

PHOSPHORUS RETENTION IN NON-TIDAL PALUSTRINE FORESTED WETLANDS OF THE MID-ATLANTIC REGION

Mark R. Walbridge and Judith P. Struthers

*Department of Biology
George Mason University
Fairfax, Virginia 22030-4444*

Abstract: We: 1) quantified the areal extent of wetlands by type in Caroline County, VA to estimate the relative importance of non-tidal palustrine forested wetlands as a component of the wetland resources in Virginia's mid-Atlantic coastal plain, 2) used a comparative literature review to identify factors that might be important in controlling P retention in these wetlands, and 3) evaluated three indices that have been used to compare P adsorption potentials in wetland soils. Non-tidal palustrine forested wetlands comprised 66.0% of the 11,372 ha of wetlands in Caroline Co. The majority were either seasonally (4000 ha) or temporarily (1596 ha) flooded wetlands dominated by broad-leaved deciduous species. These wetlands are both small (averaging 5.4 and 2.4 ha in area, respectively) and numerous in this region. Adsorption by Al and Fe (hydr)oxides and precipitation of Al, Fe, and Ca phosphates probably controls dissolved phosphate retention and long-term P storage in these wetlands, although P storage in the woody biomass of aggrading forests may also be important. Phosphorus adsorption isotherms, a single-point phosphorus adsorption index, and concentrations of oxalate-extractable (noncrystalline) Al and Fe have all been used as comparative indices of P sorption potentials in wetland soils, although the latter may represent the best single index of P sorption capacity because of its direct relationship to the mechanisms controlling P adsorption in soil. When using these indices to compare wetland P sorption potentials, it is important to consider differences in soil depth, profile heterogeneity, and bulk density between sites. Actual amounts of phosphate retained by a wetland will also be influenced by the degree of phosphate loading it receives, as determined by hydrology, phosphate sources in the watershed, and the P sorption potentials of surrounding upland soils. Because of the low P sorption potentials of sandy soils in coastal plain uplands, non-tidal palustrine forested wetlands in the mid-Atlantic coastal plain may perform particularly important functions with respect to dissolved phosphate removal and retention on the landscape.

Key Words: aluminum, coastal plain, hydrology, iron, land use, phosphate loading, P sorption capacity, soil chemistry, water quality.

INTRODUCTION

Forested wetlands include those wetlands variously described as bottomland hardwood forests (Clark and Benforado 1981, Wharton et al. 1982, McWilliams and Rosson 1990), floodplain and riparian forests (Lowrance et al. 1984, Penka et al. 1985), fringe wetlands (Lugo 1990), riverine wetlands (Brinson 1990), stream-side forests (Bell et al. 1978), and swamps (Yarbro 1983, Ewel and Odum 1984). Forested wetlands perform a number of important water quality functions on the landscape, including nitrogen and phosphorus removal (Mitsch et al. 1979a, Yarbro 1983, Brinson et al. 1984, Richardson et al. 1988), amelioration of agricultural runoff (Lowrance et al. 1984, Cooper et al. 1987), and regulation of nutrient exchange between terrestrial and aquatic ecosystems (Cuffney 1988).

With the exception of the Dismal Swamp (Day 1982, Magonigal and Day 1988, Carter 1990), non-tidal pal-

ustrine forested wetlands (PFOs) in Virginia have received little attention, particularly with respect to their potential for removing non-point source inputs of phosphorus (P) from surface, subsurface, and ground waters. Past studies have examined the geomorphologic structure and/or vegetational composition of these wetlands (e.g., Hack 1957, Parsons and Ware 1982, Osterkamp and Hupp 1984). More recent studies have focused on sediment and trace element dynamics (Hupp et al. 1993, Puckett et al. 1993).

Elucidation of the P retention functions of non-tidal PFOs in Virginia's lower piedmont and coastal plain could be particularly important because of the potential impact of these functions on the quality of water entering the Chesapeake Bay (cf. Computer Sciences Corp. 1991) and because these wetlands are currently threatened both by increasing development in this region and by changes in the criteria used to delineate

jurisdictionally protected wetlands. Coastal plain regions are frequently characterized by sandy soils, particularly in upland areas, while finer-textured clays tend to accumulate along floodplains and in riparian zones (cf. Schlesinger 1991). Because the geochemical mechanisms (e.g., adsorption and precipitation) that remove phosphate from soil solutions are associated primarily with these clay particles (Stevenson 1986), non-tidal palustrine forested wetlands in coastal plain regions may perform particularly important functions with respect to dissolved phosphate removal and retention on the landscape.

Our study had two objectives: 1) to estimate the relative importance of non-tidal palustrine forested wetlands as a component of the wetland resources in Virginia's mid-Atlantic coastal plain, and 2) to identify factors that might be important in controlling P retention in these wetlands. To accomplish our first objective, we quantified the areal extent of wetlands by type in Caroline Co., VA as representative of Virginia's mid-Atlantic coastal plain using a combination of National Wetlands Inventory (NWI) data and updated digital information provided by the Virginia Council on the Environment. We addressed our second objective by a comparative literature review of the factors controlling P retention in forested wetlands. Richardson (1985) suggested a simple index for comparing the P adsorption capacities of wetland soils. Here, we also suggest additional factors that should be included when comparing P adsorption potentials in wetland soils.

WETLAND RESOURCES IN CAROLINE CO., VA

Caroline Co. comprises an area of approximately 362,508 ha and lies primarily in the mid-Atlantic coastal plain. Although the Rappahannock River, which forms the northern border of the county, is tidally influenced below Fredericksburg, Caroline Co. is primarily a landlocked county. Wetland distributions in coastal counties may show increased importance of tidal wetlands, but estimates of wetland distributions for Caroline Co. should be comparable to other landlocked coastal plain counties in VA.

We used Virginia Council on the Environment (VCE) digital data for wetland distributions by type in the lower 42% of Caroline Co. (C. Powers, pers. comm.), and combined these data with similar distributions indicated on National Wetlands Inventory (NWI) maps for the remaining 58% of the county. When available, VCE data were used in preference to NWI data because the VCE data are more recent and are considered more accurate (C. Powers, pers. comm.).

For the NWI data, wetland areas by type were determined from appropriate NWI maps using an ER-

DAS Geographic Image Processing System, Version 7.4 software (ERDAS, Inc., Atlanta, GA) and a 386 microcomputer. Wetland areas were calculated by averaging two estimates per wetland, one drawn in a clockwise direction, the other counterclockwise. Many temporarily flooded, broad-leaved deciduous palustrine forested wetlands (PFO1As) on the NWI maps are represented as linear features (lines following stream drainages). We estimated the areas of these wetlands by multiplying linear measurements times an estimated average width of 6m.

Wetland classifications follow the U.S. Fish and Wildlife Service system (Cowardin et al. 1979). Where appropriate, category designations were updated based on information provided by the USFWS regional office in Massachusetts (G. Smith and D. Foulis, pers. comm.). Deep water habitats, unconsolidated bottom (UB) areas with water depths greater than 2 m at mean low water, were excluded from our analysis. Since these are difficult to identify from aerial photography, we followed the USFWS convention for including or excluding UB areas as wetlands (D. Foulis, pers. comm.). All palustrine UBs were assumed to be wetlands, lacustrine UBs and riverine UBs represented as polygons were assumed to be deepwater habitats, and riverine UBs represented as linear features were assumed to be wetlands.

The combined NWI and VCE databases indicate that there are approximately 11,372 ha of wetlands in Caroline Co., VA, roughly 3.1% of the total county area (Table 1). Non-tidal palustrine forested wetlands (PFOs) account for 66.0% of the total wetland area and 94.1% of all wetlands in the county are non-tidal palustrine wetlands. Tidal palustrine wetlands account for an additional 5.4%; most of these are also forested. Palustrine wetlands completely dominate the wetland resources of Caroline Co. (Table 1).

Of the estimated 7505 ha of non-tidal palustrine forested wetlands in Caroline Co., the majority (4000 ha) are seasonally flooded wetlands dominated by broad-leaved deciduous tree species (PFO1Cs); most of the remaining non-tidal palustrine forested wetlands (1596 ha) are temporarily flooded wetlands dominated by broad-leaved deciduous trees (PFO1As) (Table 2). PFO1C and PFO1A wetlands in Caroline Co. are both small, averaging 5.4 and 2.4 ha in area respectively, and numerous. Since many PFO1A wetlands are drawn as linear features on the NWI maps, our method of estimating areas for these wetlands may have caused us to underestimate their areal extent.

Based on the combined NWI and VCE databases, only a small percentage of each type of non-tidal palustrine forested wetland seems to have suffered impacts from drainage, impoundment, or beaver activity, although impacts to PFO1F wetlands (semiperman-

Table 1. Total wetland areas by type for Caroline County, Virginia.

Wetland Type	Water Regime	Vegetation	No. of Wetlands	Areal Estimates (ha)			% of Total Wetland Area
				VCE ¹	NWI ²	Total	
Palustrine	Non-tidal	Forested	2,218	3,265	4,240	7,505	66.0
		Other	2,685	1,652	1,546	3,198	28.1
	Tidal	Forested	29	0	435	435	3.8
		Other	37	0	187	187	1.6
Total Palustrine			4,969	4,917	6,408	11,325	99.6
Total Riverine			22	0	45	45	0.4
Total Lacustrine			13	0	2	2	—

¹ Estimates from the Virginia Council on the Environment for the lower 42% of Caroline County, Virginia (C. Powers and A. Frisch, pers. comm.).

² Estimates for the upper 58% of Caroline County, Virginia, based on National Wetlands Inventory (NWI) maps and areal estimates using an ERDAS Geographic Information System.

nently flooded) seem to have been somewhat more severe (Table 2).

PHOSPHORUS RETENTION IN FORESTED WETLANDS: A REVIEW

Factors Controlling Phosphorus Retention in Forested Wetlands

Phosphorus inputs to forested wetlands can occur either as suspended solids or in dissolved form. The sediment removal functions of forested wetlands are well-documented (Lowrance et al. 1986, 1988, Cooper and Gilliam 1987, Cooper et al. 1987), and significant quantities of P can be associated with the sediments deposited in forested wetlands. Such P may be associated with either the (particulate) organic or the inorganic (i.e., clay) fraction of the suspended sediment load.

For alluvial swamps, estimates of annual sediment P deposition range from 19.6–36 kg/ha (Mitsch et al. 1979 a,b). For smaller swamps and riparian forests along lower order streams, annual sediment P deposition rates are much lower, ranging from 1.7–3.0 kg/ha (Yarbro 1983, Peterjohn and Correll 1984). The higher deposition rates found for alluvial swamps along higher order streams indicate the increased importance of overbank flooding with increasing stream order as a vector of P input (cf. Brinson 1993). However, the lower deposition rates measured by Yarbro (1983) and Peterjohn and Correll (1984) are probably more characteristic of small non-tidal PFOs in the mid-Atlantic region.

Dissolved P inputs to forested wetlands are also important and can account for 50% or more of total P inputs, P retention, or the export of algal-available P. Kitchens et al. (1975) observed a 50% reduction of both phosphate and total P in winter flood waters passing through the Santee Swamp, SC. In the Creeping Swamp, NC, Yarbro (1983) estimated an annual net

removal of 2.3–2.4 kg/ha of filterable reactive P over a 2-year period. In two Pennsylvania agricultural watersheds sampled over a 4-year period that included 56 storm events, 50% of the algal-available P exported was dissolved P (Pionke and Kunishi 1992). Labile P export was controlled more by water than by sediments, with 62–78% of the labile P in stormflow occurring as soluble P. Frink (1991) found that watershed models that included a sediment transport component tended to overestimate P export from agricultural watersheds and underestimate P export from wooded and urban watersheds and suggested that this was due to an underestimation of soluble P transport as predicted by these models. While the mechanisms associated with sediment removal are primarily geomorphological (Lowrance et al. 1984, Cooper et al. 1987, Pinay et al. 1992), the mechanisms associated with dissolved P removal are primarily biogeochemical. For the remainder of this paper, we will limit our discussion of the P retention functions of forested wetlands to the biogeochemical pathways associated with dissolved phosphate removal.

Dissolved phosphate inputs to forested wetlands in the mid-Atlantic region can result from 1) non-point-source leaching of excess phosphate fertilizers (including both agricultural and residential (lawn and garden) sources, 2) non-point-source leaching from residential septic fields, 3) point-source inputs from industrial sources, and 4) point-source inputs from municipal waste treatment facilities. Dissolved phosphate inputs may enter wetlands either via surface and subsurface waters draining from surrounding uplands (Peterjohn and Correll 1984) or by overbank flooding from associated streams and rivers (Mitsch et al. 1979a), with the former pathway dominating in small forested wetlands along lower order streams (Brinson 1993).

Both biologically and geochemically mediated pathways can remove dissolved phosphate from the water column (cf. Walbridge et al. 1991). Biological mech-

Table 2. Areas of non-tidal palustrine forested wetlands (PFOs) by type for Caroline County, Virginia.

USFWS Classification ¹	Area (ha)	% by Type	Water Regime	% of Total	No. of Sites	Av. Size (ha)
PFO1A	1,595.9	99.5	temporary	21.3	659	2.4
PFO1Ad	6.6	0.4	(drained)	0.1	1	6.6
PFO1Ah	1.7	0.1	(impounded)	<0.1	3	0.6
PFO1B	2.4		saturated	<0.1	1	2.4
PFO1C	3,999.9	97.0	seasonal	53.3	745	5.4
PFO1Cb	103.2	2.5	(beaver)	1.4	99	1.0
PFO1Cd	0.8	<0.1	(drained)	<0.1	1	0.8
PFO1Ch	18.4	0.5	(impounded)	0.3	40	0.5
PFO1E	636.6	97.0	seasonal sat.	8.5	129	4.9
PFO1Eb	19.9	3.0	(beaver)	0.3	10	2.0
PFO1F	113.4	76.8	semiperm.	1.5	55	2.1
PFO1Fb	27.1	18.4	(beaver)	0.4	14	1.9
PFO1Fh	7.2	4.9	(impounded)	0.1	5	1.4
PFO1Y	1.8		sat./semi./seas.	<0.1	3	0.6
PFO4	182.0			2.4	84	2.2
PFO5	123.8			1.7	173	0.7
Intergrades						
PFO1/EM	21.1			0.3	6	3.5
PFO1/UB	1.2			<0.1	1	1.2
PFO1/3C	1.3		seasonal	<0.1	1	1.3
PFO1/4	185.0			2.5	62	3.0
PFO1/5	29.4			0.4	8	3.7
PFO4/1	110.7			1.5	27	4.1
PFO5/EM	9.0			0.1	4	2.3
PFO5/UB	25.6			0.3	23	1.1
PFO/SS	281.2			3.8	64	4.4

¹ Wetland types follow U.S. Fish and Wildlife Service classification scheme (Cowardin et al. 1979). Vegetation modifiers for forested palustrine wetlands include: 1 = broad-leaved deciduous; 3 = broad-leaved evergreen; 4 = needle-leaved evergreen; 5 = dead. Water regime modifiers for non-tidal wetlands include: A = temporary; B = saturated; C = seasonal; E = seasonal saturated; F = semipermanent; Y = saturated/semi-permanent/seasonal. Special modifiers include: b = beaver; d = partially drained/ditched; h = diked/impounded. In addition to forested wetlands (FO), other types of palustrine (P) wetlands include: EM = emergent; SS = scrub/shrub; UB = unconsolidated bottom.

anisms include uptake by soil microorganisms and plants. Geochemical mechanisms include adsorption by Al and Fe oxides and hydroxides and the precipitation of Al, Fe, and Ca phosphates.

Microbial uptake has been shown to be both rapid and highly efficient in wetland soils subjected to ambient P loadings (Richardson and Marshall 1986, Walbridge and Vitousek 1987), but soil microorganisms are readily saturated under higher phosphate loadings (Richardson and Marshall 1986, Richardson et al. 1988). Following cell death, the phosphorus contents of soil microorganisms are highly labile. For a wide range of both wetland and upland soils, it has been shown that about 40% of microbial biomass P is released as phosphate within 18 hours of cell lysis (Brookes et al. 1982, Hedley and Stewart 1982, Walbridge 1991). In a Michigan fen ecosystem, the majority of P initially immobilized by soil microorgan-

isms was transferred to the peat/litter compartment within 30 days of addition (Richardson and Marshall 1986).

A number of studies have suggested the importance of plant uptake in removing dissolved phosphate from the water column in wetland soils (Kitchens et al. 1975, Mitsch et al. 1979a, Yarbrow 1983, Brinson et al. 1984, Lowrance et al. 1984), but the potential for long-term P storage via this mechanism is limited to the net annual rate of P accumulation in plant biomass, since P taken up by short-lived plants (herbaceous annuals, perennials, and algae) will enter the litter compartment within a relatively short period of time. Lowrance et al. (1984) estimated annual P storage in aboveground biomass at 3.8 kg/ha in a periodically harvested GA riparian forest. They suggested that plant uptake and storage in wood was a potential mechanism for P retention in forested riparian zones but indicated that

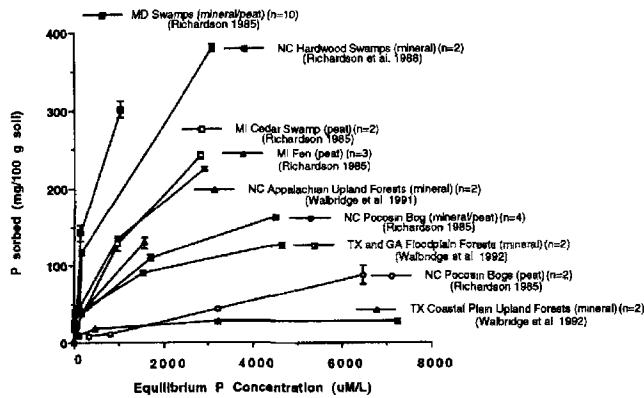


Figure 1. Phosphorus adsorption isotherms for a variety of freshwater wetland soils, with isotherms for two upland soil types included for comparison. Redrawn from Richardson (1985) with additional data from Richardson et al. (1988) and Walbridge et al. (1991, 1992). Values represent means of P sorbed during 24 hour laboratory equilibrations from initial solution concentrations ranging from 0.31 to 260 mg $\text{PO}_4\text{-P/L}$, plotted as a function of the equilibrium concentration of $\text{PO}_4\text{-P}$ remaining in solution (see Table 3 for further details regarding individual studies). Values are means of 2 or more sites per type (NC pocosin bogs (peat) represent the average of Dare and Ponzer pocosin peats reported by Richardson (1985)), or 2 or more locations per site for single site isotherms (MI cedar swamp, MI fen, and NC pocosin bog (mineral/peat)). Error bars indicate ± 1 SE.

periodic harvesting would be needed to maintain this function. Other published estimates for annual P storage in woody biomass in forested wetlands and riparian zones are somewhat lower, ranging from 0.2–1.8 kg/ha (Schlesinger 1978, Mitsch et al. 1979a, Yarbrow 1983, Peterjohn and Correll 1984). As ecosystems mature and approach steady state, inputs and outputs should come into balance, and the potential for P storage in plant biomass will approach zero (Vitousek and Reiners 1975, Omernik et al. 1981). Phosphorus storage in wood, however, could be important in aggrading non-tidal PFOs in the mid-Atlantic region.

Phosphorus taken up by plants may also accumulate in the litter compartment, but since a portion of this P will be released as phosphate during decomposition, long-term storage of organic P in the litter/soil compartment will be limited by the rate of organic matter (peat) accumulation in the soil. Richardson (1985) used extremes for P concentrations in peat and rates of peat accumulation to estimate a range of 0.05 to 2.4 kg/ha for annual P accumulation in temperate zone peats. Although few data are available for either soil characteristics or rates of peat formation in non-tidal mid-Atlantic PFOs, the predominance of mineral soils and temporarily or seasonally flooded water regimes (Table 2) suggests that rates of P accumulation in soil organic matter are probably near the low end of this range.

Thus, with the possible exception of P stored in the woody biomass of aggrading forests, biological mechanisms probably do not contribute significantly to long-term P retention in most wetlands with mineral soils. In contrast, geochemical mechanisms, adsorption by Al and Fe oxides and hydrous oxides and the precipitation of Al, Fe, and Ca phosphates, have been shown to exhibit significant potential for long-term P storage in wetland soils. Brinson et al. (1984) found an increase of 199 kg/ha of extractable P in surface soils of a NC alluvial floodplain swamp that received weekly P additions totaling 430 kg/ha over a 10-month period. In Brown Marsh Swamp, NC, which received 295 kg/ha of P in sewage effluent over a 1.5-year period, Richardson et al. (1988) measured an increase of 130 kg/ha of extractable P in surface soils (0–20 cm) and estimated a maximum P adsorption potential of 420 kg/ha. These data show that the potential for long-term P storage through adsorption and/or precipitation reactions with soil minerals greatly exceeds even the maximum potential rates of P accumulation in plant biomass and peat. The P adsorption characteristics of non-tidal mid-Atlantic PFO soils have been little studied.

Comparing P Adsorption Potentials In Wetland Soils

Phosphorus adsorption isotherms (e.g., Nair et al. 1984) are one method of indexing a soil's capacity for removing dissolved phosphate from solution. (The term isotherm is used to indicate that P adsorption is examined as a function of solution P concentration under conditions of constant temperature). Replicate soil samples are equilibrated with a range of phosphate solutions of known concentration (cf. Table 3). Phosphate is usually supplied as KH_2PO_4 dissolved in 0.01 M CaCl_2 , and equilibration periods can range from 24 hours to 14 days or longer. Following equilibration, solutions are clarified by centrifugation and/or filtration and their phosphate concentrations determined. The difference between initial and final solution phosphate content gives an estimate of dissolved phosphate removed from solution by the soil during equilibration. Adsorption isotherms are then derived by plotting P sorbed (on the y-axis) in mg P/100 g soil as a function of the equilibrium (final) P concentration of the equilibration solution (on the x-axis) in $\mu\text{M/L}$. Because P sorption capacity approaches saturation at higher levels of phosphate addition (at least during short-term experiments), the relationship is characteristically curvilinear. Although commonly referred to as P adsorption isotherms, the mechanisms associated with dissolved phosphate removal in acid soils are dominated by adsorption by Fe and Al oxides and clay minerals

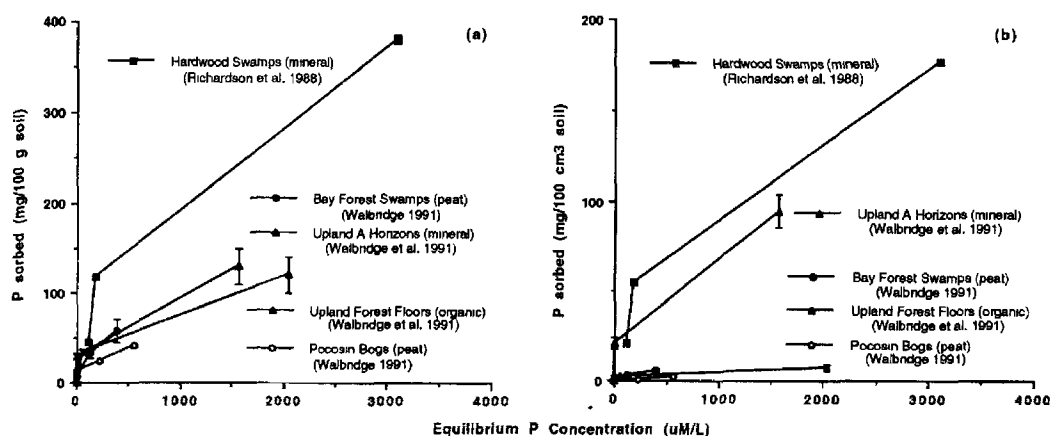


Figure 2. Phosphorus adsorption isotherms for wetland and upland soils. Values represent means of P sorbed a) per unit of soil mass (mg/100 g soil), or b) per unit of soil volume (mg/100 cm³ soil), during 24 hour or 14 day (Walbridge 1991) laboratory equilibrations from initial solution concentrations ranging from 0.31 to 400 mg PO₄-P/L, plotted as a function of equilibrium concentration of PO₄-P remaining in solution (see Table 3 for further details regarding individual studies). Error bars indicate ± 1 SE.

at lower solution phosphate concentrations and by the precipitation of insoluble Fe and Al phosphates at higher concentrations (Anderson 1981, Stevenson 1986).

Richardson (1985) used P adsorption isotherms to compare the P sorption properties of bog, fen, and swamp soils and found that wetland soils can differ greatly in their ability to remove dissolved phosphate from solution. We combined Richardson's (1985) data with more recent data on the P sorption characteristics of four additional wetland soils (Richardson et al. 1988, Walbridge et al. 1992) and added data for upland soils for comparison (Walbridge et al. 1991, 1992) (Figure 1). Forested wetlands, including those of the mid-Atlantic region for which data are available, show some of the highest P sorption capacities. However, not all forested wetland soils are characterized by high P sorption potentials. Forested floodplain swamps in the GA and TX coastal plain have comparatively low P sorption capacities, falling within the range found by Richardson (1985) for pocosin bogs in the NC coastal plain. However, these floodplain forest soils do have much higher P sorption capacities than the soils of surrounding upland forests (Figure 1).

When using P adsorption isotherms to compare the P sorption potentials of wetland soils, several additional factors should be considered. These factors include variations in soil depth, profile heterogeneity, and the mass of soil per unit land surface area.

Phosphorus adsorption isotherms are usually derived from soils collected in the upper 15–20 cm of the soil profile. Yet, soil depth certainly varies across sites, and P sorption capacity may also vary with depth in the soil profile. This second fact has been clearly shown for upland soils (e.g., Wood et al. 1984, Wal-

bridge et al. 1991) but has not been demonstrated specifically in wetland soils. However, similar patterns are likely to occur in wetland soil types that exhibit significant profile differentiation.

Soils (and soil horizons) also differ in the mass of soil per unit land surface area, due to differences in bulk density and gravel and root content. This can be particularly important when comparing soils from different wetland types (e.g., bogs vs. swamps) because wetland soils can differ greatly in organic matter content (cf. Cuttle 1983, Faulkner and Richardson 1989). Figure 2 shows P adsorption isotherms for five different types of wetland and upland soils in NC for which bulk density data were available—a coastal plain hardwood swamp (mineral soil) (Richardson et al. 1988), a bay forest swamp (organic soil) (Walbridge 1991), a pocosin bog (organic soil) (Walbridge 1991), an Appalachian upland forest soil (mineral horizon) (Walbridge et al. 1991), and an Appalachian upland forest floor (organic horizon) (Walbridge et al. 1991).

When expressed per unit of soil mass (Figure 2a), the hardwood swamp soil has a much larger P sorption capacity than the other soils, which are roughly similar. When expressed per unit of soil volume (Figure 2b), the Appalachian forest mineral soil shows a P sorption capacity nearly equal to that of the hardwood swamp (also a mineral soil), while all of the organic soils and/or soil horizons have comparatively low P sorption capacities. Thus, when P adsorption isotherms are used to compare the P sorption characteristics of soils varying in bulk density and/or organic matter content, it is essential that these relationships be expressed per unit of soil volume rather than per unit of soil mass.

When corrected for differences in soil depth, profile heterogeneity, and bulk density, these P adsorption

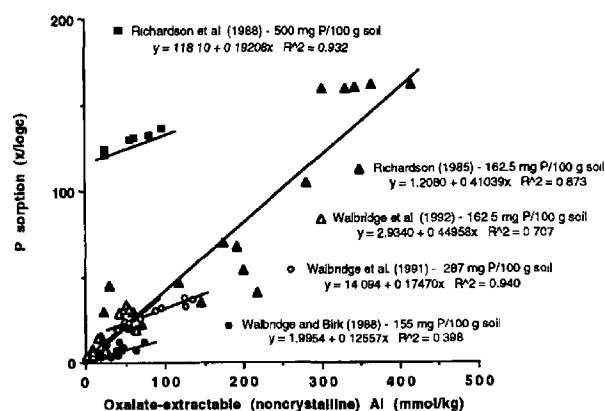


Figure 3. Phosphorus adsorption as predicted by oxalate-extractable (noncrystalline) Al in a variety of soils. Phosphorus adsorption is indexed by $(x/\log c)$, where x = P sorbed (mg P/100 g soil) and c = the corresponding equilibrium P concentration ($\mu\text{M/L}$). Amounts of $\text{PO}_4\text{-P}$ added (mg P/100 g soil) in determining this P sorption index in each study are indicated on the figure, as are appropriate linear regression equations and r^2 values.

isotherms will provide a more accurate comparative index of the P sorption potentials of different wetland soils. However, as indicated above, the procedure is somewhat complex, and a more tractable method of comparing P sorption potentials in wetland soils would be quite useful.

For acid wetland soils, Richardson (1985) found a strong correlative relationship between P sorption capacity and concentrations of oxalate-extractable (amorphous) Al and Fe in soil, with a stronger correlation for Al ($r = 0.929$) than Fe ($r = 0.621$). To develop this relationship, P sorption capacity was indexed as $x/\log c$, where x = P sorbed in mg P/100 g soil, and c = the resulting equilibrium P concentration in $\mu\text{M/L}$ (Bache and Williams 1971). Similar relationships have

since been observed between this phosphorus adsorption index (PAI) and oxalate-extractable Al and Fe in a wide range of both wetland and upland soils (Richardson et al. 1988, Walbridge et al. 1991, Walbridge et al. 1992). While both the slope and y-intercept of the relationship can vary as a function of the level of phosphate addition used to derive the index (Figure 3), under similar experimental conditions (e.g., Richardson (1985) and Walbridge et al. (1992)—see Table 3) these relationships can be nearly identical.

All three methods—P adsorption isotherms, the single-point PAI, and concentrations of oxalate-extractable Al and Fe in soil—are presented only as comparative indices of a wetland soil's potential for removing dissolved phosphate from solution, not as mechanistic models of P adsorption or precipitation. At the P addition levels commonly used to derive the PAI (Figure 3), precipitation of Al and Fe phosphates is probably the dominant mechanism controlling the removal of dissolved phosphate from solution, rather than adsorption by Al and Fe hydrous oxides (Anderson 1981). Both adsorption and precipitation are mechanisms of P fixation in acid soils, and both types of fixed phosphate are highly insoluble and are poor sources of plant-available P (Stevenson 1986).

The tendency for soils to fix P is related to clay mineralogy. Amorphous Al and Fe hydrous oxides have the strongest tendency for P fixation, followed by the crystalline Fe and Al minerals goethite and gibbsite, kaolinite, and montmorillonite (Stevenson 1986). Aluminum and Fe oxides and hydroxides sorb phosphate by a process called specific anion adsorption, in which phosphate bonds covalently with Al and Fe (cf. Stevenson 1986, Schlesinger 1991). It is the fact that a single phosphate can bind with two Al or Fe molecules to form a chelate ring that causes the low availability (solubility) of most adsorbed P. Both noncrystalline

Table 3. Experimental conditions associated with the determination of phosphorus adsorption isotherms for studies shown in Figures 1–3.

Study and System Type	Levels of $\text{PO}_4\text{-P}$ Added (mg/L)	Soil : Solution Ratio	Equilibration Time	Shaking Time
Richardson (1985) (wetlands)	16, 33, 130, 260	1:12.5	24 hours	3 × 30 minutes
Walbridge and Birk (1988) (uplands)	124	1:12.5	24 hours	3 × 30 minutes
Richardson et al. (1988) (wetlands)	40, 100, 400	1:12.5	24 hours	3 × 30 minutes
Walbridge (1991) (wetlands)	3.1, 15.5, 31.0	1:33.3	14 days	30 minutes 2 × per day
Walbridge et al. (1991) (uplands)	0.31, 3.1, 31, 310	1:9.3	24 hours	3 × 30 minutes
Walbridge et al. (1992) (uplands and wetlands)	33, 130, 260	1:12.5	24 hours	continuous

(amorphous) and crystalline Al and Fe oxides sorb P by this mechanism, but when present in significant amounts, noncrystalline forms tend to dominate P sorption reactions due to their greater reactive surface area per unit soil volume (Parfitt and Smart 1978, Hsu 1989, Schwertmann and Taylor 1989).

Despite the fact that the probable mechanism of dissolved phosphate removal during determination of the PAI represents precipitation rather than adsorption, the utility of the PAI as an index of P sorption is suggested by the significant correlations frequently observed between this index and concentrations of oxalate-extractable (noncrystalline) Al and Fe in the soil. This relationship is consistent with current understanding of the processes controlling P adsorption and fixation in soils and suggests that concentrations of oxalate-extractable Al and Fe may represent the best single indices of P sorption capacity for wetland soils. Although other factors (e.g., clay content, organic matter, and pH) also influence P adsorption, correlations between the PAI and oxalate-extractable Al and Fe are frequently so strong that addition of these other factors in a multiple regression model does not significantly improve prediction of the PAI (e.g., Richardson 1985). It may be important however, to examine the relationship between a PAI determined at a lower level of phosphate addition where adsorption controls dissolved P removal, using a multiple regression model that includes these other factors.

The tendency for clays to be deposited in floodplains (Cooper et al. 1987, Schlesinger 1991) provides a mechanism for the accumulation of Al and Fe in floodplain soils. Periodic flooding may also contribute to the formation and/or maintenance of Al and Fe in noncrystalline form (Kuo and Mikkelsen 1979). Flooding cycles can affect the degree of crystallinity of both Al and Fe in soil and can cause the transformation of normally stable crystalline Al and Fe minerals to noncrystalline (amorphous) form, increasing P sorption capacity (Willett et al. 1978, Kuo and Baker 1982, Sah and Mikkelsen 1986). It is unclear whether wetland soil minerals undergo cyclic changes in crystalline state in response to flooding and draining or whether such cycles merely lead to the persistence of the less stable noncrystalline forms. Wetland soils are also often high in organic matter content due to reduced decomposition, and the presence of organic matter can also impede the crystallization of both Al and Fe (Schwertmann 1966, Kodama and Schnitzer 1977, 1980).

Iron phosphates are sensitive to changes in redox potential. Under reduced conditions, the transformation of Fe(III) to Fe(II) can cause the release of associated phosphate to the soil solution (Ponnamperuma 1972, Gambrell and Patrick 1978). Since Al does not undergo such a transformation, phosphate bound to

soil Al may be more resistant to changes induced by flooding. This could explain the stronger correlation usually observed between P sorption and oxalate-extractable Al than Fe (Richardson 1985, Richardson et al. 1988, Walbridge et al. 1991, Walbridge et al. 1992). Additionally, acid ammonium oxalate can extract appreciable amounts of magnetite Fe, which does not bind with phosphate (Baril and Bitton 1969, Lindsay 1979). The presence of magnetite would thus affect the relationship between oxalate-extractable Fe and P sorption capacity.

In summary then, our literature review and analyses suggest that the ability of individual non-tidal mid-Atlantic PFOs to remove phosphate from incident surface, subsurface, and/or ground waters is probably largely a function of soil chemistry and can be readily indexed by a simple laboratory soil analysis. Whether the index used involves P adsorption isotherms, the single-point PAI, or concentrations of oxalate-extractable Al and Fe, comparisons between sites should include consideration of differences in soil depth, profile heterogeneity, and bulk density. Actual amounts of phosphate retained by individual wetlands will also be related to the degree of phosphate loading that wetland receives—as determined by hydrology, point and non-point sources of phosphate in the watershed, and the P sorption potentials of soils in surrounding uplands.

Hydrology, Watershed Phosphate Sources, and P Retention in Surrounding Upland Soils

Wetlands cannot remove phosphate from surface, subsurface, and/or ground waters unless these waters pass through the wetland ecosystem. A number of factors will determine the potential for hydrologic inputs to wetlands from the surrounding watershed.

Pathways of ground-water flow to the wetland must be determined. Ground-water connections between ecosystems cannot necessarily be inferred from regional topography (Freeze and Cherry 1979, Winter 1988, Phillips et al. 1993). Identification of actual pathways of ground-water flow may require detailed investigation of piezometric surfaces.

The volume of water delivered to a wetland via surface and subsurface flow will be determined by the balance between precipitation inputs, evapotranspiration losses, and changes in storage capacity in the surrounding watershed. Land-use changes that affect evapotranspiration or storage will affect watershed hydrologic budgets. Decreases in vegetative cover will result in increased runoff; extensive reforestation could have the opposite effect (Swank et al. 1988).

If P sorption potentials vary as a function of soil depth (Wood et al. 1984, Walbridge et al. 1991), the portion of the soil profile through which the majority

of hydrologic inputs pass may also influence P retention. Wetland soils may continue to remove phosphate from subsurface waters even when the water table is well below the soil surface. Landscape-level factors, such as the location of the wetland within the watershed and the wetland/watershed ratio, may also be important in determining the proportion of runoff within a watershed that reaches the wetland (cf. Johnston et al. 1990).

Hydrology will control the delivery of P from both point and non-point sources in the watershed. Most point sources are readily identifiable, but identification of non-point sources may be more problematic. Neary et al. (1989) and Riekirk et al. (1989) identified six potential watershed sources of non-point-source pollution (NPSP)—agriculture, silviculture, mining, construction, urban, and atmospheric. In the mid-Atlantic region, agriculture, silviculture, construction, and urban sources represent the most likely non-point sources of P in runoff. Depending on soil chemistries and hydrologic inputs, wetlands located in watersheds with potential or actual phosphate sources may play a more significant role in improving downstream water quality (cf. Tietjen and Carter 1981) than wetlands located in pristine watersheds.

The specific value of wetlands in improving water quality exports from watersheds with significant potential point and non-point pollution sources must also be considered in light of the P sorption potentials of soils in the surrounding uplands. Riparian forests in the northeastern United States, situated in watersheds surrounded by Spodosols with strong geochemical retention capacities in lower horizons (Wood et al. 1984), probably receive little phosphate in surface, subsurface, and ground waters. For the same reason, riparian forests lining stream drainages in western North Carolina probably receive minor inputs of phosphate from surrounding uplands (cf. Walbridge et al. 1991). However in areas of the coastal plain where sandy soils with low P sorption capacities predominate on upland sites, the P retention functions of forested wetlands lining stream drainages may be particularly important (Figure 1; Walbridge et al. 1992).

CONCLUSIONS

Non-tidal palustrine forested wetlands comprise a significant percentage of the wetland resources in landlocked regions of the Virginia's mid-Atlantic coastal plain. As development continues in this region and the definitions of jurisdictionally protected wetlands change, these wetlands may come under increasing developmental pressures. The P retention functions of these wetlands have been little studied and are poorly understood, but these wetlands have potential value

for improving water quality inputs to downstream aquatic ecosystems that ultimately enter the Chesapeake Bay.

Literature review suggests that soil chemistry is probably the most important factor controlling the removal and retention of dissolved phosphate from incident surface, subsurface, and ground waters in non-tidal mid-Atlantic PFOs, although P storage in woody biomass could be important in aggrading forests. Phosphorus sorption potential can be indexed by analyzing P adsorption isotherms, single-point P adsorption indices, or concentrations of oxalate-extractable (non-crystalline) Al and Fe in soil. When using these indices to compare P sorption potentials in wetland soils, differences in soil depth, profile heterogeneity, and bulk density should also be considered. Actual phosphate retention by individual wetlands will also be determined by the degree of phosphate loading a wetland receives—a function of hydrology, phosphate sources in the watershed, and the P sorption potentials of soils in surrounding uplands. Because of the low P sorption potentials often observed in sandy coastal plain upland soils, non-tidal PFOs in the mid-Atlantic coastal plain may perform particularly important functions with respect to dissolved phosphate removal and retention on the landscape.

ACKNOWLEDGMENTS

Paper presented at the workshop on "Saturated Forested Wetlands in the Mid-Atlantic Region: The State of the Science", January 26–28, 1992, Annapolis, MD, jointly sponsored by the U.S. EPA, the USDA-Forest Service, and the USFWS. The authors thank C. Powers and A. Frisch for providing Virginia Council on the Environment data for wetland distributions in Caroline County, B. Topol and the Rappahannock Area Development Council for providing NWI maps for Caroline County, B. Haack and B. Freeman for the use of and help with the ERDAS GIS system at George Mason University, G. Smith and D. Foulis, USFWS—Massachusetts, for assistance with USFWS classification protocol, and C. J. Richardson, Duke University, for providing access to original data published in Richardson (1985). A.K. Darke and two anonymous reviewers provided helpful comments on an earlier draft of this manuscript.

LITERATURE CITED

- Anderson, M.A. 1981. Expectations and limitations for aqueous adsorption chemistry. p. 327–349. *In* M.A. Anderson and A.J. Rubin (eds.) *Adsorption of Inorganics at Solid-Liquid Interfaces*. Ann Arbor Scientific, Ann Arbor, MI, USA.
- Bache, B.W. and E.G. Williams. 1971. A phosphate sorption index for soils. *Journal of Soil Science* 22:289–301.

- Baril, R. and G. Bitton. 1969. Teneurs elevees de fer libre et l'identification taxonomique de certains sols du Quebec contenant de la magnetite. *Canadian Journal of Soil Science* 59:1-9.
- Bell, D.T., F.L. Johnson, and A.R. Gilmore. 1978. Dynamics of litter fall, decomposition, and incorporation in the streamside forest ecosystem. *Oikos* 30:76-82.
- Brinson, M.M. 1990. Riverine forests. Chapter 5. In A.E. Lugo, M. Brinson, and S. Brown (eds.) *Forested Wetlands. Ecosystems of the World Volume 15*. Elsevier, New York, NY, USA.
- Brinson, M.M. 1993. Changes in the functioning of wetlands along environmental gradients. *Wetlands* 13: (in press).
- Brinson, M.M., H.D. Bradshaw and E.S. Kane. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. *Journal of Applied Ecology* 21:1041-1058.
- Brookes, P.C., D.S. Powlson, and D.S. Jenkinson. 1982. Measurement of microbial biomass phosphorus in soil. *Soil Biology and Biochemistry* 14:319-329.
- Carter, V. 1990. The Great Dismal Swamp: an illustrated case study. Chapter 8. In A.E. Lugo, M. Brinson, and S. Brown (eds.) *Forested Wetlands. Ecosystems of the World Volume 15*. Elsevier, New York, NY, USA.
- Clark, J.R. and J. Benforado (eds.). 1981. *Wetlands of Bottomland Hardwood Forests*. Elsevier, New York, NY, USA.
- Computer Sciences Corporation. 1991. Trends in Phosphorus in the Chesapeake Bay (1984-1990). Contract No. 68-WO-0043. U.S. Environmental Protection Agency, Washington, DC, USA.
- Cooper, J.R. and J.W. Gilliam. 1987. Phosphorus redistribution from cultivated fields into riparian areas. *Soil Science Society of America Journal* 51:1600-1604.
- Cooper, J.R., J.W. Gilliam, R.B. Daniels, and W.P. Robarge. 1987. Riparian areas as filters for agricultural sediment. *Soil Science of America Journal* 51:416-420.
- Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of Wetlands and Deep-water Habitats of the United States. U.S. Fish and Wildlife Service Office of Biological Services (79/31), Washington, DC, USA.
- Cuffney, T.F. 1988. Input, movement and exchange of organic matter within a subtropical coastal blackwater river-floodplain system. *Freshwater Biology* 19:305-320.
- Cutler, S.P. 1983. Chemical properties of upland peats influencing the retention of phosphate and potassium ions. *Journal of Soil Science* 34:75-82.
- Day, F.P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology* 63:670-678.
- Ewel, K.C. and H.T. Odum (eds.). 1984. *Cypress Swamps*. University Presses of Florida, Gainesville, FL, USA.
- Faulkner, S.P. and C.J. Richardson. 1989. Physical and chemical characteristics of freshwater wetland soils. Chapter 4. In D.A. Hammer (ed.) *Constructed Wetlands for Wastewater Treatment*. Lewis Publishers, Chelsea, MI, USA.
- Freeze, R.A. and J.A. Cherry. 1979. *Groundwater*. Prentice-Hall, Inc., Englewood Cliffs, NJ, USA.
- Frink, C.R. 1991. Estimating nutrient exports to estuaries. *Journal of Environmental Quality* 20:717-724.
- Gambrell, R.P. and W.H. Patrick, Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. p. 375-423. In D.D. Hook and R.M.M. Crawford (eds.) *Plant Life in Anaerobic Environments*. Ann Arbor Scientific Publishers Inc., Ann Arbor, MI, USA.
- Hack, J.T. 1957. Studies of Longitudinal Stream Profiles in Virginia and Maryland. Geological Survey Professional Paper 294-B. U.S. Government Printing Office, Washington, DC, USA.
- Hedley, M.J. and J.W.B. Stewart. 1982. Method to measure microbial phosphate in soils. *Soil Biology and Biochemistry* 14:377-385.
- Hsu, P.A. 1989. Aluminum hydroxides and oxyhydroxides. p. 331-378. In J.B. Dixon and S.B. Weed (eds.) *Minerals in Soil Environments*, Second Edition. Soil Science Society of America, Madison, WI, USA.
- Hupp, C.R., M.D. Woodside, and T.M. Yanosky. 1993. Sediment and trace element trapping in a forested wetland, Chickahominy River, Virginia. *Wetlands* 13: (in press).
- Johnston, C.A., N.E. Detenbeck, and G.J. Niemi. 1990. The cumulative effect of wetlands on stream water quality and quantity: a landscape approach. *Biogeochemistry* 10:105-141.
- Kitchens, W.M., J.M. Dean, L.H. Stevenson, and J.H. Cooper. 1975. The Santee Swamp as a nutrient sink. p. 349-366. In F.G. Howell, J.B. Gentry, and M.H. Smith (eds.) *Mineral Cycling in Southeastern Ecosystems*. CONF-740513. U.S. Energy Research and Development Administration, Washington, DC, USA.
- Kodama, H. and M. Schnitzer. 1977. Effect of fulvic acid on the crystallization of Fe (III) oxides. *Geoderma* 19:279-291.
- Kodama, H. and M. Schnitzer. 1980. Effect of fulvic acid on the crystallization of aluminum hydroxides. *Geoderma* 24:195-205.
- Kuo, S. and A.S. Baker. 1982. The effect of soil drainage on phosphorus status and availability to corn in long-term manure-amended soils. *Soil Science Society of America Journal* 46:744-747.
- Kuo, S. and D.S. Mikkelsen. 1979. Distribution of iron and phosphorus in flooded and nonflooded soil profiles and their relation to P absorption. *Soil Science* 127:18-25.
- Lindsay, W.L. 1979. *Chemical Equilibria in Soils*. Wiley, New York, NY, USA.
- Lowrance, R., S. McIntyre, and C. Lance. 1988. Erosion and deposition in a field/forest system estimated using cesium-137 activity. *Journal of Soil and Water Conservation* 43:195-199.
- Lowrance, R., J.K. Sharpe, and J.M. Sheridan. 1986. Long-term sediment deposition in the riparian zone of a coastal plain watershed. *Journal Soil and Water Conservation* 41:266-271.
- Lowrance, R., R. Todd, J. Fail, O. Hendrickson, R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *Bioscience* 34:374-377.
- Lugo, A.E. 1990. Fringe wetlands. Chapter 6. In A.E. Lugo, M. Brinson, and S. Brown (eds.) *Forested Wetlands. Ecosystems of the World Volume 15*. Elsevier, New York, NY, USA.
- McWilliams, W.H. and J.F. Rosson. 1990. Composition and vulnerability of bottomland hardwood forests of the Coastal Plain Province in the South Central United States. *Forest Ecology and Management* 33/34:485-501.
- Megonigal, J.P. and F.P. Day. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal swamp. *American Journal of Botany* 75:1334-1343.
- Mitsch, W.J., C.L. Dorge, and J.R. Wiemhoff. 1979a. Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60:1116-1124.
- Mitsch, W.J., M.D. Hutchinson, and G.A. Paulson. 1979b. The Moccasin Wetlands of the Kankakee River in Illinois—An Assessment of Their Value. Illinois Institute of Natural Resources, Doc 79/17, Chicago, IL, USA.
- Nair, P.S., T.J. Logan, A.N. Sharpley, L.E. Sommers, M.A. Tabatabai, and T.L. Yuan. 1984. Interlaboratory comparison of a standardized phosphorus adsorption procedure. *Journal of Environmental Quality* 13:591-595.
- Neary, D.G., W.T. Swank, and H. Riekkirk. 1989. An overview of nonpoint source pollution in the Southern United States. p. 1-7. In D.D. Hook and R. Lea (eds.) *Proceedings of the Symposium: The Forested Wetlands of the Southern United States*. July 12-14, 1988, Orlando, FL. General Technical Report SE-50. USDA-Forest Service, Southeastern Forest Experiment Station, Asheville, NC, USA.
- Omernik, J.M., A.R. Abernathy, and L.M. Male. 1981. Stream nutrient levels and proximity of agricultural and forest land to streams: some relationships. *Journal of Soil and Water Conservation* 36:227-231.
- Osterkamp, W.R. and C.R. Hupp. 1984. Geomorphic and vegetative characteristics along three northern Virginia streams. *Geological Society of America Bulletin* 95:1093-1101.
- Parfitt, R.L. and R. St. C. Smart. 1978. The mechanism of sulfate adsorption on iron oxides. *Soil Science Society of America Journal* 42:48-50.
- Parsons, S.E. and S. Ware. 1982. Edaphic factors and vegetation in Virginia Coastal Plain swamps. *Bulletin of the Torrey Botanical Club* 109:365-370.
- Penka, M., M. Vyskot, E. Klimo, and F. Vasicek. 1985. *Floodplain Forest Ecosystem. I. Before Water Management Measures*. Elsevier, New York, NY, USA.
- Peterjohn, W.T. and D.L. Correll. 1984. Nutrient dynamics in an

- agricultural watershed: observations on the role of a riparian forest. *Ecology* 65:1466-1475.
- Phillips, P.J., J.M. Denver, R.J. Shedlock, and P.A. Hamilton. 1993. Relation of forested wetlands and water quality in different hydrologic and geomorphic settings of the Delmarva Peninsula. *Wetlands* 13: (in press).
- Pinay, G., A. Fabre, P. Vervier, and F. Gazelle. 1992. Control of C, N, P, distribution in soils of riparian forests. *Landscape Ecology* 6:121-132.
- Pionke, H.B. and H.M. Kunishi. 1992. Phosphorus status and content of suspended sediment in a Pennsylvania watershed. *Soil Science* 153:452-462.
- Ponnamperuma, F.N. 1972. The chemistry of submerged soils. *Advances in Agronomy* 14:29-96.
- Puckett, L.J., M.D. Woodside, B. Libby, and M.R. Schening. 1993. Sinks for trace metals, nutrients and sediments in wetlands of the Chickahominy River near Richmond, Virginia. *Wetlands* 13: (in press).
- Richardson, C.J. 1985. Mechanisms controlling phosphorus retention capacity in freshwater wetlands. *Science* 228:1424-1427.
- Richardson, C.J. and P.E. Marshall. 1986. Processes controlling movement, storage and export of phosphorus in a fen peatland. *Ecological Monographs* 56:279-302.
- Richardson, C.J., M.R. Walbridge, and A. Burns. 1988. Soil chemistry and phosphorus retention capacity of North Carolina coastal plain swamps receiving sewage effluent. Water Resources Research Institute of the University of North Carolina, Raleigh, NC, USA. UNC-WRRI-88-241.
- Riekirk, H., D.G. Neary, and W.T. Swank. 1989. The magnitude of upland silvicultural nonpoint source pollution in the South. p. 8-18. In D.D. Hook and R. Lea (eds.) *Proceedings of the Symposium: The Forested Wetlands of the Southern United States*. July 12-14, 1988, Orlando, FL. General Technical Report SE-50. USDA-Forest Service, Southeastern Forest Experiment Station, Asheville, NC, USA.
- Sah, R.N. and D.S. Mikkelsen. 1986. Sorption and bioavailability of phosphorus during the drainage period of flooded-drained soils. *Plant and Soil* 92:265-278.
- Schlesinger, W.H. 1978. Community structure, dynamics, and nutrient cycling in the Okefenokee cypress swamp-forest. *Ecological Monographs* 48:43-65.
- Schlesinger, W.H. 1991. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego, CA, USA.
- Schwertmann, U. 1966. Inhibitory effect of soil organic matter on the crystallization of amorphous ferric hydroxide. *Nature* 212: 645-646.
- Schwertmann, U. and R.M. Taylor. 1989. Iron oxides. p. 380-438. In J.B. Dixon and S.B. Weed (eds.) *Minerals in Soil Environments*, Second Edition. Soil Science Society of America, Madison, WI, USA.
- Stevenson, F.J. 1986. *Cycles of Soil: C, N, P, S, Micronutrients*. John Wiley and Sons, New York, NY, USA.
- Swank, W.T., L.W. Swift, and J.E. Douglass. 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances. In W.T. Swank and D.A. Crossley (eds.) *Forest Hydrology and Ecology at Coweeta*. Ecological Studies 66: 297-312.
- Tietjen, W.L. and J.C. Carter. 1981. Retention of urban derived phosphorus by an alluvial swamp of the Coastal Plain of Georgia. Report ERC 05-81. Environmental Resources Center, Georgia Institute of Technology, Atlanta, GA, USA.
- Vitousek, P.M. and W.A. Reinert. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25:376-381.
- Walbridge, M.R. 1991. Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. *Ecology* 72:2083-2100.
- Walbridge, M.R. and E.M. Birk. 1988. P availability in *Pinus taeda* L. stands at the Savannah River Plant. *Bulletin of the Ecological Society of America* 69:331. (Abstract).
- Walbridge, M.R., R.G. Knox, and P.A. Harcombe. 1992. Phosphorus availability along a landscape gradient in the Big Thicket National Preserve. *Bulletin of the Ecological Society of America* 73:377. (Abstract).
- Walbridge, M.R., C.J. Richardson, and W.T. Swank. 1991. Vertical distribution of biological and geochemical phosphorus subcycles in two southern Appalachian forest soils. *Biogeochemistry* 13:61-85.
- Walbridge, M.R. and P.M. Vitousek. 1987. Phosphorus mineralization potentials in acid organic soils: processes affecting $^{32}\text{PO}_4^{3-}$ isotope dilution measurements. *Soil Biology and Biochemistry* 19: 709-717.
- Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. *The Ecology of Bottomland Hardwood Swamps of the Southeast: a Community Profile*. FWS/OBS-81/37, USDI Fish and Wildlife Service, Biological Services Program, Washington, DC, USA.
- Willett, I.R., W.A. Muirhead, and M.L. Higgins. 1978. The effects of rice-growing on soil phosphorus immobilization. *Australian Journal of Experimental Agriculture and Animal Husbandry* 18: 270-275.
- Winter, T.C. 1988. A conceptual framework for assessing cumulative impacts on hydrology of nontidal wetlands. *Environmental Management* 12:605-620.
- Wood, T., F.H. Bormann, and G.K. Voigt. 1984. Phosphorus cycling in a northern hardwood forest: biological and chemical control. *Science* 223:391-393.
- Yarbro, L.A. 1983. The influence of hydrologic variations on phosphorus cycling and retention in a swamp stream ecosystem. p. 223-245. In T.D. Fontaine and S.M. Bartell (eds.) *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, MI, USA.

Manuscript received 11 August 1992; revision received 12 March 1993; accepted 19 March 1993.