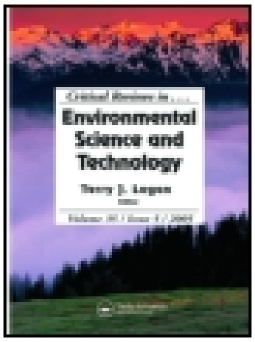

Critical Reviews in Environmental Control

ISSN: 1040-838X (Print) (Online) Journal homepage: http://www.tandfonline.com/loi/best19

Sediment and nutrient retention by freshwater wetlands: Effects on surface water quality

Carol A. Johnston Ph.D.

To cite this article: Carol A. Johnston Ph.D. (1991) Sediment and nutrient retention by freshwater wetlands: Effects on surface water quality, Critical Reviews in Environmental Control, 21:5-6, 491-565, DOI: 10.1080/10643389109388425

To link to this article: https://doi.org/10.1080/10643389109388425

Critical Reviews in Environmental Control, 21(5,6):491–565 (1991)

Sediment and Nutrient Retention by Freshwater Wetlands: Effects on Surface Water Quality*

Carol A. Johnston, Ph.D.

Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota, 5013 Miller Trunk Highway, Duluth, MN 55811

* Contribution 77 of the Center for Water and the Environment.

ABSTRACT: Freshwater wetlands alter surface water quality in ways which benefit downstream use. This review summarizes the mechanisms of freshwater wetland interaction with sediment and nutrients that affect surface water quality. The mechanisms vary in magnitude and reversibility, and differ among wetland types. They include sedimentation, plant uptake, litter decomposition, retention in the soil, and microbial processes. Sedimentation is a relatively permanent retention mechanism whereby particulates and associated contaminants are physically deposited on the wetland soil surface. Plant uptake and litter decomposition provide short- to long-term retention of nutrients, depending on rates of leaching, translocation to and from storage structures, and the longevity of plant tissues. Plant litter can also provide a substrate for microbial processing of nutrients. Wetland soils sorb nutrients, and provide the environment for aerobic and anaerobic microorganisms that process nutrients. Wetland storage compartments, fluxes, and net retention rates are discussed for nitrogen and phosphorus.

KEY WORDS: wetlands, water quality, sediment, nitrogen, phosphorus, plants, litter, microbes, soil, retention.

I. INTRODUCTION

Freshwater wetlands are complex ecosystems that interact with contaminants in a number of ways. The general perception that wetlands improve water quality has led to their use for wastewater disposal in many parts of the world,[1,2] but many of the mechanisms by which wetlands retain and process waterborne inputs are still poorly understood. The purpose of this review is to summarize information from the literature about the various mechanisms by which naturally occurring freshwater wetlands interact with surface water, and to draw conclusions about their importance to water quality.

1040-838X/91/$.50

This review focuses on wetland processes which affect sediment and nutrients. In general, processes that decrease waterborne sediment and nutrient concentrations are considered to benefit water quality, although reduction below minimal threshold concentrations may not provide additional benefit and may even be detrimental to the productivity of downstream ecosystems. This review does not deal with the impacts of water quality impairment on wetland "health", but rather on the ability of the wetland to retain and process contaminants to the benefit of other surface waters. Literature compilations by Nixon and Lee[3] and Johnston et al.[4] served as major reference sources.

A. Characteristics of Wetlands

Wetlands are defined by the U.S. Fish and Wildlife Service as "lands where saturation with water is the dominant factor determining the nature of soil development and the types of plant and animal communities living in the soil and on its surface."[5] Wetlands are distinguished from uplands by soil wetness, and from deep water habitats by water depth. Although areas with submergent aquatic vegetation and standing water up to 2 m in depth fall within the U.S. Fish and Wildlife Service definition of wetland, most of the wetlands considered in this review have shallower water, and floating, emergent, or woody vegetation. Wetlands with herbaceous vegetation (especially those with standing surface water) are generically called marshes, while those with woody vegetation are called swamps.

Wetland soils vary in texture and organic matter content. Organic soils contain at least 12 to 18% organic carbon, depending on clay content, while mineral soils contain less.[6] "Peatlands" are wetlands with organic soils and little or no surface water. The terms "bog" and "fen" are used, respectively, to refer to acidic and alkaline peatlands, although use of the terminology varies.[7]

Water is the primary medium of material transfer into and out of wetlands. Freshwater wetlands receive water from precipitation, groundwater, and/or surface water, conveyed in the form of runoff, streams, rivers, lakes, and human wastewater discharges. These water sources convey varying amounts of sediment and nutrients. In general, the highest inputs are from anthropogenically altered sources (wastewater discharges, surface waters, and runoff from urban and agricultural lands), while the lowest are from precipitation and groundwater. An individual wetland may receive water from any and all of these sources, often with substantial seasonal variation (e.g., seasonal precipitation trends, spring flooding). There is an equivalent variety of possible output paths (into surface water, groundwater, and evapotranspiration), making it difficult to construct the hydrologic budgets necessary to quantify accurately wetland-water interactions.[8,9]

B. Processing of Materials by Wetland Ecosystems

Once a substance enters a wetland, it may be stored, altered by chemical or biological action, or discharged via water or atmospheric fluxes.[10] A generic model of these interactions contains 7 different storage compartments and 28 different flux pathways for materials in wetlands (Figure 1). While some of these storage and discharge mechanisms are well understood, the difficulty in quantifying others has resulted in highly variable published results on the effects of wetlands on water quality.

Retention in wetlands results from cumulative fluxes into storage compartments of the wetland ecosystem: soils, vegetation, and plant litter (Figure 1). If annual inputs are greater than outputs, the storage compartment is a "sink", removing the substance from circulation. Storage compartments that are sinks gradually accumulate substances, those that are sources are gradually depleted of them, and those in which annual inputs equal outputs have no net effect.

Total storage of a substance in a particular compartment ("standing stock") is expressed as mass per unit area, and is computed by multiplying the mass or volume of the storage medium (e.g., biomass per square meter; soil volume per square meter) by the concentration of the substance per unit of that mass or volume, such as grams of nitrogen per gram dry weight of biomass (mg/gdw), or grams of phosphorus per milliliter of water. The flux of a substance between compartments is expressed as mass per unit area over time. In this paper, concentrations are expressed as percent dry weight, mg/gdw, or μg/gdw, standing stocks are expressed as mg m^{-2} or g m^{-2}, and fluxes are expressed as mg m^{-2} $year^{-1}$ or g m^{-2} $year^{-1}$.

Measurement of standing stocks gives a snapshot view of the total amount of nutrients contained in a storage compartment at a particular time. Some standing stocks (e.g., nutrients stored in tree boles or soils) change very little over time, while the standing stocks in dynamic storage compartments (e.g., leaves, herbaceous plants) change substantially during the course of a year. The timing of standing stock measurement can therefore affect the results obtained.

The importance of a storage compartment to water quality depends on both the rate of flux into a storage compartment and the duration of retention in that compartment ("turnover time"). A given flux into a short-term storage compartment (e.g., wetland surface water) is less desirable from the standpoint of water quality than a comparable flux into a long-term storage compartment (e.g., burial in soil). If the flux rate into a long-term storage compartment is small, however, its net effect on water quality will also be small but nevertheless positive when compared to the alternative of exporting standing stocks.

The size of a standing stock is not necessarily indicative of its net effect on water quality. A large standing stock may be the result of small annual additions over a long period of time. For example, new annual nutrient storage in tree boles is typically very small, but standing stocks of nutrients in tree boles may be substantial because tree longevity results in long turnover times.

The conversion of an element from one form to another can benefit water quality even if there is no net retention by a storage compartment. For example, inorganic nitrogen (NH_4 and NO_3) can degrade water quality by promoting algae blooms, but other forms of nitrogen cannot be taken up by algae. Therefore, the conversion of dissolved inorganic nitrogen to organic nitrogen can benefit water quality without a change in total N concentration.

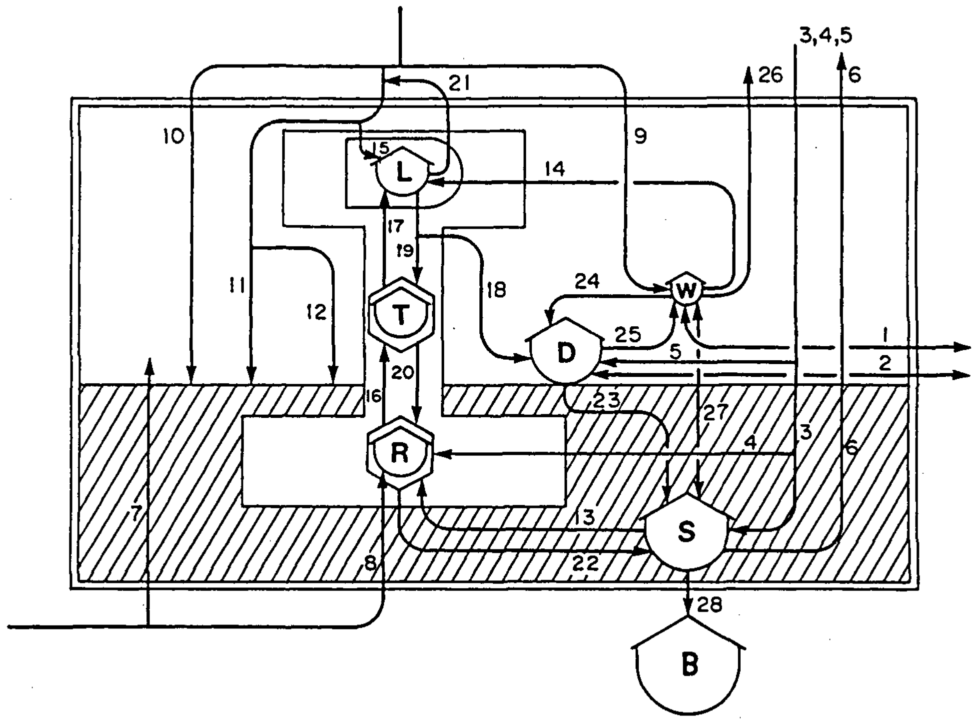

FIGURE 1. General model of major fluxes and standing stocks of materials in wetland ecosystems. Standing stocks: L = aboveground shoots or leaves; T = trunks and branches, woody plants; R = roots and rhizomes; W = materials dissolved or suspended in surface water; D = litter or detritus; S = near-surface sediments; B = deep sediments below the rooting zone. Fluxes: 1,2 = exchanges of dissolved and particulate materials with adjacent waters; 3–5 = N fixation in sediments, rhizosphere, and litter; 6 = denitrification; 7,8 = groundwater inputs to surface water and roots; 9,10 = atmospheric deposition to water and land; 11,12 = aqueous deposition from canopy and stemflow; 13 = uptake by roots; 14,15 = foliar uptake from surface water and rainfall; 16 = translocation from roots to trunks and stems; 17 = translocation from trunks and stems to leaves; 18 = litterfall; 19,20 = readsorption of materials from leaves through trunks and stems to roots and rhizomes; 21 = leaching from leaves; 22 = death or sloughing of root material; 23 = incorporation of litter into sediment; 24,25 = uptake by and release from decomposing litter; 26 = volatilization of ammonia; 27 = sediment-water exchange; 28 = long-term burial in sediments, outputs to groundwater. (From Nixon, S. W. and Lee, V., *Wetlands and Water Quality,* Wetlands Research Program, Tech. Rep. Y-86-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 1986. With permission.)

Input-output (''black box'') studies treat the whole wetland as a storage compartment. Fluxes into and out of a wetland, represented by arrows entering and leaving the bounding box in Figure 1, are measured to determine the net effect of the wetland on water quality. These studies are typically done for wetlands with single, well-defined surface water inlets and outlets, negligible groundwater inputs and outputs, and high anthropogenic inputs.

Wetland literature contains numerous studies of standing stocks, particularly in vegetation, but studies of fluxes are less common. There are few comprehensive studies that quantify all the fluxes among wetland vegetation, litter, surface water, groundwater, soil, and atmospheric compartments, and even fewer such studies with data for multiple years. Where long-term studies have been conducted, they have shown that initial trends may not be indicative of long-term retention capacities, and may even be reversed over time.[11–13]

II. SEDIMENT RETENTION

A. Mineral Sediment Deposition

Sediment deposition in wetlands benefits downstream water quality by reducing the turbidity and suspended solids concentration of surface waters, and by retaining phosphorus and contaminants that are sorbed to the sediments retained.[14] Although some reworking of sediments may occur due to fluvial activity in floodplain wetlands and wind resuspension in shallow lakes,[15] sedimentation is a relatively irreversible mechanism.[16]

The capacity of flowing water to transport sediment depends on its velocity and the size of particles being transported.[17,18] Erosion occurs at velocities above the critical erosion velocity for a given particle size, transport occurs at velocities below the critical erosion velocity but above the fall velocity, and deposition occurs at velocities lower than the critical erosion velocity but higher than the fall velocity.[17] Stream velocity can be calculated by means of the Manning equation:

$$V = \frac{1.49}{n} R^{2/3} S^{1/2} \tag{1}$$

where V = velocity, R = hydraulic radius (cross-sectional area divided by wetted perimeter), S = stream gradient, and n = roughness coefficient. Velocity will decrease with a decrease in hydraulic radius, a decrease in stream gradient, or an increase in the roughness coefficient. All three of these conditions occur when a stream floods a wetland, and the resultant decrease in water velocity permits the sediment load of the stream to settle out. This process may be accelerated by the flocculation of clay particles and high molecular weight humic acids.[16,19]

A number of methods have been used to estimate rates of sedimentation in wetlands (Table 1). Methods for measuring short-term sedimentation (i.e., ≤ 1 year) include sediment traps constructed from polyethylene bottles,[22] leaf squares placed in hardware cloth holders,[31] and dust, clay, or glitter horizons sprinkled on the soil surface prior to a flood event.[24,25] Longer-term methods use radioisotope dating with ^{137}Cs or ^{210}Pb to estimate the number of years over which a measured mass or thickness of soil has accumulated,[21,26–29,32] sometimes in combination with changes in soil morphology indicative of a change in sediment supply.[30,33] Novitzki[34] used input-output suspended solids budgets to estimate sedimentation rates, but Kadlec and Robbins[29] found little change in suspended solids concentrations in streams flowing through wetlands, despite relatively high

TABLE 1
Annual Thickness and Mass Accumulation Rates for Mineral Soils and Sediments

Wetland description	Location	State	Thickness accretion (cm year^{-1})	Mass accumulation (g m^{-2} year^{-1})	Method	Ref.
Riparian forest	Tifton	GA	0.22	3500–5200	Depth to argillic horizon	20
Sagittaria wetland	Big Lake	IA	1.70	—	^{137}Cs dating	21
Alluvial cypress swamp	Cache River	IL	0.80	5600	Sediment traps	22
Lake Ellyn (drained)	Du Page County	IL	2.00	—	Sediments accumulated in impounded lake	23
Cypress swamp	Barataria Basin	LA	−0.60	—	Dust, clay, glitter marker horizons	24
Barataria Bay marshes	Barataria Basin	LA	0.60	—	White-clay marker horizons	25
Streamside with hurricane	Barataria Basin	LA	1.50	—	White-clay marker horizons	25
Streamside without hurricane	Barataria Basin	LA	1.10	—	White-clay marker horizons	25
Inland with hurricane	Barataria Basin	LA	0.90	—	White-clay marker horizons	25
Inland without hurricanes	Fourleague Bay marshes	LA	0.56	—	White-clay marker horizons	25
Streamside without hurricane	Fourleague Bay marshes	LA	0.13	—	White-clay marker horizons	25
Capitol Lake, near swamp inlet	Baton Rouge	LA	2.60	17.9	^{137}Cs dating	26
Freshwater bay bottom	Barataria Basin	LA	0.65	—	^{137}Cs dating	27
Lac des Allemands	Barataria Basin	LA	0.44–0.81	—	^{137}Cs dating	28
River bottom, South Channel	Pentwater	MI	~0	~0	^{210}Pb dating	29
North Channel inside of bend	Pentwater	MI	—	4700	^{210}Pb dating	29
North Channel outside of bend	Pentwater	MI	0.04	50	^{210}Pb dating	29
Marsh edge at outlet pool	Pentwater	MI	0.10	110	^{210}Pb dating	29
Cattail	Pentwater	MI	0.41	1400	^{210}Pb dating	29
Sedge Meadow	Pentwater	MI	0.29	1000	^{210}Pb dating	29
Cranberry Bog inlet stream delta	Stevensville	MI	0.06	330	^{210}Pb dating	29
Cranberry Bog outlet floodplain	Stevensville	MI	0.23	2300	^{210}Pb dating	29
Forest edge	Panther Swamp	NC	1.0–1.50	—	^{137}Cs and sediment-soil morphology	30
Ephemeral streams	Cypress Creek	NC	0.25–0.75	—	^{137}Cs and sediment-soil morphology	30
Forest edge	Cypress Creek	NC	0.75–2.50	—	^{137}Cs and sediment-soil morphology	30

Intermittent streams	Cypress Creek	NC	0.25–0.75	—	^{137}Cs and sediment-soil morphology	30
Floodplain swamp	Cypress Creek	NC	0–0.25	—	^{137}Cs and sediment-soil morphology	30
Floodplain swamp	Panther Swamp	NC	0–0.50	—	^{137}Cs and sediment-soil morphology	30
Intermittent streams	Panther Swamp	NC	0.25–1.00	—	^{137}Cs and sediment-soil morphology	30
Low areas	Creeping Swamp	NC	—	305	Flood event *sedimentation*	31
Intermediate elevations	Creeping Swamp	NC	—	148	Flood event sedimentation	31
Higher elevations	Creeping Swamp	NC	—	39	Flood event sedimentation	31
Prairie Potholes	Various	SD	—	430–800	^{137}Cs dating	32
Riparian forest levee	Cecil	WI	1.30	7840	^{137}Cs and sediment-soil morphology	33
Riparian forest backwater area	Cecil	WI	0.50	472	^{137}Cs and sediment-soil morphology	33
Wet meadow	Madison	WI	—	956	Suspended solids budget	34
Arithmetic Mean			0.69	1680		
Range			−0.6–2.6	0–7840		

Note: Negative values indicate erosion.

sedimentation rates measured with radioisotopes. Other methods for estimating sediment accretion include depth to the argillic horizon,[20] dendrogeomorphic measurement,[35] and drainage basin modeling.[36]

Sedimentation rates are expressed in terms of vertical accretion (cm year^{-1}) and mass accumulation (g m^{-2} year^{-1}: Table 1). Mass accumulation rates are more meaningful for inter-wetland comparisons of sedimentation rates because vertical accretion rates vary substantially with differing soil bulk densities (i.e., soil mass per unit volume). For example, even though the study by DeLaune et al.[26] had the highest thickness accretion rates reported in Table 1, it had one of the lowest mass accretion rates due to the flocculent nature of the lake bottom sediments.

The study by Kadlec and Robbins[29] illustrates the within-wetland variability in sedimentation rates, even between sites in close proximity. The mass accretion rate measured at the inside of a bend of the North Channel in Pentwater Marsh was very high (4700 g m^{-2} year^{-1}), while the rate measured at the outside of the bend was one of the lowest reported (50 g m^{-2} year^{-1}). Johnston et al.[33] also reported highly variable mass accumulation rates within an individual wetland, ranging from 7840 g m^{-2} year^{-1} in a natural levee deposited by a 1-m wide stream, to only 472 g m^{-2} year^{-1} in backwater areas farther from the stream. Because of this variability, extrapolating data from a few sample cores to a much larger area may yield erroneous results.[37]

The highest mass accumulation rates were generally measured in wetlands receiving: (1) seasonal flooding from sediment-laden rivers and streams,[20,22,29,33] or (2) surface water runoff from upland cultivated fields (“forest edge”[30]). With the exception of Pentwater Marsh,[29] the wetlands with the highest sedimentation rates were forested, possibly because floodplain forests are adapted to the seasonal flooding regimes associated with the highest sedimentation rates. Sediment delivery from surface water inputs, rather than wetland characteristics per se, was the major factor influencing sediment retention by wetlands.

Average rates of thickness accretion and mass accumulation for mineral soil wetlands were 0.69 cm year^{-1} and 1680 g m^{-2} year^{-1}, respectively. Sediment deposition is not routinely measured in wetlands, however, and tends to be studied in wetlands which receive appreciable amounts of sediment. Therefore, these accumulation rates are probably higher than those occurring in most wetlands.

Sediment retention within individual wetlands can have an important cumulative effect on water quality at the watershed scale.[38] In an analysis of erosion yields from eight watersheds containing wetlands, Phillips[39] found that less than 65% of the sediment eroded from upland areas was transported out of the watersheds studied (Table 2, column B). Of the sediment that reached streams within the watershed, 23 to 93% was retained by wetlands through which those streams flowed (Table 2, column C).

B. Organic Soil Accumulation

Organic soil (“peat”) is formed by the accumulation of organic matter where

TABLE 2
Sediment Storage in Wetlands, Percent of Watershed Erosion

Basins	State or country	Area (km²)	A Sediment stored in wetlands (% of total erosion)	B Sediment leaving basin (% of total erosion)	C Sediment stored in wetlands (% of inputs to streams)	Ref.
Lone Tree Cr.	CA	1.7	19	62	23	40
Upper Neuse	NC	1997	15	14	52	41, 42[a]
Upper Tar	NC	1119	21	8	72	39
Dry Creek	NE	52	31	64	33	43
Coon Creek, 1853–1938	WI	360	58	6	91	44
Coon Creek, 1938–1975	WI	360	37	7	84	44
Gullied basin	SE Australia	340	37[b]	10	79	45
11 Small basins	Luxembourg[c]	3.5	14	34	29	46
Yendacott	Devon, U.K.	1.0	45	3	93	47

Note: Values in column C = A/(A + B).

[a] Sediment budget estimated by Phillips[39] from data published in these sources.
[b] "Floodplain" deposits as identified by Melville and Erskine[45] are equated to alluvial storage, and "floodout" deposits to non-wetland storage.
[c] Values are means for the 11 basins.

After Phillips, J. D., *Water Resourc. Bull.*, 25, 867, 1989.

biomass production exceeds decomposition rate. Most organic soils occur in wetlands because rates of decay are slow due to the lack of oxygen. Unlike mineral sediment deposition, which depends on inputs of soil material from outside of the wetland, organic soil accumulation depends primarily on the production and decomposition of material *in situ*.

Formation of peat consists primarily of three processes: (1) loss of organic matter by leaching or attack by animals and microorganisms; (2) loss of physical structure; and (3) change of chemical state (i.e., the production of new types of molecules by microorganisms and spontaneous chemical reactions).[48,49] A number of factors can affect the rate of organic matter accumulation:[50]

1. Nature of plant material (different plant species decompose at different rates)
2. Climate (influences decomposition rates, depth to permafrost, regional flora and fauna)
3. Fire (initial destruction of peat and vegetation, ashes increase available nutrients in peat for several years after fire)
4. Geologic factors (glacial readvance, erosion)
5. Flooding (can cause anaerobic conditions)
6. Human disturbance (logging, cultivation, drainage, burning, blocking drainages with road fills, etc.)

As with mineral soils, rates of organic soil accumulation may be measured by use of radioisotope dating (Table 3). Hemond[52] used ^{210}Pb dating to measure organic matter accumulation, but ^{14}C dating of wood buried in peat or the peat itself is more commonly used.[50,51,53–57] Modeling of decomposition in bogs has also been used to estimate organic soil accumulation.[57]

Both thickness accretion and mass accumulation rates generally decrease with depth within a peat profile because the organic matter continues to decompose and be compacted over time. Therefore, the depth of sampling influences averaged accumulation calculations; Heilman's[51] measurements of surface peat accretion are five to seven times Heinselman's[50] deep (0 to 216 cm) peat measurements. The average thickness accretion rate for organic soils (0.12 cm year^{-1}: Table 3) was one sixth the average accretion rate for mineral soils (0.69 cm year^{-1}: Table 1). However, average mass accumulation was over an order of magnitude lower for organic soils (96 g m^{-2} year^{-1}: Table 3) than mineral soils (1680 g m^{-2} year^{-1}: Table 1) due to the low bulk densities of organic soils. Measured rates of *Sphagnum* moss accretion and mass accumulation are much higher than those for organic soils[58–62] because the moss is largely undecomposed. Mass accumulation rates fall within the range of *Sphagnum* productivity values summarized by Johnston[63] (10 to 680 g m^{-2} year^{-1}).

III. NITROGEN AND PHOSPHORUS RETENTION

Nitrogen and phosphorus are nutrients essential to plant growth, but excessive concentrations of these nutrients can be detrimental to lake and stream water

TABLE 3
Annual Thickness and Mass Accumulation Rates for Organic Soils

Wetland description	Location	State or country	Sample depth (cm)	Thickness accretion (cm year^{-1})	Mass accumulation (g m^{-2} year^{-1})	Dating method	Ref.
Sphagnum peat	Fairbanks	AK	0–41	0.25	150	^{14}C	51
Sphagnum peat	Fairbanks	AK	0–71	0.38	280	^{14}C	51
Thoreau's Bog	Concord	MA	60	0.30	—	^{210}Pb	52
Glacial L. Agassiz peatland	Littlefork	MN	0–216	0.05	—	^{14}C	50
Myrtle Lake peatland	Littlefork	MN	0–430	0.14	—	^{14}C	53
Sedge meadow	Cecil	WI	0–50	0.17	—	^{14}C	54
Marsh site	Okefenokee	GA	0–380	0.06	80	^{14}C	55
Shrub site	Okefenokee	GA	0–180	0.05	68	^{14}C	55
Cypress site	Okefenokee	GA	0–360	0.06	74	^{14}C	55
Lagg	Manitoba	Canada	80–85	0.03	52	^{14}C	56
Muskeg	Manitoba	Canada	200–205	0.03	27	^{14}C	56
Bog forest	Manitoba	Canada	185–190	0.04	36	^{14}C	56
Moor House	—	U.K.	—	0.01	—	Bog model	57
Arithmetic mean				0.12	96		
Range				0.01–0.38	27–280		

quality, resulting in algae blooms, decreased light penetration, loss of dissolved oxygen, and ultimately the eutrophication of lakes. Therefore, the retention of nitrogen and phosphorus in wetlands can benefit downstream water quality. Since wetland plants require nitrogen and phosphorus for growth, small additions of nutrients are generally not harmful. Nutrient additions that are high in proportion to normal inputs, however, can alter the species composition of wetland vegetation and cause other biological changes.[64]

A. Sources of Nitrogen and Phosphorus to Wetlands

1. Atmospheric Deposition

All wetlands receive inputs of nitrogen and phosphorus from precipitation and atmospheric deposition. Atmospheric inputs are the major source of nutrients to wetlands for which precipitation is the primary source of water,[52,65,66] but nutrient concentrations in precipitation are typically much lower than those in surface waters, particularly surface waters receiving point and nonpoint-source pollution. Loadings from precipitation average about 0.5 g N m^{-2} $year^{-1}$ and 0.04 g P m^{-2} $year^{-1}$ (Table 4), while loadings from wastewater applications in wetlands typically exceed 6.0 g N m^{-2} $year^{-1}$ and 1.7 g P m^{-2} $year^{-1}$.[12] Atmospheric N deposition tends to be highest in the humid eastern U.S. and lowest in the drier west coast areas, while the spatial distribution of atmospheric P deposition lacks an apparent pattern (Table 4). Deposition rates of N and P are an order of magnitude lower in Alaska than in the 48 contiguous states (Table 4).

2. Nitrogen Fixation

Nitrogen fixation, the process whereby gaseous N_2 is converted into organic N by prokaryotic organisms containing the enzyme nitrogenase, is a source of nitrogen to some wetlands. A wide variety of symbiotic (associated with nodulated host plants) and asymbiotic (free-living) organisms can fix nitrogen. Nitrogen-fixing organisms occur in the water column, on the soil surface, in aerobic and anaerobic flooded soils, in the root zone of plants, and on the leaf and stem surfaces of plants.[88]

The prevailing method for measuring nitrogen fixation is the acetylene reduction activity (ARA) method, in which soil and/or plants are incubated in a 10% acetylene atmosphere over a period of time. The acetylene is reduced by nitrogenase to ethylene, which is measured by gas chromotography,[89] and used to estimate nitrogen fixation assuming a ratio of 3 mol ethylene formed to 1 mol dinitrogen (N_2) fixed.[90] An alternative but more expensive method is to measure the uptake of $^{15}N_2$ with a mass spectrometer or emission spectrometer.[91] In wetland studies in which ARA assays were calibrated against ^{15}N measurements, the molar

TABLE 4
Atmospheric Deposition of Nitrogen and Phosphorus

Location	State or country	N form(s)	N (mg m^{-2} year^{-1})	P (mg m^{-2} year^{-1})	Ref.
Barrow	AK	NO_3 + NH_4	23	—	67
Barrow	AK	—	—	1.2	68
Poker Flat	AK	NO_3 + NH_4	12	—	69
New Haven	CT	—	—	12	70
Lewes	DE	NO_3	340	—	71
Gainesville	FL	TN	1050	90	72
Sapelo Island	GA	NO_3 + NH_4	300	—	73
Putnam Co.	GA	—	—	92–95	74
Okefenokee Swamp	GA	NO_3	332	22	75
Chicago	IL	—	—	25	70
Southern IL	IL	—	—	110	22
Falmouth	MA	TN	800	100	76
Rhode River	MD	TN	1370	45	77
Houghton Lake	MI	TN	520	30	78
Marcell	MN	—	—	9–15	79
Marcell	MN	TN	728	60	80
Tar River Swamp	NC	TN	580	49	81
Creeping Swamp	NC	—	—	60–79	31
Coweeta	NC	—	—	9–13	82
Piedmont	NC	—	—	28	83
Mirror Lake	NH	NO_3 + NH_4	660	4	84
Hubbard Brook	NH	—	—	63	85
New York State	NY	—	—	22–64	70
Finger Lakes	NY	—	—	29	70
Ithaca	NY	NO_3 + NH_4	1000	18	84
Brookhaven	NY	NO_3 + NH_4	405	—	71
Ithaca	NY	NO_3 + NH_4	560	—	71
Whiteface	NY	NO_3 + NH_4	520	—	71
Cincinnati	OH	—	—	80	70
Cochocton	OH	—	—	17	70
Western Oregon	OR	—	—	27	70
Penn State	PA	NO_3 + NH_4	625	—	71
Narragansett	RI	—	—	7	70
Savannah River	SC	—	—	30	86
Walker Branch	TN	—	—	54	87
Charlottesville	VA	NO_3 + NH_4	515	—	71
Cedar River	WA	—	—	30	70
Seattle	WA	—	—	150	70
Various locations	WI	TN	114	5	34
Great Lakes region	—	—	—	10–50	70
SD, NE, MN	—	NO_3	220–450	—	69
West Coast	—	NO_3	60–110	—	69
MT, ND, WY	—	NO_3	110–220	—	69
Southeastern U.S.	—	NO_3	220	—	69
Arithmetic mean			490	43	
Range			12–1370	1.2–110	

Note: TN = total N.

ratio of ethylene production to $^{15}N_2$ fixation ranged from 3.5 to 4.4,[92,93] higher than the 3:1 ratio normally assumed. Therefore, studies that have used the 3:1 assumption may somewhat overestimate actual values.[90]

Most nitrogen fixation studies are conducted in the laboratory on small samples of soil or plants. While this allows researchers greater control over experimental conditions, the collection and incubation process may disturb the sample. Results are also affected by sample size and incubation time.[94] *In situ* incubation techniques for nitrogen fixation have been used by several wetland researchers to avoid the problems inherent in laboratory incubations,[92,95,96] but the spatial variability in ARA over very short distances makes extrapolation of results from *in situ* measurements or laboratory incubations uncertain.[94]

A number of environmental factors influence the rate of nitrogen fixation in flooded soil.[88] The availability and quality of carbon compounds appears to be the primary factor limiting growth of heterotrophic nitrogen-fixing bacteria because these microorganisms must obtain their energy from carbon compounds synthesized by other organisms. Added labile carbon substrates have been shown to stimulate nitrogen fixation in flooded soils,[91] and excretion of organic compounds from plant roots helps make the rhizosphere a favorable environment for heterotrophic nitrogen fixation.[97] Factors that inhibit nitrogen fixation include high ambient concentrations of inorganic nitrogen, low light intensities (decreases autotrophic nitrogen fixation), high oxygen concentrations (inhibits nitrogenase), high redox potential (fixation is greater under reduced than under oxidized conditions), and high (>8.0) or low (<5.0) pH levels[88,97] Growing season length also appears to affect fixation rates, with average fixation in tropical regions (2.5 g N m^{-2} $year^{-1}$) greater than fixation in temperate and arctic regions (1.3 g N m^{-2} $year^{-1}$: Table 5).

Although asymbiotic fixation can provide more than half of the total nitrogen input to wetlands hydrologically dependent on precipitation,[52,67] nitrogen inputs from fixation are generally small compared to those from surface water inputs to wetlands,[66] particularly surface waters containing anthropogenically derived N.[72] Therefore, asymbiotic fixation in wetlands is probably not a significant source of nitrogen to downstream waters.

Symbiotic nitrogen fixation occurs in root nodules of host plants such as legumes and certain wetland shrubs (e.g., *Alnus* spp. and *Myrica gale* and *M. cerifera*). Only a few researchers have tried to quantify symbiotic nitrogen inputs to wetlands, and the rates reported varied over two orders of magnitude (Table 6). Symbiotic fixation rates are typically higher than asymbiotic fixation rates (Tables 5 and 6), although a Netherlands study reported that asymbiotic nitrogen fixation approximately equaled symbiotic nitrogen fixation by *Alnus glutinosa* in a recharge fen.[107] Studies that estimated fixation rates based on soil nitrogen concentrations[113,114] reported higher values than those based on acetylene reduction from excised nodule material[112] or exhumed *Alnus* roots.[107]

While symbiotic nitrogen fixation is clearly an important mechanism of nitrogen input to wetlands having the appropriate host vegetation, the distribution and relative abundance of such wetlands is unknown. The importance of symbiotic

TABLE 5
Asymbiotic Nitrogen Fixation in Wetlands

Wetland description	Location	State or country	N (g m^{-2} year^{-1})	Ref.
Temperate regions				
Tundra, polygonal troughs, and marshes	Barrow	AK	0.12	98
Tundra, high center polygon	Barrow	AK	0.04	98
Tundra, low center polygon	Barrow	AK	0.09	98
Tundra, wet meadow	Barrow	AK	0.02	98
Cypress dome (sewage enriched), *Azolla*	Gainesville	FL	0.07	72
Cypress dome, cypress roots, and *Azolla*	Gainesville	FL	Neglible	72
Cypress dome (sewage enriched), litter	Gainesville	FL	0.12	99
Cypress dome, litter	Gainesville	FL	0.39	99
Panicum hemitomon marsh	Deltaic Plain	LA	6.7	100
Flooded rice field soil	Crowley	LA	2–3	91[a]
Thoreau's Bog	Concord	MA	1.00	92
Scirpus atrovirens marsh	Petersham	MA	0.4–2.0	101[b]
Peat bog	Petersham	MA	0.05	102
Hibiscus marsh	Choptank River	MD	0.70	103
Sphagnum peatland bog	Marcell	MN	0.05–0.07	66
Typha latifolia stand (*in situ*)	St. Paul	MN	1.80	96
Glyceria and *Typha* rhizomes	Ontario	Canada	6.00	104
Beaver pond	Sept-Iles, Quebec	Canada	5.10	105
Poor fen	Southern Germany	G.D.R.	0.53	106
Fen	Southern Germany	G.D.R.	2.10	106
Bog	Southern Germany	G.D.R.	0.07	106
Recharge fen, peat muck	Vechtplassen	Netherlands	0.11	107
Recharge fen, *Sphagnum*	Vechtplassen	Netherlands	Negligible	107
Discharge fen, peat muck	Vechtplassen	Netherlands	1.27	107
Blanket bog	Pennine	U.K.	0.05–3.20	108

TABLE 5 (continued)
Asymbiotic Nitrogen Fixation in Wetlands

Wetland description	Location	State or country	N ($g\ m^{-2}\ year^{-1}$)	Ref.
Arithmetic mean			1.33	
Range			0–6.7	
Tropical regions				
Typha angustata wetlands	Union Territory	India	2.2–2.38	109[a]
Planted rice soil	—	Ivory Coast	7.20	110
Papyrus marsh	—	Kenya	0.01	111[a]
Rice field, Puro soil (*in situ*)	—	Philippines	1.85–3.33	95[c]
Rice field, Santa Domingo soil (*in situ*)	—	Phillipines	0.23–0.57	95[c]
Arithmetic mean			2.50	
Range			0.01–7.2	

Note: Rates are as reported in original references except where footnoted. Studies by Reddy and Patrick[91] and Chapman and Hemond[92] used ^{15}N; all other studies were done by the acetylene reduction activity method.

[a] Daily rate × 365 days.
[b] Daily rate × 200 days.
[c] Fixation rate per "cropping season".

TABLE 6
Nitrogen Fixation in Wetlands with Nitrogen-Fixing Symbionts

Wetland description	Location	State or country	N fixation rate ($g\ m^{-2}\ year^{-1}$)	Ref.
Myrica gale open peatland	Petersham	MA	3.4	112
Myrica gale lakeside wetland	Petersham	MA	2.4	112
Alnus rugosa wetland	Union	CT	8.5	113
Alnus rugosa wetland	Montreal, PQ	Canada	16.8	114
Alnus glutinosa fen	Vechtplassen	Netherlands	0.1	107

Note: Rates are as reported in original references.

N fixation in wetlands to downstream water quality is also unknown, although a study of nitrogen fixation by an upland *Alnus* stand showed increased aquatic productivity downstream.[115] Because symbiotic fixation becomes incorporated in plant tissues, rendering in unavailable until the organic matter is decomposed, this source of nitrogen is probably not detrimental to downstream water quality.

B. Nutrient Concentrations and Standing Stocks in Wetlands

1. Nutrient Concentrations in Soil

Nutrient concentrations reported for wetland soils span several orders of magnitude: 0.02 to 65.0 mg N/gdw and 0.001 to 7.0 mg P/gdw (Tables 7 and 8). While it is difficult to derive generalities from such variable data, organic soils average about twice as much N (17 mg/gdw) as mineral soils (8 mg/gdw) on a per-mass basis. Average phosphorus concentrations per unit weight (0.6 mg/gdw) were comparable for both organic and mineral soils (Tables 7 and 8).

The differences in nutrient concentrations between organic and mineral soils are altered, however, by expressing soil nutrient concentrations on a per-volume basis because organic soils have much lower bulk densities than mineral soils. Volumetric concentrations of total N were only slightly higher for organic soils than for mineral soils in a Wisconsin wetland (5.3 and 4.8 g/l, respectively), and volumetric concentrations of total P were three times higher in the mineral soils (0.75 g/l) than they were in the organic soils (0.26 g/l).[33] Volumetric N concentrations calculated from Florida wetland soils were lower for organic (2.3 g/l) than mineral soils (6.8 g/l), even though organic soils had much higher concentrations by weight (23.7 vs. 9.2 mg/gdw for mineral soils).[121] Volumetric units permit more valid comparisons of nutrient concentrations in organic vs. mineral soils and are more realistic in terms of vegetative nutrient supply because plant roots occupy a volume rather than a mass of soil. Although several authors have advocated volumetric reporting of nutrient concentrations in wetland soils, its use is still uncommon.[33,147,148]

TABLE 7
Concentrations of Nitrogen and Phosphorus in Mineral Wetland Soils

Wetland or soil type	Location	State or country	Sample depth (cm)	Total N (mg/gdw)	Total P (mg/gdw)	Organic matter (% dry weight)	Ref.
Muskeg	Fairbanks	AK	5–25	—	0.007–0.009	12	116
Carex aquatilis wetland	Fairbanks	AK	5–25	—	0.008–0.016	1.9–3.3	116
Arctagrostis tundra	Barrow	AK	0–3	0.06	0.013	—	117
Dupontia tundra	Barrow	AK	3–13	0.07	0.022	—	117
Dupontia tundra	Barrow	AK	0–3	0.02	0.005	—	117
Arctagrostis tundra	Barrow	AK	3–13	0.06	0.033	—	117
Mixed hardwood swamp, sewage enriched	Wildwood	FL	0–8	5–65	—	—	118
Floodplain forest	Gainesville	FL	0–20	—	0.35	8	119
Cypress domes, 4 natural sites	Gainesville	FL	0–20	—	0.14–0.30	8–49	119
Scrub cypress	Naples	FL	0–20	—	0.001	<1	119
Cypress domes, 2 nutrient-enriched sites	Gainesville	FL	0–20	—	0.55–1.01	18	119
Freshwater marsh receiving wastewater	Clermont	FL	0–25	—	0.90	—	120
Riviera fine sand	St. Johns Co.	FL	0–10	3.8	—	10	121
Floridana fine sand	Lee Co.	FL	0–10	14.3	—	26	121
Astor sand	Lake Co.	FL	0–10	11.7	—	15	121
Chobee fine sandy loam	Palm Beach Co.	FL	0–10	9.9	—	15	121
Eureka fine sandy loam	Marion Co.	FL	0–10	8.6	—	12	121
Valkaria fine sand	Lee Co.	FL	0–10	0.2	—	1	121
Delray fine sand	Okeechobee Co.	FL	0–10	10.7	—	13	121
15 cypress domes	Gainesville	FL	0–150	2.4–15.1	—	—	122
Cypress swamp, 26 sewage-enriched cores	Waldo	FL	0–50	—	0.21–1.05	6–40	123
Capitol Lake, near swamp inlet	Baton Rouge	LA	0–69	—	0.14–1.70	—	26
Cypress-Tupelo Swamp	—	LA	—	11.0	1.01	37	124
Alluvial Swamp	Tar River	NC	0–10	11.0	1.17	35	125
Creeping Swamp	Pitt County	NC	—	—	1.30	—	31
Devils Lake	—	ND	—	2.3	0.38	—	126
Freshwater tidal marsh	Camden	NJ	0–5	7.2–8.6	1.2–1.5	—	127
Silt loam alluvium	Cecil	WI	0–15	7.1	0.93	—	57

Sandy loam alluvium	Cecil	WI	0–15	0.9	0.43	—	57
Sand alluvium	Cecil	WI	0–15	1.1	0.22	—	57
Marsh	Ontario	Canada	—	15.2	1.28	—	128
Swamp	Ontario	Canada	—	12.1	0.69	—	128
Exhausted pegasse soil	NW District	British Guiana	0–24	6.7	—	26	129
Six shallow Danish lakes, 15 cores	Jylland	Denmark	0–25	12–27	1–7	3–12	130
Arithmetic mean				8.3	0.69		
Range				0.02–65.0	0.001–7.0		

Note: Mineral soils have <12 to 18% organic carbon (about 25 to 38% organic matter), depending on clay content.[5,6]

TABLE 8
Concentrations of Nitrogen and Phosphorus in Organic Wetland Soils

Wetland or soil type	Location	State or country	Sample depth (cm)	Total N (mg/gdw)	Total P (mg/gdw)	Organic matter (% dry weight)	Ref.
Organic soils							
Wet tundra	Barrow	AK	5–25	—	0.003–0.015	78	116
Picea mariana bog	Fairbanks	AK	0–51	4.3–5.9	—	—	51
Peat bog	Bethany	CT	0–10	5–15	—	—	131
Appalachicola Swamp Forest	Tallahasse	FL	—	12.5–17.6	0.22–0.36	67–98	132, 133
Everglades muck	Marion Co.	FL	0–10	18.2	—	95	121
Pickney fine sand	Franklin Co.	FL	0–10	8.2	—	56	121
Surrency sand	Alachua Co.	FL	0–10	15.6	—	88	121
Samsula muck	Alachua Co	FL	0–10	29.7	—	99	121
Brighton peat	Lake Co.	FL	0–10	23.3	—	100	121
Peat soil, *Cladium* mire	Everglades	FL	0–40	27.3	0.17	—	134
Okefenokee Swamp, marsh site	—	GA	—	30.0	0.53	95	58
Okefenokee Swamp, cypress site	—	GA	—	21.0	0.57	95	58
Okefenokee Swamp, shrub site	—	GA	—	20.0	0.57	96	58
Freshwater marsh, 2 sites streamside	Barataria Basin	LA	0–50	15.0	0.93	41	135
Freshwater marsh, 2 sites backmarsh	Barataria Basin	LA	0–50	18.0	0.94	52	135
Freshwater tidal marsh	Pembroke	MA	0–100	1.8	0.16	40–75	136
Thoreau's Bog	Concord	MA	—	7.0	—	—	52
Atlantic white cedar wetlands	Annapolis	MD	—	14.4	1.20	65	137
Chamaedaphne-Betula	Houghton	MI	—	25.4	0.90	71	138
Alkaline peatland, *Larix laricina*	Roseau	MN	5–80	24.0	1.10	—	139
Alkaline peatland, *Picea mariana*	Roseau	MN	5–80	15.0	1.30	—	139
Peat soils	Various	NC	—	9–24	—	68	140
Peat soil, 36 fens	Various	U.S.	0–40	19.4	—	66	141
Freshwater marsh, *Typha-Scirpus*	Theresa	WI	0–20	17.5	—	40	142
Sapric soil	Cecil	WI	0–15	14.7	0.79	—	57
Virgin pegasse soil	NW District	British Guiana	0–24	10.2	—	55	129
Small valley mire, peat cores	York	U.K.	0–60	—	0.19–0.68	—	143
Raised bog, *Trichophorum-Carex*	Galway	U.K.	0–20	18.0	0.20	—	144
3 fens, Vechtplassen area	Utrecht	Netherlands	—	16–25	0.8–1.3	—	145
Marginal fen, *Carex-Sphagnum*	Aneboda	Sweden	0–20	25.0	0.70	—	146
Ambrotrophic bog, *Rhynchospora-Sphagnum*	Aneboda	Sweden	0–20	11.0	0.30	—	146
Arithmetic mean				17.1	0.64		
Range				1.8–30.0	0.003–1.3		

Note: Organic soils have at least 12 to 18% organic carbon (about 25 to 38% organic matter), depending on clay content.[5,6]

2. Nutrient Concentrations in Vegetation

Nitrogen and phosphorus are taken up and assimilated by growing plants. Numerous studies have measured nutrient concentrations in the aboveground portions of herbaceous wetland plants (Table 9), and it was observed 20 years ago that "there appears to be little need for additional research of this type on emergent aquatic plants."[174] Vegetation nutrient concentrations tend to be highest early in the growing season, decreasing as the plant matures and senesces.[150,155,167,169,175] When measured at peak standing crop, concentrations of N and P reported for emergent wetland vegetation averaged 1.9 and 0.2% of dry weight, respectively (Table 9). While there was some interspecific variation in nutrient concentrations, most studies reported concentrations in the range of 1 to 3% dry weight for nitrogen and 0.1 to 0.3% dry weight for phosphorus. Concentrations in free-floating wetland vegetation were somewhat higher, averaging 3.1% N and 0.5% P dry weight (Table 9).

Average N and P concentrations in the leaves of woody wetland plants (2.1 and 0.2% dry weight, respectively: Table 10) were similar to those in herbaceous wetland plants. Nutrient concentrations were much lower, however, in woody tissues. Shrub stems had N and P concentrations averaging 0.6 and 0.06% dry weight, respectively, while tree boles and roots had concentrations averaging 0.4 and 0.01% dry weight, respectively (Table 10).

Nutrient concentrations in fallen wetland plant litter (Table 11) were generally lower than concentrations in their live counterparts, best illustrated by studies that measured nutrient concentrations in live plant parts and litter at the same site.[120,161,184] Nutrients were leached out of newly fallen litter or translocated back into perennial tissues prior to litterfall, decreasing nutrient concentrations. An exception to this trend can occur when microbes associated with plant litter take up ("immobilize") nutrients from the environment, thereby increasing concentrations.[161,183]

Over time, leaching and immobilization continue to alter litter nutrient concentrations throughout litter decomposition and can cause very different trends among species. In an Iowa study, *Sparganium eurycarpum* and *Carex atherodes* litter exhibited net gains in N and P concentrations after 330 days of decomposition, *Scirpus validus* and *Typha glauca* litter exhibited net losses after 330 and 525 days, respectively, and *Scirpus fluviatilis* litter exhibited a net gain of P and a new loss of N after 525 days. *S. fluviatilis* had still not lost 50% of its initial dry weight after 525 days of decomposition.[183]

3. Nutrient Standing Stocks in Soil

Soils contain by far the largest standing stocks of nutrients of any wetland storage compartment (Tables 12 and 13). Although reported values range widely due to the lack of standard depth criteria, soil nutrient standing stocks are at least one and sometimes two orders of magnitude higher than standing stocks in veg-

TABLE 9
Concentrations of Nitrogen and Phosphorus in the Aboveground Portions of Herbaceous Wetland Vegetation at Peak Standing Crop (% dry weight)

Species	Location	State or country	N	P	Ref.
Emergent					
Acorus calamus	Trenton	NJ	2.06	—	149
Altemanthera philoxeroides	Montgomery	AL	2.20	0.39	150
Andropogon sp.	Aiken	SC	—	0.15	151
Bidens laevis	Trenton	NJ	2.22	—	149
Carex aquatilis	Wet tundra, Barrow	AK	2.18	0.15	152
C. aquatilis	Tundra biome, Barrow	AK	2.9–3.3	0.2–0.3	153
C. lacustris	Ithaca	NY	1.72	0.25	154
C. lacustris	Ithaca	NY	1.70	0.17	155
C. lacustris	Theresa	WI	0.60	0.16	156
C. lacustris	—	MN	—	0.17	157
C. lacustris	Great Lake marshes	Various	1.20	0.10	158
C. lacustris	North central	IA	1.30	0.13	159
C. lanuginosa	Ithaca	NY	3.27	0.45	154
C. rostrada	Ithaca	NY	1.47	0.24	154
Carex spp.	Houghton Lake	MI	1.60	0.12	78
C. stricta	—	MN	—	0.17	157
C. tenuiflora	Ottawa, Ontario	Canada	1.70	0.15	160
C. trisperma	Ottawa, Ontario	Canada	1.20	0.15	160
Cladium jamaicense	Everglades	FL	—	0.04	161
C. jamaicense	Everglades	FL	—	0.02	134
Dupontia fisheri	Wet tundra, Barrow	AK	1.60	0.09	152
D. fisheri	Tundra biome, Barrow	AK	2.4–3.0	0.2–0.4	153
Eleocharis quadrangulata	Par Pond, Aiken	SC	0.90	0.13	162
Erianthus sp.	Aiken	SC	—	0.07	151
Eriophorum anguistifolium	Wet tundra, Barrow	AK	2.10	0.11	152

E. vaginatum	Atkasook	AK	2.30	0.29	163
E. vaginatum	Eagle Creek	AK	2.00	0.40	164
Glyceria grandis	Hamilton, Ontario	Canada	1.5–1.7	0.13–0.21	165
Impatiens capensis	Trenton	NJ	2.08	—	149
Juncus effusus	17 sites, SE U.S.	U.S.	0.9–1.3	0.05–0.20	166
J. effusus	Steed Pond, Aiken	SC	1.3–1.8	0.16–0.30	166
Justicia americana	Auburn	AL	1.60	0.09	150
Nuphar advena	Trenton	NJ	2.13	—	149
Peltandra virginica	Trenton	NJ	2.15	—	149
Petasites frigidus	Wet tundra, Barrow	AK	2.26	0.22	152
P. frigidus	Tundra biome, Barrow	AK	2.8–3.5	0.2–0.3	153
Phragmites communis	Norfolk	U.K.	3.94	0.18	167
Polygonum arifolium	Trenton	NJ	1.93	—	149
P. punctatum	Aiken	SC	—	0.32	151
Pontedaria cordata	Trenton	NJ	2.11	—	149
Sagittaria lancifolia, control	Clermont	FL	—	0.05–0.27	120
S. lancifolia, enriched	Clermont	FL	—	0.11–0.45	120
S. latifolia	Aiken	SC	—	0.58	151
S. latifolia	Trenton	NJ	1.91	—	149
Saururus cernuus	25 sites, SE U.S.	U.S.	1.4–2.6	~0.2	168
Scirpus americanus	Par Pond, Aiken	SC	0.83	0.13	169
S. cyperinus	Aiken	SC	—	0.19	151
Sparganium eurycarpum	Ithaca	NY	3.35	0.64	154
Sphagnum flavicomans	Bethany	CT	0.5–0.8	—	131
Sphagnum spp.	Concord	MA	0.70	—	52
Tillandsia usneoides	Okefenokee Swamp	GA	0.8–1.0	0.03–0.04	75
Typha angustifolia	Everglades	FL	—	0.14–0.19	170
T. glauca	Ithaca	NY	2.47	0.53	154
T. latifolia	28 sites, SE U.S.	U.S.	0.7–2.3	0.05–0.40	171
T. latifolia	Par Pond, Aiken	SC	0.51	0.09	169
T. latifolia	Aiken	SC	—	0.16	151
T. latifolia	Great Lake marshes	Various	2.90	0.10	158
T. latifolia	Trenton	NJ	2.01	—	149

TABLE 9 (continued)
Concentrations of Nitrogen and Phosphorus in the Aboveground Portions of Herbaceous Wetland Vegetation at Peak Standing Crop (% dry weight)

Species	Location	State or country	N	P	Ref.
Zizania aquatica	Trenton	NJ	2.12	—	149
Emergent marsh	Genessee Co.	NY	2.41	0.52	171
Herbaceous spp.	Pinelands	NJ	1.97	—	172
Hamilton marsh, control	Trenton	NJ	2.60	0.19	127
Hamilton marsh, sewage enriched	Trenton	NJ	2.41–3.39	0.14–0.24	127
Woodbury Creek marsh	Camden	NJ	2.54	0.18	127
Arithmetic mean			1.94	0.21	
Range			0.5–3.94	0.02–0.64	
Free floating					
Eichhornia crassipes	17 sites, Orlando	FL	1.3–3.3	0.14–0.80	162
Lemna minor	Genessee Co.	NY	4.30	0.75	171
Salvinia rotundifolia, control	Wekiva River, Sanford	FL	1.94	0.21	173
Mixed *Spirodela* and *Salvinia*	Wekiva River, Sanford	FL	2.94–4.14	0.38–0.73	173
Spirodela polyriza, transplanted	Wekiva River, Sanford	FL	3.3–4.2	0.52–0.68	173
Salvinia rotundifolia, transplanted	Wekiva River, Sanford	FL	3.13–3.85	0.55–0.74	173
Spirodela polyrhiza, control	Wekiva River, Sanford	FL	2.21	0.33	173
Arithmetic mean			3.08	0.51	
Range			1.3–4.3	0.14–0.75	

TABLE 10
Concentrations of Nitrogen and Phosphorus in Woody Wetland Vegetation (% dry weight)

Species	Location	State or country	N	P	Ref.
Leaves					
Acer rubrum	Dismal Swamp	VA	1.65–1.88	0.09–0.16	176
A. rubrum	—	NC	1.67	0.16	177
A. rubrum	Pinelands	NJ	1.93	—	172
A. rubrum	—	NY	1.90	0.23	178
Alnus serrulata	Aiken	SC	—	0.20	151
Betula nana	Atkasook	AK	3.80	—	163
B. nana	Eagle Creek	AK	2.80	0.50	164
B. pumila	Houghton Lake	MI	2.06	0.11	78
Chamaecyparis thyoides	Dismal Swamp	VA	—	0.14	176
Chamaedaphne calyculata	Houghton Lake	MI	1.69	0.09	78
Clethra alnifolia	Pinelands	NJ	1.92	—	172
Gaylussacia frondosa	Pinelands	NJ	1.34	—	172
Hardwoods, cypress dome	Alachua County	FL	—	0.08	119
Hardwoods, floodplain forest	Alachua County	FL	—	0.21	119
Hardwoods, control dome	Alachua County	FL	—	0.06	179
Hardwoods, sewage dome	Alachua County	FL	—	0.17	179
Hardwoods, riparian forest	Rhode River	MD	1.63	0.16	180
Ledum palustre	Atkasook	AK	3.00	0.39	163
L. palustre	Eagle Creek	AK	1.80	0.30	164
Leucothoe racemosa	Pinelands	NJ	1.49	—	172
Magnolia virginiana	Pinelands	NJ	2.10	—	172
Myrica cerifera	Aiken	SC	—	0.11	151
Nyssa sylvatica	Dismal Swamp	VA	1.65–1.93	0.10–0.21	176
N. sylvatica	—	NC	1.74	0.17	177
N. sylvatica	Pinelands	NJ	1.48	—	172
N. sylvatica	—	NC	—	0.11	181

TABLE 10 (continued)
Concentrations of Nitrogen and Phosphorus in Woody Wetland Vegetation (% dry weight)

Species	Location	State or country	N	P	Ref.
Quercus alba	—	MN	1.94	0.40	182
Q. alba	Dismal Swamp	VA	1.69	0.12	176
Q. alba	—	NC	2.15	0.12	177
Q. alba	—	NY	2.60	0.14	178
Q. laurifolia	Dismal Swamp	VA	1.78	0.12	176
Rhododendron viscosum	Pinelands	NJ	1.76	—	172
Rubus chamaemorus	Atkasook	AK	4.50	—	163
Salix nigra	Aiken	SC	—	0.25	151
S. pulchra	Wet tundra, Barrow	AK	3.80	0.49	152
S. pulchra	Atkasook	AK	4.40	0.60	163
Salix spp.	Houghton Lake	MI	2.00	0.12	78
Shrubs, new growth	Okefenokee Swamp	GA	0.96–1.69	0.04–0.09	75
Taxodium distichum	Dismal Swamp	VA	—	0.17	176
T. distichum, scrub cypress	Collier County	FL	—	0.05	119
T. distichum, cypress dome	Alachua County	FL	—	0.10	119
T. distichum, floodplain forest	Alachua County	FL	—	0.17	119
T. distichum, needles & twigs	Okefenokee Swamp	GA	1.43	0.10	75
T. distichum, control dome	Alachua County	FL	—	0.08	179
T. distichum, sewage dome	Alachua County	FL	—	0.26	179
Vaccinium corymbosum	Pinelands	NJ	1.55	—	172
V. uglinosum	Eagle Creek	AK	3.00	0.50	164
V. vitis-idea	Eagle Creek	AK	0.70	0.25	164
Arithmetic mean			2.12	0.19	
Range			0.70–4.50	0.04–0.60	

Shrub stems					
Betula pumila	Houghton Lake	MI	0.91	0.08	78
Chamaedaphne calyculata	Houghton Lake	MI	0.72	0.07	78
Clethra alnifolia	Pinelands	NJ	0.71	—	172
Gaylussacia frondosa	Pinelands	NJ	0.41	—	172
Leucothoe racemosa	Pinelands	NJ	0.40	—	172
Rhododendron viscosum	Pinelands	NJ	0.48	—	172
Salix spp.	Houghton Lake	MI	0.71	0.07	78
Shrubs	Okefenokee Swamp	GA	0.35	0.02	75
Vaccinium corymbosum	Pinelands	NJ	0.49	—	172
Arithmetic mean			0.57	0.06	
Range			0.35–0.91	0.02–0.08	
Tree boles and roots					
Acer rubrum boles	Pinelands	NJ	0.60	—	172
Hardwood boles	Rhode River	MD	0.08	0.010	180
Hardwood roots	Rhode River	MD	0.16	0.044	180
Hardwood boles, control dome	Alachua County	FL	—	0.006	179
Hardwood boles, sewage dome	Alachua County	FL	—	0.011	179
Magnolia virginiana boles	Pinelands	NJ	0.68	—	172
Nyssa sylvatica boles	Pinelands	NJ	0.60	—	172
Taxodium distichum, scrub cypress	Collier County	FL	—	0.004	119
T. distichum, floodplain forest	Alachua County	FL	—	0.006	119
T. distichum	Okefenokee Swamp	GA	0.24	0.009	75
T. distichum, control dome	Alachua County	FL	—	0.003	179
T. distichum, sewage dome	Alachua County	FL	—	0.005	179
Arithmetic mean			0.39	0.011	
Range			0.08–0.68	0.003–0.044	

TABLE 11
Concentrations of Nitrogen and Phosphorus in Wetland Plant Litter (Standing Dead and Fallen Litter) (% dry weight)

Wetland or litter type	Location	State	N	P	Ref.
Herbaceous plant litter					
Cladium jamaicense, standing dead	Everglades	FL	—	0.01	161
Typha angustifolia, standing dead	Everglades	FL	—	0.02	161
Scirpus validus, leaves	Hancock County	IA	0.4	0.06	183
Typha glauca, leaves	Hancock County	IA	0.5	0.06	183
Sparganium eurycarpum, leaves	Hancock County	IA	0.6	0.01	183
Typha glauca, leaves	Hamilton County	IA	1.3	0.24	183
Scirpus fluviatilis, leaves	Hamilton County	IA	1.0	0.20	183
Carex atherodes, leaves	Hancock County	IA	0.3	0.05	183
Sagittaria lancifolia, enriched	Clermont	FL	—	0.04–0.25	120
S. lancifolia, control	Clermont	FL	—	0.06–0.07	120
Woodbury Creek Marsh	Camden	NJ	1.3	0.12	184
Arithmetic mean			0.75	0.09	
Range			0.3–1.3	0.01–0.24	
Tree and shrub leaf litter					
Acer rubrum	Great Dismal Swamp	VA	1.0–1.2	0.06–0.07	185, 186
Chamaecyparis thyoides	Great Dismal Swamp	VA	1.2	0.07	185, 186
Nyssa aquatica	Okefenokee Swamp	GA	0.7–1.1	0.04	187
N. aquatica	Pitt County	NC	1.1	0.07	81
Other spp. (*Taxodium, Fraxinus*)	Pitt County	NC	1.3	0.09	81
Nyssa aquatica	Great Dismal Swamp	VA	1.3–1.8	0.07–0.11	185, 186
N. sylvatica	Great Dismal Swamp	VA	1.1–1.3	0.05–0.08	185
Quercus spp.	Great Dismal Swamp	VA	1.2–1.3	0.06–0.07	185, 186
Taxodium ascendens	Okefenokee Swamp	GA	0.6–0.7	0.03	187
T. distichum, control	Gainesville	FL	—	0.42–0.54	188

T. distichum, enriched	Gainesville	FL	—	0.42–1.13	188
T. distichum, enriched	Waldo	FL	—	0.52–0.97	123
T. distichum	Great Dismal Swamp	VA	1.4–1.8	0.10–0.12	185, 186
Annual mean, mixed leaves	Okefenokee Swamp	GA	0.7–1.1	0.03–0.05	187
Woody bog litter	York	U.K.	—	0.60–0.80	143
Arithmetic mean			1.16	0.23	
Range			0.6–1.8	0.03–1.13	
Tree and shrub reproductive material					
Annual mean, flowers	Okefenokee Swamp	GA	1.1–1.6	0.07–0.13	187
Reproductive material	Pitt County	NC	1.4	0.17	81
Woody litter					
Annual mean, twigs and bark	Okefenokee Swamp	GA	0.5–1.0	0.02–0.04	187
Wood	Pitt County	NC	0.9	0.04	81

TABLE 12
Standing Stocks of Nitrogen in Vegetation, Litter, and Soil (g m^{-2})

Type of wetland	Location	State or country	Leaves and herbs	Wood	Roots and rhizomes	Litter	Soil	Soil depth (cm)	Ref.
Emergents									
Alternanthera philoxeroides	Montgomery	AL	24.1	—	—	—	—	—	150
A. philoxeroides	Gainesville	FL	24.0–42.5	—	—	—	—	—	189
Calluna-Eriophorum bog	Pennines	U.K.	12.0	—	—	20.0	342	(0–30)	108
Carex lacustris marsh	Ithaca	NY	18.3	—	4.8	—	—	—	155
C. rostrata fen	Ithaca	NY	14.8	—	3.7	—	—	—	190
Carex spp.	Houghton Lake	MI	4–6	—	—	—	—	—	191
Cladium jamaicense marsh	Everglades	FL	5.5–8.9	—	—	—	1527–1579	Root zone	134
Freshwater tidal marsh	North River	Manitoba	18.0	—	—	—	—	—	192
Freshwater tidal marsh	Trenton	NJ	29.0	—	24.4	—	—	—	193
Glyceria grandis fens	Ontario	Canada	45.7–72.0	—	—	—	—	—	165
Juncus effusus	Aiken	SC	26.1	—	—	—	—	—	166
Justicia americana	Lake Ogletree	AL	15.3	—	29.0	—	—	—	150[a]
Papyrus swamp	—	Uganda	61.6	—	—	—	—	—	194
Phragmites communis	—	Czechoslovakia	41.0	—	—	—	—	—	195
P. communis	—	Czechoslovakia	28.0	—	—	—	—	—	196
P. communis	Norfolk	U.K.	43.3	—	—	—	—	—	167
Sagittaria marsh, high treatment	Clermont	FL	4.8	—	14.9	11.2	—	—	197
Sagittaria marsh, low treatment	Clermont	FL	9.0	—	19.3	5.3	—	—	197
Scirpus americanus	Aiken	SC	1.7	—	—	—	—	—	169
S. fluviatilis	Goose Lake	IA	6.6	—	—	—	—	—	183
S. fluviatilis marsh	Theresa	WI	15.4	—	5.3	8.1	1696	(3–15)	198
Subarctic mire	Stordalen	Sweden	5.9	—	—	—	—	—	199
Tundra biome site	Barrow	AK	0.6–2.4	—	—	—	—	—	152
Typha angustifolia	Norfold	U.K.	13.0	—	—	—	—	—	167
T. glauca	Goose Lake	IA	16.5	—	—	—	—	—	183
T. glauca marsh	Eagle Lake	IA	28.2	—	3.9	—	—	—	200
T. latifolia	Aiken	SC	6–12	—	—	—	—	—	162
T. latifolia	—	Czechoslovakia	25.1	—	—	—	—	—	196
T. latifolia (Par Pond)	Aiken	SC	5.4	—	—	—	—	—	169
T. latifolia marsh	Lake Mendota	WI	31.0	—	—	—	—	—	201
Arithmetic mean			20.7	—	13.2				
Range			0.6–72.0	—	3.7–29.0				

Floating macrophytes									
Eichhornia crassipes	Gainesville	FL	30–90	—	—	—	—	—	189
E. crassipes	Auburn	AL	5–34	—	—	—	—	—	202
Hydrocotyle umbellata	Gainesville	FL	9–30	—	—	—	—	—	189
Lemna minor	Gainesville	FL	0.4–5.0	—	—	—	—	—	189
Pistia stratiotes	Gainesville	FL	9–25	—	—	—	—	—	189
Salvinia rotundifolia	Gainesville	FL	1.5–9.0	—	—	—	—	—	189
Arithmetic mean			20.7						
Range			0.4–90						
Woody									
Chamaedaphne peatland	Houghton Lake	MI	6.2	—	—	9.8	683	(0–20)	78
Murray River floodplain	Victoria	Australia	12.5	5.0	5.6	9.2	—	—	203[b]
Nyssa aquatica swamp	Pitt County	NC	—	—	—	4.50–6.12	—	—	204
Sphagnum bog	Marcell	MN				—	6900	(0–400)	66, 205
Taxodium distichum swamp	Okefenokee	GA	4.7	94.8	—	24.1	5365	(0–290)	75
Arithmetic Mean			7.8			12.1			
Range			4.7–12.5			4.5–24.1			

[a] Aboveground stocks determined by dividing whole-plant standing stocks by the ratio of total standing stock/aerial standing stock as of June 14 (2.9).

[b] Values are means from seven artificially irrigated plantations containing *Eucalyptus camaldulensis, E. grandis, E. saligna, Casuarina cunningham, Pinus radiata, Populus deltoides,* and *Populus deltoides* × *P. nigra*.

TABLE 13
Standing Stocks of Phosphorus in Vegetation, Litter, and Soil (g m^{-2})

Type of wetland	Location	State or country	Leaves and herbs	Wood	Roots and rhizomes	Litter	Soil	Soil depth (cm)	Ref.
Emergents									
Alternanthera philoxeroides	Montgomery	AL	2.69	—	—	—	—	—	150
A. philoxeroides	Gainesville	FL	3.0–5.3	—	—	—	—	—	189
Carex lacustris marsh	Ithaca	NY	1.60	—	1.20	—	—	—	155
C. rostrata fen	Ithaca	NY	1.90	—	0.70	—	—	—	190
Carex spp.	Houghton Lake	MI	0.2–0.4	—	—	—	—	—	191
Cladium jamaicense marsh	Everglades	FL	0.25	—	—	—	9.7–25.7	Root zone	134
Freshwater tidal marsh	Trenton	NJ	3.60	—	2.90	—	—	—	193
Glyceria grandis fen	Ontario	Canada	5.2–6.8	—	—	—	—	—	165
Juncus effusus	Aiken	SC	3.02	—	—	—	—	—	166
Justicia americana	Lake Ogletree	AL	0.65	—	2.03	—	—	—	150[a]
Manitowoc River	Brillion	WI	1.00	—	—	—	—	—	206
Phragmites communis	—	Czechoslovakia	5.30	—	—	—	—	—	195
P. communis	—	Czechoslovakia	2.90	—	—	—	—	—	196
P. communis	Norfolk	U.K.	2.00	—	—	—	—	—	167
Sagittaria marsh, high treatment*	Clermont	FL	(3.58)	—	(15.11)	(2.14)	(81)	(0–150)	120
Sagittaria marsh, low treatment	Clermont	FL	0.69	—	2.19	0.41	96	(0–150)	120
Scirpus americanus	Aiken	SC	0.18	—	—	—	—	—	169
S. fluviatilis	Goose Lake	IA	1.38	—	—	—	—	—	183
S. fluviatilis marsh	Theresa	WI	3.33	—	2.00	1.13	—	—	198
S. fluviatilis marsh	Brillion	WI	0.70	—	—	—	—	—	207[b]
Tundra biome site	Barrow	AK	0.1–0.33	—	—	—	—	—	152
Typha angustifolia	Norfolk	U.K.	3.20	—	—	—	—	—	167
T. angustifolia marsh	Brillion	WI	0.49	—	—	—	—	—	207[b]
T. glauca	Goose Lake	IA	3.17	—	—	—	—	—	183
T. glauca marsh	Eagle Lake	IA	3.74	—	1.39	—	—	—	200
T. latifolia	Aiken	SC	0.7–1.7	—	—	—	—	—	162
T. latifolia	—	Czechoslovakia	1.60	—	—	—	—	—	196
T. latifolia (Par Pond)	Aiken	SC	0.71	—	—	—	—	—	169
T. latifolia marsh	Lake Mendota	WI	3.20	—	2.50	—	—	—	201
Arithmetic mean			2.15		1.84				
Range			0.1–6.8		0.7–2.9				

Floating macrophytes									
Eichhornia crassipes	Gainesville	FL	6–18	—	—	—	—	—	189
E. crassipes ponds	Auburn	AL	0.5–3.0	—	—	—	—	—	202
Hydrocotyle umbellata	Gainesville	FL	2.3–7.5	—	—	—	—	—	189
Lemna minor	Cache River	IL	3.3	—	—	—	—	—	22
L. minor	Gainesville	FL	0.1–1.6	—	—	—	—	—	189
Nuphar luteum	Chowan River	NC	0.20	—	—	—	—	—	208
Pistia stratiotes	Gainesville	FL	2.0–5.7	—	—	—	—	—	189
Salvinia rotundifolia	Gainesville	FL	0.4–2.4	—	—	—	—	—	189
Arithmetic mean			3.53						
Range			0.1–18.0						
Woody									
Chamaedaphne peatland	Houghton Lake	MI	0.41	—	—	0.43	24	(0–20)	78
Murray River floodplain	Victoria	Australia	1.70	1.00	1.10	1.50	—	—	203[c]
Nyssa aquatica swamp	Pitt County	NC	—	—	—	0.28–0.96	—	—	204
Nyssa-Acer-Fraxinus swamp	Pitt County	NC	1.24	4.25	—	0.45	33	(0–25)	31
Taxodium ascendens swamp	Okefenokee	GA	0.32	4.28	—	1.94	—	—	75[d]
T. distichum dome	Gainesville	FL	0.56	2.67	—	0.21	16	(0–20)	209
T. distichum dome	Gainesville	FL	0.73	—	0.28	0.63	16	—	210
T. distichum strand	Waldo	FL	1.08	2.81	8.06	1.93	179	(0–50)	123[e]
T. distichum swamp	Cache River	IL	1.20	5.10	2.80	—	120	(0–24)	22
T. distichum swamps	Various	FL	0.08–1.50	0.18–3.52	—	—	—	—	119
Arithmetic Mean			0.89	3.14		0.96	64		
Range			0.08–1.70	0.18–4.28		0.21–1.94	16–179		

[a] Aboveground stocks determined by dividing whole-plant standing stocks by the ratio of total standing stock/aerial standing stock as of June 14 (4.1).
[b] End of season harvest.
[c] Values are means from seven artificially irrigated plantations containing *Eucalyptus camaldulensis, E. grandis, E. saligna, Casuarina cunningham, Pinus radiata, Populus deltoides,* and *Populus deltoides* × *P. nigra.*
[d] Litter includes 0.39 g m^{-2} in standing dead trees.
[e] Litter includes 0.5 g m^{-2} in large wood detritus.

* Values not included in computations.

etation. Even in the Okefenokee Swamp, where nitrogen standing stocks in the mature cypress forest were the highest of any wetland system studied (99.5 g m^{-2}), soil nitrogen standing stocks were 50 times those in vegetation.[75] In a Michigan peatland, the soil compartment contained >97% of all N and P in the wetland system.[78] Standing stocks are proportional to concentration per unit volume over the depth sampled.

A major reason that soils constitute such a large standing stock is the very long turnover times for soil nutrients, estimated by dividing the standing stock by annual inputs to the compartment. In contrast to P turnover in leaves and litter, which averages about 2 years, the turnover time in soils is about 100 years (Table 14). The shortest turnover time for soil P (8 years) occurred in a floodplain forest with rapid sedimentation due to flooding during the period of study.[22] Turnover time in bog soils may be much longer; N accumulation rates in a Minnesota bog indicated turnover times of over 5600 years.[66] Therefore, once nutrients enter the soil compartment, they are retained there for a very long time.

4. Nutrient Standing Stocks in Herbaceous Vegetation

Nutrient standing stocks in vegetation are computed by multiplying concentrations by biomass per unit area, usually measured for herbaceous vegetation at peak standing crop. Although nutrient concentrations for herbaceous vegetation and leaves generally fall within a narrow range (about 1 to 3% N and 0.1 to 0.3% P), biomass values are much more variable, even within a single species.[63] For example, aboveground standing crops of *T. latifolia* throughout the U.S. varied from 0.38 to 1.34 kg m^{-2}.[211] An even wider range of values (0.67 to 3.98 kg m^{-2}) was reported for *Phragmites australis* in Scottish lakes.[212]

As a result of this variability in biomass, aboveground nutrient standing stocks for wetland emergents are highly variable, ranging from 0.4 to 72 g N m^{-2} and 0.1 to 6.8 g P m^{-2} (Tables 12 and 13). The highest values generally occurred in marshes with high biomass,[165,194,195] but the high N standing stock reported by Mason and Bryant[167] for *P. communis* was due primarily to high N concentrations (3.94% dry weight: Table 9) in the plant tissues. Nutrient standing stocks for floating macrophytes are also variable, with highly productive species such as *Eichhornia crassipes* having the highest values (Tables 12 and 13).

In northern temperate latitudes, aboveground nutrient standing stocks in herbaceous vegetation increase early in the growing season, peak sometime during early to late summer, and decline during autumn senescence. Overwinter aboveground standing stocks are generally negligible due to annual die-back, but some aboveground tissue may persist even frozen in the ice and snow of northern wetlands.[213] Aboveground N standing stocks in *C. lacustris*, for example, were 3.9 g m^{-2} in winter, as compared to 18.3 g m^{-2} in August.[155] Aboveground standing stocks tend to peak earlier at lower latitudes; peak nitrogen standing stocks occurred in May in South Carolina,[169] in July in New Jersey,[214] and in August in New York State.[155,175] Although N, P, and biomass standing stocks

TABLE 14
Estimated Turnover Time for Phosphorus in Vegetation, Litter, and Soil of Woody Wetlands, in Years

Type of wetland	Location	State or country	Leaves and herbs	Wood	Roots and rhizomes	Litter	Soil	Soil depth (cm)	Ref.
Taxodium distichum dome	Gainesville	FL	4.0	267	—	1.4	64	(0–20)	209
Nyssa-Acer-Fraxinus swamp, 1977	Pitt County	NC	2.4	51	—	1.6	106	(0–25)	31
Nyssa-Acer-Fraxinus swamp, 1978	Pitt County	NC	3.2	47	—	1.1	87	(0–25)	31
Taxodium distichum swamp	Cache River	IL	1.0	73	93	—	8	(0–24)	22
T. distichum strand	Gainesville	FL	0.8	40	20	2.1	85	(0–20)	123
Chamaedaphne peatland	Houghton Lakes	MI	2.4	—	—	3.3	225	(0–20)	78[a]
Taxodium ascendens swamp	Okefenokee	GA	1.5	214	—	—	—	—	75
Arithmetic mean			2.2	115	57	1.9	96		
Range			0.8–4.0	40–267	20–93	1.1–3.3	8–225		

[a] Similar turnover times were reported for nitrogen.

are generally considered to peak concurrently, Chapin[215] showed that N peaked 2 weeks before biomass in tundra foliage, and Boyd[169] showed that N peaked a month before P in *Typha*.

Nutrient additions to wetlands can alter both the timing and magnitude of peak aboveground standing stocks. The application of high levels of effluent (10.2 cm/week) to a Florida marsh resulted in peak aboveground P standing stocks of 3.6 g m^{-2}, five times those in a low effluent treatment area.[120] Peak P standing stock occurred a month earlier in the high treatment area than in the low treatment area.

Although there are fewer studies of nutrient standing stocks in belowground structures of herbaceous wetland plants, these storage compartments are clearly important. In southeastern U.S. marshes,[120,150,197] belowground nutrient standing stocks were two to three times higher than aboveground stocks, while in northern U.S. marshes belowground to aboveground standing stocks ranged from 1:1 to 1:7 for N and 1:1 to 1:3 for P (Tables 12 and 13).

The ratio of P in litter relative to aboveground standing stocks in a Florida wetland (1:1.7) was unchanged by nutrient additions even though total standing stocks increased five times in each compartment.[120] Nutrient additions also increased N standing stocks in the litter, but decreased N standing stocks in aboveground biomass so that litter-to-aboveground ratios switched from 1:2 to 2:1. Litter-to-aboveground standing stocks were also 2:1 for N in a British *Calluna-Eriophorum* bog.[108] Litter nutrient standing stocks that exceed the amounts in live vegetation can occur where low decomposition rates result in the accumulation of litter from several years, where immobilization increases litter nutrient concentrations, or where sediment is deposited on litter during flooding. Litter standing stocks were lower than aboveground stocks of N (1:2) and P (1:3) in a Wisconsin *S. fluviatilis* marsh.[198]

5. Nutrient Standing Stocks in Woody Vegetation

The biomass of wetland forests is much higher than that of herbaceous wetlands.[216] Aboveground biomass values summarized by Conner and Day[217] for 18 southeastern U.S. swamp forests averaged 25.4 kg m^{-2}, and a number of authors have reported values for *Taxodium distichum* swamps exceeding 30 kg m^{-2}.[75,123,217–220] A summary of data from over 50 freshwater forested wetlands by Lugo et al.[221] showed that riverine wetlands have higher average aboveground biomass (24.2 kg m^{-2}) than forested wetlands in hydrologic basins (16.3 kg m^{-2}). Bog forests have less biomass than other wetland forests, but more than most herbaceous wetlands: reported values range from 4.4 to 10 kg m^{-2}.[59,205]

In mature wetland forests, woody plant parts constitute the vast majority of biomass.[221] Therefore, even though mean nutrient concentrations in wood are low relative to concentrations in leaf biomass (Table 10), total nutrient storage is greatest in woody plant parts (Tables 12 and 13), up to 20 times the amount in leaves.[75] In young forest plantations where leaves make up a larger proportion of aboveground biomass, however, nutrient standing stocks in wood were only about half the amount in leaves.[203]

There are few studies of belowground forest biomass and nutrient standing stocks due to the inaccessibility of root systems (Tables 12 and 13). Belowground woody standing stock values were generally estimated by assuming a belowground biomass amount proportional to aboveground biomass and multiplying by nutrient concentrations in roots. The exception is the Stewart et al.[203] study in Australia in which entire root systems of 5-year-old trees were excavated. While it may not be possible to extrapolate measurements from such young trees to mature forests, these data infer that nutrient standing stocks in roots may be comparable to those in aboveground woody structures.

Due to the longevity of trees, turnover times for P in wood are very long, on the order of decades of centuries (Table 14). Tree roots also seem to constitute a long-term storage compartment for P, although this would likely depend on the size of the roots. Turnover times for leaves and litter in forested wetlands are much shorter, usually 3 years or less (Table 14). Unlike herbaceous wetland plant litter, nutrient standing stocks in forested wetland litter tended to be less than standing stocks in green tissues and constituted a small proportion of total standing stocks in biomass (Table 12).

C. Nutrient Fluxes among Wetland Compartments

The storage of nutrients in a wetland compartment is not permanent. With the exception of deep sediments below the rooting zone where nutrients are essentially isolated from biotic cycling, nutrients move both into and out of storage compartments. The net benefit to water quality, therefore, is not a function of storage compartment size, but rather net annual retention (i.e., inputs minus outputs).

When considering the effect of wetlands on water quality, the fluxes of primary interest are those involving surface water (Figure 1). However, since all of the wetland elements are interconnected, fluxes that do not directly affect surface water may ultimately influence water quality. For example, a large proportion of annual nutrient fluxes into plants are returned to the wetland surface as litter, which releases nutrients into surface water as it decomposes. Therefore, it is important to understand the mechanisms and rates of transfer for each of these flux paths in order to assess the net effect of a wetland on water quality.

1. Fluxes between Water and Soil

Fluxes from water and soil are generally beneficial to water quality because of the long turnover times for nutrients in soil (Table 14). Water-to-soil fluxes include deposition of organic matter and sediments, and sorption of water-soluble nutrients. While sorption is a reversible mechanism, sediment and organic matter accretion usually are not.

The deposition of sediment can result in large fluxes of nutrients, particularly phosphorus, from surface waters to wetland soils. Nutrient fluxes via sediment deposition were high in wetlands with mineral soils, averaging 15 g N m^{-2} $year^{-1}$ and 1.5 g P m^{-2} $year^{-1}$ (Table 15). Much of this deposition occurred during flood events.[22,31] Nutrient deposition rates were higher adjacent to streams than in backwater areas,[33,135] and higher in cultivated watersheds than in uncultivated ones.[32]

Nutrient fluxes associated with organic soil accumulation were about an order of magnitude lower than those associated with mineral sediment deposition, averaging 1.6 g N m^{-2} $year^{-1}$ and 0.26 g P m^{-2} $year^{-1}$ (Table 15). This is due in part to the lower average mass accumulation rates for organic soils as compared to mineral soils (Tables 1 and 3). Also, wetlands with organic soils typically have much lower nutrient inputs than wetlands with mineral soils. Unlike mineral sediment fluxes from flood events, in which allochthonous materials are carried into the wetland and deposited directly on the soil surface, nutrients in organic soil are primarily derived from atmospheric inputs and nutrient cycling *in situ*.

There has been considerable debate about the ability of wetland soils to sorb nutrients, particularly phosphorus. Laboratory leaching experiments by a number of researchers have shown that wetland soils can remove substantial amounts of ammonium and phosphorus.[222,223] While the ability of organic soils to sorb phosphorus was initially forwarded as a justification for their use in wastewater treatment systems,[224,225] Richardson[13] demonstrated that organic soils were *less* suitable than mineral soils for phosphorus sorption. The phosphorus adsorption potential of wetland soils was best predicted by the amorphous (i.e., acid oxalate-extractable) aluminum and iron content of the soil, which is higher in mineral than organic soils.[13] The presence of these compounds under anaerobic conditions results in more soil phosphate being sorbed where solution phosphate is high, and more soil phosphate being solubilized where solution phosphate is low.[226,227] Phosphorus desorption rates are much higher in saltwater estuaries than they are in freshwater systems, where P is bound by sediment particles with little recycling to the water column.[228,229] Rates of ammonium removal are positively correlated with percent carbon,[230] which is highest in organic wetland soils.

2. Plant Fluxes

The flux of nutrients into, within, and out of wetland plants is very complex, involving a number of pathways (Figure 1). Plant uptake is the net annual flux of nutrients into plant roots (fluxes 8 and 13). Once taken up, nutrients may remain in the roots or be translocated upward into aboveground woody tissues (flux 16) and/or herbaceous tissues (flux 17). Leaching, the removal of soluble nutrients from mature and stand dead plants by precipitation, can return substantial amounts of nutrients to wetland surface waters (flux 21). As tissues senesce, nutrients may be retranslocated downward (fluxes 19 and 20), or leave the plant as litterfall (flux 18) or root sloughing (flux 22).

TABLE 15
Annual Accumulation of Nitrogen and Phosphorus in Wetland Soils (g m^{-2} year^{-1})

Wetland description	Location	State	N Deposition	P Deposition	Method	Ref.
Mineral soils						
Bald cypress-tupelo swamp	Cache River	IL	—	3.60	Sediment traps	22
Lac des Allemands	Barataria Basin	LA	7.1	1.10	^{137}Cs dating	28
Backmarsh area	Barataria Basin	LA	9.0	0.50	^{137}Cs dating	135
Streamside marsh	Barataria Basin	LA	16.0	1.00	^{137}Cs dating	135
Bottomland hardwoods, higher elevations	Creeping Swamp	NC	—	0.10	Flood event sedimentation	31
Bottomland hardwoods, area-weighted mean	Creeping Swamp	NC	—	0.17	Flood event sedimentation	31
Bottomland hardwoods, middle elevations	Creeping Swamp	NC	—	0.20	Flood event sedimentation	31
Bottomland hardwoods, low areas	Creeping Swamp	NC	—	0.28	Flood event sedimentation	31
Prairie potholes, cultivated watersheds	Eastern Counties	SD	1.7	0.57	Flux of inorganic matter from watershed	32
Prairie potholes, uncultivated watersheds	Eastern Counties	SD	1.4	0.30	Flux of inorganic matter from watershed	32
Riparian forest levee	Cecil	WI	52.4	8.20	^{137}Cs dating	33
Arithmetic mean			14.6	1.46		
Range			1.4–52.4	0.1–8.2		
Organic soils						
Cypress site	Okefenokee Swamp	GA	0.9	0.04	^{14}C dating	58
Marsh site	Okefenokee Swamp	GA	2.5	0.05	^{14}C dating	58
Shrub site	Okefenokee Swamp	GA	1.4	0.04	^{14}C dating	58
Black spruce bog	Marcell	MN	0.7–1.2	—	Ash inputs, ambrosia pollen	66
Sphagnum bog	—	Sweden	1.0	0.09	Moss growth	56
Riparian forest backwater area	Cecil	WI	2.7	1.10	^{137}Cs dating	33
Arithmetic mean			1.6	0.26		
Range			0.9–2.7	0.04–1.1		

With the exception of floating plants such as *Lemna minor* and *E. crassipes*, wetland plants obtain most (95 and 99%) of their nutrients from the soil in which they are rooted, rather than from overlying surface waters.[231] After the senescing macrophytes fall to the soil surface, much of the phosphorus in reincorporated into the sediments via litter decomposition, but some is leached into overlying surface waters. Therefore, vegetation uptake does not directly benefit water quality, and in some cases may even degrade it by transferring nutrients from soil to water. Rooted emergents indirectly benefit water quality, however, by transporting oxygen belowground.[232]

Given the large number of studies for nutrient standing stocks in wetland plants, it is surprising that few workers have attempted to quantify net annual retention of nutrients in plant biomass (Tables 16 and 17). One reason for the lack of such studies is the complexity of within-plant fluxes (Figure 1). Another reason may be that many wetland botanists think of nutrient uptake only within the context of a growing season, and only with respect to live plants. The evaluation of wetland effects on water quality, however, requires a perspective encompassing the entire biogeochemical cycle.

a. Herbaceous Plants

In herbaceous wetland plants, net annual retention is equal to annual uptake minus losses from leaching and litterfall (Table 16). While it is often assumed that the nutrient standing stocks represent annual uptake in herbaceous wetland vegetation, a large proportion of nutrients in aboveground biomass of many wetland perennials is translocated upward from belowground storage structures in the spring, and downward from the shoots in the fall. This internal recycling of nutrients helps plants conserve nutrients, but reduces their net uptake of nutrients.

Studies of within-plant nutrient cycling help distinguish net retention from annual uptake. Klopatek[198] found that 26% of the N and 38% of the P uptake by *S. fluviatilis* was retained overwinter, the rest being lost via leaching and litterfall (Table 16). Of the 5.32 g N m^{-2} and 2.0 g P m^{-2} retained annually, 2.03 g N m^{-2} and 0.44 g P m^{-2} had been retranslocated from aboveground to belowground structures. In a similar study, Prentki et al.[201] reported 30% overwinter retention of P by *Typha latifolia* (1.3 g m^{-2}), of which 0.75 g m^{-2} had been retranslocated from aboveground. Nutrient retention percentages in tundra wetlands were even higher, exceeding 50% of annual uptake.[68]

The detailed study by Prentki et al.[201] illustrated changes in P storage by *T. latifolia* over an entire growing season. Belowground stocks started at 2.5 g m^{-2} in March, but declined early in the growing season as P was translocated to aboveground structures. By mid-June, 40% of the aboveground standing stock consisted of P reallocated from belowground plant parts, and upward translocation had ceased. At this point, belowground P reserves began to be replenished.

Lindsley et al.[235] showed a similar pattern of spring translocation and fall storage for N and P in *Sparganium eurycarpum*, which also has an extensive

TABLE 16
Nitrogen and Phosphorus Cycling by Herbaceous Wetland Vegetation (g m^{-2} $year^{-1}$)

Wetland type	Location	State or country	Plant uptake	Fluxes out of plants: Leaching	Fluxes out of plants: Litterfall	Net annual retention[a]	Percent retention	Ref.
Nitrogen								
Scirpus fluviatilis	Goose Lake	IA	—	1.49	3.15	—	—	183[b]
S. fluviatilis	Theresa	WI	20.75	7.34	8.09	5.32	26	198
Tundra biome site	Barrow	AK	1.79	—	0.80	0.99	55	68
Typha glauca	Goose Lake	IA	—	1.13	6.09	—	—	183[b]
T. glauca	Eagle Lake	IA	—	0.10	3.80	—	—	183[b]
Arithmetic mean				2.52	4.39			
Range				0.1–7.34	0.8–8.09			
Phosphorus								
Tundra biome site	Barrow	AK	0.12	—	0.05	0.06	54	68
Typha swamp	Everglades	FL	—	—	0.47–0.73	—	—	161
Scirpus fluviatilis	Goose Lake	IA	—	0.37	0.63	—	—	183[b]
T. glauca	Goose Lake	IA	—	0.10	1.13	—	—	183[b]
T. glauca	Eagle Lake	IA	—	0.20	0.60	—	—	200[b]
Scirpus fluviatilis	Theresa	WI	5.33	2.20	1.13	2.00	38	198
Typha latifolia	Madison	WI	4.3	—	2.50	1.3	30	201[c]
Arithmetic mean				0.72	0.95			
Range				0.1–2.2	0.05–2.5			

[a] Calculated as plant uptake minus fluxes out of plants.
[b] Includes standing dead litter as of April of the following year.
[c] Losses from belowground sloughing were 0.6 g m^{-2} $year^{-1}$.

TABLE 17
Nitrogen and Phosphorus Cycling by Woody Wetland Vegetation (g m^{-2} $year^{-1}$)

Wetland type	Location	State or country	Plant uptake	Wood increment	Fluxes out of plants		Net annual retention[a]	Percent retention	Ref.
					Leaching	Litterfall			
Nitrogen									
Acer-Nyssa swamp	Great Dismal Swamp	VA	—	—	—	3.35	—	—	185
Chamaecyparis thyoides swamp	Great Dismal Swamp	VA	—	—	—	2.19	—	—	185
Chamaedaphne peatland	Houghton Lake	MI	3.00	—	—	2.30	0.7	23	78
Nyssa aquatica swamp	Pitt County	NC	—	—	0.45	7.28	—	—	81
N. sylvatica swamp	Okefenokee Swamp	GA	—	—	—	3.94	—	—	187
Quercus-Acer-Nyssa swamp	Great Dismal Swamp	VA	—	—	—	2.08	—	—	185
Shrub swamp	Okefenokee Swamp	GA	—	—	—	2.11	—	—	187
Sphagnum bog	Concord	MA	3.80	—	—	3.80	0	0	52[b]
Sphagnum bog	Marcell	MN	6.60	—	—	6.60	0	0	66[b]
Taxodium distichum swamp	Okefenokee Swamp	GA	—	—	—	3.85	—	—	187
T. distichum swamp	Great Dismal Swamp	VA	—	—	—	2.66	—	—	185
T. distichum swamp	Okefenokee Swamp	GA	—	—	—	3.82	—	—	75
Arithmetic mean						3.67			
Range						2.08–7.28			
Phosphorus									
Acer-Nyssa swamp	Great Dismal Swamp	VA	—	—	—	0.19	—	—	185
Chamaecyparis thyoides swamp	Great Dismal Swamp	VA	—	—	—	0.13	—	—	185
Chamaedaphne peatland	Houghton Lake	MI	0.17	—	—	0.10	0.07	41	78
Nyssa aquatica swamp	Tar River	NC	—	—	0.11	0.54	—	—	81
N. sylvatica swamp	Okefenokee Swamp	GA	—	—	—	0.21	—	—	187
Nyssa-Acer-Fraxinus swamp	Pitt County	NC	0.53	0.06,0.12	0,0.05	0.34,0.35	0.19,0.12	36,23	31[c]
Quercus-Acer-Nyssa swamp	Great Dismal Swamp	VA	—	—	—	0.12	—	—	185
Shrub swamp	Okefenokee Swamp	GA	—	—	—	0.08	—	—	187
Taxodium distichum dome	Gainesville	FL	0.15	0.01	—	0.15	0	0	209
T. distichum dome	Gainesville	FL	—	—	—	0.16	—	—	188
T. distichum strand	Waldo	FL	1.55	0.07[e]	—	0.69	0.86	56	123[d]
T. distichum swamp	Okefenokee Swamp	GA	—	—	—	0.20	—	—	187
T. distichum swamp	Great Dismal Swamp	VA	—	—	—	0.18	—	—	185

T. distichum swamp	Cache River	IL	0.87	0.07	0.03	0.77	0.07	8	22
T. distichum swamp	Okefenokee Swamp	GA	0.23	0.00	0.08	0.16	0.00	0	75
Arithmetic mean			0.58	0.05	0.06	0.27	0.16	23	
Range			0.15–1.55	0–0.12	0–0.11	0.08–0.77	0–0.19	0–56	

[a] Calculated as plant uptake minus fluxes out of plants.
[b] Annual litterfall was assumed to equal annual uptake.
[c] First value is for 1977, second value is for 1978.
[d] Values estimated by simulation model, based on field data.[233,234]
[e] Root increment was 0.40 g m^{-2} $year^{-1}$.

rhizome system. In *Scirpus validus*, however, the trend for belowground standing stocks of N was different from that for P; although upward translocation decreased belowground N standing stocks early in the growing season, belowground P standing stocks continuously increased between June and September because P was being concentrated in the rhizomes.[235] Belowground stocks of both N and P in *Scirpus* were two to three times higher than aboveground stocks throughout most of the growing season. Overwinter belowground nutrient stocks were low for *Sagittaria latifolia*, and negligible for *Zizania aquatica*, an annual.

Leaching can rapidly deplete aboveground nutrients at the end of the growing season. Leaching and translocation reduced P standing stocks in *Scirpus fluviatilis* and *T. latifolia* by 37 and 65% between August 15 and November 15.[183] Annual leaching losses from this and other herbaceous plant studies averaged 2.5 g N m^{-2} and 0.7 g P m^{-2} (Table 16).

Litterfall from herbaceous plants involves the fragmentation and toppling of dead plant matter. Unlike annual litterfall from woody deciduous plants, herbaceous litterfall can take more than a year, particularly in persistent emergent species. Davis and van der Valk[183] reported that 9 and 18% of peak nutrient standing stocks in *T. glauca* and *S. validus*, respectively, remained in standing dead litter 13 months after the end of the growing season. The litter of *S. validus*, however, had completely fallen underwater by 3 months after peak standing crop. Litterfall losses averaged 4.4 g N m^{-2} $year^{-1}$ and 1.0 g P m^{-2} $year^{-1}$, 20 to 45% of annual plant uptake (Table 16).

b. Woody Plants

In addition to the within-plant fluxes described for herbaceous wetland plants, nutrients taken up by trees and shrubs may be incorporated into woody tissues. While cumulative standing stocks of nutrients stored in wood can be high due to their slow turnover rate (Table 13), annual additions of nutrients to woody tissues (i.e., wood increment) are small, averaging only 0.05 g P m^{-2} $year^{-1}$ (Table 17). This is comparable to the amount lost annually from leaching.

Nutrient fluxes via litterfall from wetland forests, particularly southeastern swamps, have been studied by a number of researchers (Table 17). Forest litterfall fluxes for nitrogen (2.1 to 7.3 g m^{-2} $year^{-1}$) fall within the range of values reported for herbaceous litterfall (0.8 to 8.1 g m^{-2} $year^{-1}$: Table 16), but average phosphorus fluxes are lower for woody than herbaceous plant litterfall (0.3 and 1.0 g m^{-2} $year^{-1}$, respectively). Estimates of percent phosphorus retention by woody wetland vegetation were variable, ranging from 0 to 56% (Table 17). The highest retention estimate included storage in root biomass,[123] which was ignored by most researchers.

3. Litter Decomposition

Litter is a dynamic storage compartment, both in terms of its short turnover time (about 2 years: Table 14), and interaction with wetland surface waters (Figure 1). The litter decay constant, k, is derived from the exponential decay formula,

$$-k = \ln(X/X_o)/t \tag{2}$$

where X_o is the dry weight initially present and X is the dry weight remaining at the end of the period of measurement, t, in years.[236] The half-life for litter decay (i.e., the time at which half the initial litter has been decomposed) is calculated as:

$$t_{1/2} = 0.693/k \tag{3}$$

Rates of litter decomposition vary substantially among different wetland species. Litter decay constants summarized for wetland species by Johnston et al.[4] ranged from an exceptionally high value of 18.1 for rapidly decomposing *Sagittaria latifolia*[183] to a low of 0.06 for recalcitrant tundra vegetation.[237] Decay constants for herbaceous plants and leaves usually fall between 0.2 to 2.0, while those for slower decaying twigs and wood generally range from 0.1 to 0.3. Brinson et al.[125] reported a mean annual decomposition coefficient of 0.3 for northern peatlands, significantly lower than the 0.9 average for other wetlands. Tundra vegetation showed decreasing decomposition in the order: soft leaves > hard leaves and shrub shoots > mosses, lichens, and wood.[237] Among aquatic plants, floating-leaved water lilies (*Nuphar variegatum*) decayed fastest, submersed plants decayed at an intermediate rate, and emergent bulrushes decayed at the slowest rate.[238]

Environmental factors are important in determining decomposition rates. Moisture is particularly relevant in wetlands, where decomposing litter experiences conditions ranging from complete submergence to complete exposure.[125] Wetter conditions were associated with faster decomposition of *Nyssa aquatica* and *N. sylvatica* leaves, but slower decomposition of *Acer rubrum* leaves.[210,239] Nessel[210] reported faster decomposition of *Taxodium ascendens* leaves under wet conditions, but Duever et al.[240] found the opposite. Loss of *Peltandra virginica* litter in a freshwater tidal marsh was rapid, and increased with frequency of flooding.[241]

Differences in decomposition rates under different moisture regimes may be due to oxygen availability rather than moisture per se, with continuously anaerobic conditions being least favorable for decomposition.[125] Godshalk and Wetzel[238] experimentally demonstrated lower decomposition of aquatic plants under anaerobic conditions, while Reddy and Patrick[242] demonstrated that alternate aerobic and anaerobic conditions result in less loss of soil carbon than continuously aerated conditions.[242] Other factors affecting decomposition rates include plant physicochemical properties, initial N concentrations and C:N ratios, and temperature.[125,243]

Changes in nutrient concentrations during decomposition are not necessarily proportional to loss of biomass. Initial nutrient loss rates are often higher than mass losses due to leaching.[167,169,244–246] Nutrient immobilization by microbes associated with plant litter has the opposite effect, increasing nutrient concentrations over time.[183,244,246,247] Increases in P concentration can also be due to silt deposition on fallen litter.[183,241]

Studies of *P. virginica* litter showed different trends of N loss/gain during decomposition in different environments.[241] Submerged or creekbank-buried *Peltandra* showed an increase from an initial concentration of 2.9 to 4.0–5.5% N after 10 to 20 days, followed by a decline to 3.0–3.8% N after 50 days. The C:N ratio declined from an initial level of 15.5 to 7.6–10.6 after 29 days, followed by a rise to 12.3–15.2 after 50 days. In contrast, the N content of litter placed on the irregularly flooded high marsh rose steadily from 2.9 to 6.1% after 20 days, and 6.5% after 50 days. The C:N ratio dropped from 15.5 to 9.2 after 10 days, and reached 7.0 after 50 days. The authors attributed this different pattern to colonization of high marsh litter by autotrophic bacteria and nitrogen-fixing blue-green algae.

As plant litter decomposes, the nutrients it contains may be transported out of the system in soluble or particulate form (Figure 1: flux 25), or be incorporated into the soil (flux 23). The fate of nutrients released from plant litter determines to a large extent the effect of this mechanism on water quality; incorporation of nutrients into the soil could be beneficial to water quality, while export to downstream waters could be detrimental. While fluxes from litter can be assumed to remain on site in hydrologically closed wetlands such as peatlands[248] and cypress domes,[209] litter-derived nutrients may be exported downstream from flow-through wetlands.[31] Research is needed to quantify these pathways of nutrient movement following litter decomposition.

4. Fluxes to the Atmosphere

a. Denitrification

Denitrification is the process whereby nitrate (NO_3^-) is reduced by facultative anaerobic bacteria to nitrous oxides or dinitrogen gas, as shown by the overall reaction:

$$5(CH_2O) + 4NO_3^- + 4H^+ \rightarrow 5CO_2 + 2N_2 + 7H_2O \qquad (4)$$

This reaction is irreversible, and occurs only under anoxic conditions (Eh = +350 to +100 mV), where nitrate is used as an electron acceptor in place of oxygen. The actual sequence of biochemical changes from nitrate to elemental gaseous nitrogen is: $2NO_3^- \rightarrow 2NO_2^- \rightarrow 2NO \rightarrow N_2O \rightarrow N_2$.[249] Both N_2O and N_2 contribute to atmospheric nitrogen (Figure 1: flux 6).

Denitrification is commonly held to be a major pathway of nitrogen removal from wetlands. Unlike nutrient storage mechanisms, denitrification ultimately exports nitrogen out of the wetland system into the atmosphere and can apparently proceed indefinitely without harm to the wetland. A number of authors have reviewed denitrification and related microbial nitrogen transformation processes.[250–253]

In order to denitrification to proceed, there must be an available supply of nitrate (Equation 4). Wetlands that are hydrologically isolated receive nitrate primarily from precipitation and nitrification; those that are not, also receive nitrate inputs from surface waters.[254–256] Since denitrification requires anoxic conditions, the downward flux of nitrate from the oxidized soil surface into the anaerobic zone is a factor that limits denitrification rates.[257–259] Reddy and Patrick[252] reported diffusion coefficients for NO_3-N movement in soils ranging from 0.04 to 1.94 cm^2/day.

Nitrification, the oxidation of ammonium by *Nitrosomonas* ($NH_4^+ \rightarrow NO_2^-$) and *Nitrobacter* ($NO_2^- \rightarrow NO_3^-$), is an important source of nitrate for denitrification. Unlike nitrate, ammonium is stable under anaerobic conditions, but is susceptible to oxidation in the aerobic soil layer and overlying water column. The major supply of ammonium to the aerobic soil layer comes from mineralization of organic N and the upward diffusion of ammonium from the underlying anaerobic layer.[252] This upward diffusion rate is a major factor controlling the rate of nitrification in wetland sediments[258] because nitrate produced by nitrification is denitrified very quickly.[260] Denitrification rates are maximized by the coupling of nitrification and denitrification via diffusion across the aerobic-anaerobic soil boundary.[261–264] DeLaune and Smith[265] reported that nitrification accounted for approximately 70% of the denitrification rate in soil-water columns. High rates of denitrification occur where the close proximity of aerobic and anaerobic zones (e.g., anoxic microsites in fecal pellets or plant detrital particles) minimizes the path length for diffusion,[266] or where alternating aerobic and anaerobic conditions occur.[267]

Different measurement methods for denitrification provide variable results in part because they measure or block other portions of the nitrogen cycle. Laboratory incubations measuring NO_3^- loss from water overlying a submerged soil sample may overestimate denitrification rates because they measure assimilative (i.e., microbial uptake) as well as dissimilative (i.e., denitrification) N losses. While Bartlett et al.[268] reported that assimilative N losses constituted only 5 to 10% of nitrate reduction in freshwater wetlands, Dierberg and Brezonik[222] reported a fivefold difference between N loss rates determined by leaching through soil columns vs. acetylene reduction. Another commonly used method involves the short-term measurement of N_2O production by submerged soils in the presence of acetylene (C_2H_2), which blocks the reduction of N_2O to N_2.[269] However, the acetylene block method also inhibits nitrification and may therefore underestimate denitrification rates by cutting off the natural supply of nitrate. The use of stable isotope dilution (^{15}N) can overcome this problem by providing simultaneous estimates for nitrification and denitrification.[263,265] The advantages and disadvantages of different denitrification measurement techniques are summarized by Tiedje.[270]

In addition to nitrate, the denitrification reaction also requires the presence of readily available C (Equation 4). Reddy et al.[271] found that denitrification rates were influenced by the rate at which available C was mineralized and made available to denitrifiers. Significant correlations have also been found relating nitrate loss to water-soluble C[272] and extractable C,[273] and denitrification rates have been shown to increase with the addition of glucose[274] and sucrose.[262] Other environmental factors known to influence denitrification rates include redox potential,[275,276] soil moisture,[277] temperature,[278,279] pH,[280] presence of denitrifiers,[281,282] soil type,[283] and the presence of overlying floodwater.[257,284]

Tremendous variation exists among denitrification rates based on laboratory incubations: loss rates per unit soil mass range over four orders of magnitude, while those expressed per unit area range over three orders of magnitude. The highest denitrification potentials reported were for Finnish conifer swamps with very low bulk density (0.06 to 0.08 g cm^{-3}) organic soils.[285] Results from laboratory incubations are difficult to extrapolate to annual rates due to high spatial and temporal variation, and few workers have attempted it (Table 18). Annual denitrification potentials for soils incubated with added nitrogen averaged 7.6 g m^{-2} $year^{-1}$, while denitrification rates without amendments averaged only 0.07 g m^{-2} $year^{-1}$.

In situ measurements of N_2O flux (Table 19) provide a more realistic estimate of actual losses of nitrogen from wetlands via denitrification, but are also subject to measurement error.[270] Several of the *in situ* studies measured fluxes of ^{15}N and N_2O from the soil surface using chambers placed over wetland soils, while others used the acetylene block technique. As with laboratory incubations, much higher denitrification rates were obtained for soils with added nitrogen. Rates for sites with added N ranged from 16 to 134 g m^{-2} $year^{-1}$, while rates for unamended soils were much lower, averaging only 0.2 g m^{-2} $year^{-1}$ (Table 19). A French study[296] showed that *in situ* rates (25 mg m^{-2} day^{-1}) were one seventh the potential rates determined by laboratory incubation (175 mg m^{-2} day^{-1}).

b. Ammonia Volatilization

Ammonia volatilization (Figure 1: flux 26), the conversion of ammonium ions to ammonia gas, is not considered to be an important mechanism of N loss from flooded soils and sediments except where high ammonium concentrations exist in conjunction with high pH.[252] Reddy and Graetz[225] reported rapid ammonia volatilization losses from wastewater aerated with CO_2-free air, while little volatilization occurred in the water aerated with CO_2-containing air. During periods of high pH and ammonium concentrations, Murphy and Brownlee[302] observed high disappearance rates of ammonia from a hypertrophic prairie lake in southwestern Manitoba, which they attributed to ammonia volatilization.

c. Phosphine

Although the reduction of phosphate to phosphine gas (PH_3) in wetlands was speculated upon by early workers, Burford and Bremner[272] could detect no such

TABLE 18
Denitrification Rates Determined by Laboratory Incubation of Wetland Soils

Wetland or soil type	Location	State or country	Daily N loss per soil mass (μg gdw^{-1} day^{-1})	Daily N loss per area (mg m^{-2} day^{-1})	Annual N loss per area (g m^{-2} year^{-1})	Method	Time incubated (days)	Amendments	Ref.
Incubations with added amendments									
Cypress dome	Gainesville	FL	—	—	2.01	Acetylene block	?	Sewage	286
Cypress dome	Gainesville	FL	—	—	5.5	Acetylene block	?	NO_3	222
Cypress dome	Gainesville	FL	—	—	28.2	NO_3 loss from water	?	NO_3	222
Soil without plants	—	FL	—	120	—	NO_3 loss from water	56	Sewage	121
14 soils	Various	FL	—	60–290	—	NO_3 loss from water	12	NO_3	121
Soil with plants	—	FL	—	200	—	NO_3 loss from water	56	Sewage	121
Titi swamp	Apalachicola N.F.	FL	—	3.0–8.6	—	NO_3 loss from water	1–7	NO_3	287
Savannah wetland	Apalachicola N.F.	FL	—	3.4–41.5	—	NO_3 loss from water	1–7	NO_3	287
Sediment (no plants)	Lake Okeechobee	FL	—	8–14	—	^{15}N	26	NH_4	288
Pontederia cordata	Lake Okeechobee	FL	—	14–122	—	^{15}N	26	NH_4	288
Juncus effusus	Lake Okeechobee	FL	—	67–102	—	^{15}N	27	NH_4	288
Freshwater swamp	Bayou Sorrel	LA	—	350	—	NO_3 loss from water	12	NO_3	256
Freshwater marsh soils	—	LA	—	75	—	NO_3 loss from water	12	NO_3	289
Aerobic/anaerobic	Crowley	LA	0.94–1.76	—	—	^{15}N	128	NH_4	242
Anaerobic incubation	Crowley	LA	0.5	—	—	^{15}N	128	NH_4	242

TABLE 18 (continued)
Denitrification Rates Determined by Laboratory Incubation of Wetland Soils

Wetland or soil type	Location	State or country	Daily N loss per soil mass (μg gdw^{-1} day^{-1})	Daily N loss per area (mg m^{-2} day^{-1})	Annual N loss per area (g m^{-2} year^{-1})	Method	Time incubated (days)	Amendments	Ref.
Aerobic incubation	Crowley	LA	0.04	—	—	^{15}N	128	NH_4	242
Lac des Allemands	Barataria Basin	LA	0.01	2.5	0.03	Acetylene block	27	NH_4	290
Lac des Allemands	Barataria Basin	LA	—	0.3–124	5.5	Acetylene block	112	NH_4	290
Lac des Allemands	Barataria Basin	LA	1.5	—	—	Acetylene block	2	NO_3	290
Lac des Allemands	Barataria Basin	LA	—	—	1.4	^{15}N	168	NH_4	290
Carlisle muck	—	MI	15	—	—	^{15}N	2	NO_3	273
Carlisle muck	—	MI	25	—	—	^{15}N	2	NO_3, glucose	273
15 soils, flooded	Various	U.S.	26–118	—	—	NO_3 loss from water	1	NO_3	291
15 soils	Various	U.S.	34–161	—	—	NO_3 loss from water	1	NO_3	291
Wetland soil, 0–6 cm	Thredbo	Australia	97–150	—	—	Acetylene block	1	Sewage	292
W. Humber River	Toronto, ON	Canada	—	170	—	Acetylene block	2	NO_3	293
Stream sediments	Toronto, ON	Canada	0.1–1.2	0.2–8	—	Acetylene block	0.1	NO_3	294
Watercress bed	Toronto, ON	Canada	1.1–3.2	17–30	—	Acetylene block	0.1	NO_3	294
Phragmites swamp	Lake Arneskov	Denmark	—	50	—	NO_3 loss from water	1	NO_3, N-serve	295
Paludified spruce marsh	—	Finland	0.4–12	—	—	Acetylene block	6–21	NO_3	285
Tall-sedge fen	—	Finland	31–40	—	—	Acetylene block	6–21	NO_3	285

Alnus glutinosa swamps	—	Finland	3–211	—	—	Acetylene block	6–21	NO_3	285
Conifer swamps	—	Finland	295–533	—	—	Acetylene block	6–21	NO_3	285
Bogs	—	Finland	11–32	—	—	Acetylene block	6–21	NO_3	285
Recharge fen	Vechtplassen	Netherlands	—	—	20.0	Acetylene block	1	NO_3	107
Discharge fen	Vechtplassen	Netherlands	—	—	5.9	Acetylene block	1	NO_3	107
Blanket Bog	Pennine	U.K.	—	—	0.1	NO_3 loss from water	30	NO_3	108
Floodplain forest	Toulouse	France	—	25.0	—	?	?	NO_3	296
Arithmetic mean					7.6				
Range			0.01–533	0.3–350	0.03–28.2				
Incubations with no amendments									
Wetland soil, 0–6 cm	Thredbo	Australia	16	—	—	Acetylene block	1	None	292
Hemlock swamp interior	Toronto, ON	Canada	—	0–0.6	—	Acetylene block	0.1	None	297
Hemlock swamp margin	Toronto, ON	Canada	—	42–44	—	Acetylene block	0.1	None	297
Phragmites swamp	Lake Arneskov	Denmark	—	0–55	—	NO_3 loss from water	?	None	298
Cypress dome	Gainesville	FL	—	—	0.15	Acetylene block	?	None	286
Thoreau's Bog	Concord	MA	—	—	0.1	Acetylene block	4	None	52
Recharge fen	Vechtplassen	Netherlands	0.1	—	0.03	Acetylene block	1	None	107
Discharge fen	Vechtplassen	Netherlands	Negligible	—	Negligible	Acetylene block	1	None	107
Arithmetic mean					0.07				
Range			0.1–16	0–55	0.03–0.15				

TABLE 19
Denitrification Rates Determined in the Field

Wetland or soil type	Location	State or country	Annual N loss (g m^{-2} $year^{-1}$)	Method	Amendments	Ref.
Sites with amendments added		LA	134	^{15}N	NO_3, NH_4	299
Lac des Allemands	Barataria Basin					
Alluvial cypress swamp, Tar River	Pitt County	NC	29	^{15}N	NO_3, NH_4	125
Alluvial cypress swamp with sewage	Pitt County	NC	16	Mass balance	Sewage	204
Arithmetic mean			60			
Range			16–134			
Sites with no amendments		AK	0.002	^{15}N	None	67
Coastal plain tundra	Barrow					
Lac des Allemands	Barataria Basin	LA	0.34	Acetylene block	None	290
Alder/willow riparian zone	Lake Tahoe	NV	0.18	Acetylene block	None	300
Wet meadow	Madison	WI	0.11–0.14	Acetylene block	None	301
Drained marsh	Madison	WI	0.23–0.74	Acetylene block	None	301
Undrained marsh	Madison	WI	0.002–0.006	Acetylene block	None	301
Arithmetic mean			0.19			
Range			0.002–0.34			

gas production. Even if phosphine were produced, they showed that it would be sorbed by the soil and would not escape to the atmosphere. Therefore, gas fluxes do not appear to affect P dynamics.

D. Input-Output Studies

Input-output studies are those in which wetland outputs are subtracted from inputs to determine the net effect of wetlands on water quality. Nutrient sources such as precipitation, N fixation, runoff, groundwater, and surface water flow are measured as inputs, while nutrient losses via denitrification and water leaving the wetland are measured as outputs. Input-output investigations may be part of a more comprehensive mass balance study, in which all nutrient storage and fluxes are quantified, or they may be conducted without trying to determine within-wetland processes (i.e., black box studies).

Retention rates in input-output studies are typically calculated by subtracting outputs from inputs. This yields positive values when materials are stored or converted to gaseous forms in the wetland, and negative values when materials released from wetland soils and plants cause outputs to exceed inputs. Input minus output calculations for individual element forms (e.g., NO_3, NH_4) can indicate transformations occurring within a wetland, but must be summed to determine net element retention. For example, if all of the NH_4 entering a wetland were converted to dissolved organic N by the time it reached the outflow, there would be an apparent 100% retention of NH_4 even though net N retention was 0%.

1. Wetlands without Direct Anthropogenic Inputs

Bogs and mires are the most studied type of wetland with regard to N cycling (Table 20). These systems are relatively simple hydrologically, receiving nutrients inputs primarily from precipitation. Small bogs may also receive nutrients from surface water runoff,[66,80] but most bogs do not receive streamwater inputs. As a result, N inputs to bogs are low. Outputs may be to groundwater or to a surface water outlet.

Bogs are very retentive of the N they receive, conserving 50 to 100% of total N inputs (Table 20). Nitrogen fixation was the largest source of N to most of the bogs, even though total amounts fixed were generally low (Table 5). Net retention per unit area was relatively low, averaging only 0.9 g m^{-2} $year^{-1}$, and turnover times were long. Average N retention times in bog vegetation ranged from 2 to 9.8 years, longer than retention times for deciduous forests and shorter than those for coniferous forests.[66] Turnover times for microorganism biomass (0.28 year) and soluble and exchangeable inorganic N (7.5 years) were over an order of magnitude longer than those in deciduous forest ecosystems.[199] Denitrification was not a major source of loss from any of the bogs studied in terms of loss rates or percentages.

TABLE 20
Net Retention of Nitrogen by Wetlands with No Direct Anthropogenic Inputs, Based on Input Minus Output

Wetland type	Water source	Outlet type	Location	State or country	Retention ($g\ m^{-2}\ year^{-1}$) (% of inputs) NO_3-N[a]		NH_4-N		Organic N[b]		Net retention of total N inputs[a]		Net denitrification of total N inputs		Ref.
Bogs															
Coastal plain tundra	Precipitation	None	Barrow	AK	−0.001	−28%	0.016	78%	0.063	91%	0.078	84%	0.002	9%	67
Stordalen mire	Precipitation	None	Stordalen	Sweden	0.03	100%	0.07	100%	0.31	100%	0.42	100%	0	0%	199
Thoreau's Bog	Precipitation	Stream	Concord	MA	0.50	100%	0.05	20%	0.90	90%	1.45	83%	—	—	52
Moor House blanket bog	Precipitation	Stream	Pennines	U.K.	0.00	0%	0.60	100%	1.50	45%	2.10	53%	0.10	3%	108[c]
Marcell bog	Runoff	Stream	Marcell	MN	0.18	86%	0.15	69%	0.30	36%	0.63	50%	—	—	80
Marcell bog	Runoff	Stream	Marcell	MN	0.24	57%	0.40	90%	0.01	2%	0.68	47%	0.18	12%	66[d]
Arithmetic mean							0.22	76%	0.51	61%	0.89	69%	0.07	6%	
Range							0.02–0.15	20–100%	0.01–1.5	2–100%	0.08–2.10	47–100%	0–0.1	0–12%	
Other wetlands															
Okefenokee Swamp	Streams	River	—	GA	0.44	98%	0.34	96%	−0.089	−9%	0.68	39%	—	—	303

Cypress Swamp	Streams	Estuary	Barataria Basin	LA	—	—	—	—	—	—	1.33	50%	—	—	304
Little River watershed	Runoff	Riparian	Tifton	GA	—	—	—	—	—	—	0.73	14%	3.15	61%	305
Rhode River watershed	Runoff	Riparian	Annapolis	MD	—	—	—	—	—	—	7.38	89%	—	—	180

[a] Aqueous outputs and denitrification outputs subtracted from inputs.
[b] Includes inputs from N fixation.
[c] Used maximum rate of N fixation (3.2 g m^{-2} $year^{-1}$).
[d] Authors assumed maximum possible denitrification (NO_3 loading in throughfall).

Retention percentages for different nitrogen forms were highly variable due to the complexity of the N cycle in wetlands (Table 20). Nitrate retention percentages varied from −28 to 100%, the negative value indicating that NO_3^- outputs exceeded inputs due to the nitrification of ammonium within the wetland.[67] Net nitrate retention was zero in the Moor House blanket bog, where NO_3^- inputs in precipitation equaled outputs via denitrification. Ammonium retention ranged from 20 to 100% of inputs, while organic N retention ranged from 2 to 100%. There were large differences in retention rates of different N forms, even when workers studied the same bog, shared the same precipitation and surface runoff data, and derived similar total N retention rates and percentages.[66,80]

Nitrogen retention by two southeastern U.S. swamp systems was comparable to that of the bog systems on a per unit area basis, but lower in terms of percent of inputs (Table 20). The Okefenokee Swamp retained 96 to 98% of inorganic N inputs, but was a net exporter of organic N, resulting in total N retention of 0.68 g m^{-2} $year^{-1}$, 39% of total N inputs.[303] A Louisiana cypress swamp retained 1.33 g N m^{-2} $year^{-1}$, 50% of its inputs.[304]

Riparian forests in agricultural watersheds retained or denitrified more of their N inputs than any other wetland system (Table 20). Denitrification losses from a Georgia riparian forest were 3.15 g m^{-2} $year^{-1}$ (61% of inputs), and net retention was 0.73 g m^{-2} $year^{-1}$.[305] Fluxes to storage (annual nutrient accrual in vegetation) plus net retention exceeded total inputs measured, indicating an additional source of nitrogen internal to the system (e.g., mineralization of N stored in the soil). Nitrogen inputs minus outputs were also high for a Maryland riparian forest (7.35 g m^{-2} $year^{-1}$, 89% of inputs).[180] Although listed as N retention in Table 20, the authors speculated that some of this difference may have been due to denitrification, which was not measured.

The effectiveness of riparian forests in denitrifying or retaining N may be due to a combination of factors. First, their average N inputs were five times higher than inputs to bogs (6.8 and 1.4 g m^{-2} $year^{-1}$, respectively). Second, their diffuse surface runoff and groundwater inputs maximized contact between water and soil, where key nitrogen transformations take place. These findings infer that the hydrology of wetlands may be an important determinant of their effectiveness for N retention.

Phosphorus retention rates for wetlands ranged from a low of 0.07 g m^{-2} $year^{-1}$ for the Marcell bog[80] to a high of 3.48 g m^{-2} $year^{-1}$ for a floodplain wetland along the Cache River in Illinois[22] (Table 21). The Marcell bog retention rate was low because it receives relatively little P in surface runoff from its forested watershed, even though it retains 61% of its inputs. Retention by the Cache River floodplain wetland was high because it receives 3.6 g P m^{-2} $year^{-1}$ via sediment deposition during spring flood events (Table 15). This retention represents only 4% of the P inputs to the wetland, most of which pass by unaltered in river flow. Other studies reported P retention rates ranging from 0.17 to 0.73 g m^{-2} $year^{-1}$, with percent retention ranging from 9 to 80% (Table 21).

The 2-year study of Creeping Swamp by Kuenzler et al.[31] provides an indication of interannual variability in P retention and underscores the importance

TABLE 21
Net Retention of Phosphorus by Wetlands with No direct Anthropogenic Inputs, Based on Input-Output

					Net Retention ($g\ m^{-2}\ year^{-1}$) (% of total inputs)						
Wetland type	Water source	Outlet type	Location	State	PO_4-P		DOP-P		Total P		Ref.
Fresh marsh, control	NA	NA	Clermont	FL	—	—	—	—	0.20	53%	120[a]
Mendota Marsh	Lake	Lake	Madison	WI	—	—	—	—	0.56	10%	201
Little River watershed	Runoff	Riparian	Tifton	GA	—	—	—	—	0.17	30%	305
Rhode River watershed	Runoff	Riparian	Annapolis	MD	—	—	—	—	0.29	80%	180
Marcell bog	Runoff	Stream	Marcell	MN	0.02	60%	0.05	61%	0.07	61%	80
Cornish Creek Gum Swamp	Stream	Stream	Newton County	GA	—	—	—	—	0.45	9%	306
Cypress Swamp	Streams	Estuary	Barataria Basin	LA	—	—	—	—	0.17	46%	304
Okefenokee Swamp	Streams	River	—	GA	0.04	93%	0.388	73%	0.43	75%	303
Creeping Swamp, 1978	Streams	Stream	Pitt County	NC	0.30	79%	—	—	0.73	57%	31
Creeping Swamp, 1977	Streams	Stream	Pitt County	NC	0.28	42%	—	—	0.32	30%	31
Alluvial cypress swamp	River	River	Cache River	IL	—	—	—	—	3.48	4%	22
Arithmetic Mean[b]									0.34	45%	
Range									0.07–3.48	4–80%	

[a] Mesocosm study.
[b] Data from Mitsch et al. excluded from mean.

of flood events in wetland P dynamics. Phosphorus retention was twice as high in 1978 as in 1977 (Table 21) due in large part to a flood event that increased sedimentation and P uptake by algae. The wetland retained 61% of the particulate P inputs in 1978, while particulate P outputs were approximately equal to inputs in 1977.

Percent P retention was approximately equal to or greater than percent N retention in the majority of the studies which constructed budgets for both.[80,303,304] Percent P retention was lower than percent N retention, however, in the riparian wetlands studied.[180,305]

2. Wetlands with Direct Anthropogenic Inputs

Studies of wetlands that have been used as waste discharge sites provide insight into nutrient retention capacities under extremely high nutrient inputs (Table 22). All of the wetlands studied were net sinks for N, in some cases retaining or denitrifying 100 times as much nitrogen as the amount retained by natural wetlands (Table 20). The percentages of nitrogen inputs retained ranged from 21 to 95%, with no apparent relationship between loading rate and percent retention. The long-term disposal of sewage into the Reedy Creek wetland from 1979 to 1985[307] and the Bellaire wetland from 1976 to 1981[11] indicated no decrease in N retention capacity over time, despite loading rates as high as 95 g m^{-2} $year^{-1}$ to the Reedy Creek wetland.

However, the situation was quite different with regard to P. The Reedy Creek wetland exported more P than it received during 6 out of 7 years of operation, and in 1983 exported 171% of its inputs.[307] The Bellaire wetland initially retained P, but began to export P after 5 years of operation, and continued to be a net source of P even after wastewater inputs were discontinued in 1982.[11]

Short-term studies of P retention all had positive values, indicating that P inputs exceeded outputs, but percent retention varied from 7 to 98% (Table 22). The lowest percent retention occurred where wastes were discharged into a stream flowing through a wetland, rather than the wetland itself,[34] while the highest occurred in a wetland mesocosm[120] and a cypress dome lacking a surface water outlet.[72] Given the rapid shift from a P sink to a P source experienced in the Bellaire wetland, the sustainability of high P retention rates is questionable.

IV. CONCLUSIONS

Wetlands are retentive ecosystems, trapping sediment and nutrients to the benefit of downstream waters. Their ability to do so depends to a large extent on their hydrology, which controls the source, amount, and spatial and temporal distribution of sediment and nutrient inputs they receive. Unlike terrestrial ecosystems, which receive inputs primarily from the atmosphere, wetlands can receive inputs from the atmosphere, runoff, surface waters, and groundwater. While

TABLE 22
Net Retention and/or Denitrification of Nutrients by Wetlands Receiving Anthropogenic Inputs, Based on Surface Water Inputs Minus Surface Water Outputs

Wetland name	Wetland type	Enriched with	Location	State	Total N		Total P		Ref.
Reedy Cr. Wetland, 1979	Swamp	Sewage	Orlando	FL	53.20	71%	−19.36	−103%	307
Reedy Cr. Wetland, 1980	Swamp	Sewage	Orlando	FL	75.50	84%	−19.20	−80%	307
Reedy Cr. Wetland, 1981	Swamp	Sewage	Orlando	FL	74.92	95%	5.72	23%	307
Reedy Cr. Wetland, 1982	Swamp	Sewage	Orlando	FL	71.01	87%	−11.63	−52%	307
Reedy Cr. Wetland, 1983	Swamp	Sewage	Orlando	FL	72.62	77%	−17.07	−171%	307
Reedy Cr. Wetland, 1984	Swamp	Sewage	Orlando	FL	57.53	76%	−2.71	−30%	307
Reedy Cr. Wetland, 1985	Swamp	Sewage	Orlando	FL	61.74	77%	−2.35	−28%	307
Thuja peatland, 1976	Bog	Sewage	Bellaire	MI	1.84	75%	1.07	91%	11
Thuja peatland, 1977	Bog	Sewage	Bellaire	MI	6.75	80%	3.01	88%	11
Thuja peatland, 1978	Bog	Sewage	Bellaire	MI	9.63	80%	1.58	72%	11
Thuja peatland, 1979	Bog	Sewage	Bellaire	MI	6.21	77%	1.47	64%	11
Thuja peatland, 1980	Bog	Sewage	Bellaire	MI	9.07	75%	1.46	65%	11
Thuja peatland, 1981	Bog	Sewage	Bellaire	MI	4.46	81%	−0.33	−27%	11
Thuja peatland, 1982	Bog	—	Bellaire	MI	0.76	61%	−0.04	−2%	11
Thuja peatland, 1983	Bog	—	Bellaire	MI	—	—	−0.03	−1%	11
Fresh marsh, enriched	Marsh	Sewage	Clermont	FL	—	—	37.09	98%	120
Water hyacinth marsh	Marsh	Sewage	Gainesville	FL	—	—	7.70	16%	308
Boggy Gut Wetland	Marsh	Sewage	Hilton Head Is.	SC	44.97	83%	12.12	62%	309
Cattail marsh	Marsh	Sewage	Brillion	WI	—	—	4.80	68%	206
Nevin Wetland	Marsh	Hatchery waste	Madison	WI	15.05	21%	0.11	7%	34
Mixed hardwood swamp	Swamp	Sewage	Wildwood	FL	—	—	0.79	87%	118
Cypress Dome	Swamp	Sewage	Gainesville	FL	11.10	74%	10.44	92%	72
Cypress-Tupelo Swamp	Swamp	Agricultural drainage	Barataria Basin	LA	3.87	26%	1.69	41%	310
Tupelo Swamp	Swamp	Nutrients	Tar River	NC	—	—	25.10	57%	204[a]
Arithmetic mean					10.34	64%	—	—	
Range					0.76–75.5	21–95%	−19.4–37.1	−171%–98%	

[a] Retention over a 10-month period.

these multiple sources contribute to the retention ability of a wetland, they make it difficult to generalize about wetland functions affecting water quality.

Vegetation has been the focus of much nutrient cycling research in wetlands. This was a logical extention of research in terrestrial ecosystems, where nutrient cycling was controlled to a large extent by vegetation. In wetlands, however, physical and microbial processes are generally more important than vegetative uptake in controlling sediment and nutrient retention. Unfortunately, existing classification systems for wetlands best describe vegetation, rather than the hydrologic and soil properties that have a greater influence on the distribution and fate of materials related to water quality.

As in terrestrial systems, much more is known about concentrations than standing stocks, and much more is known about standing stocks than fluxes between storage compartments. Fluxes are difficult to quantify, especially when they involve microbially mediated processes, belowground phenomenon, or periodic events such as floods that can greatly influence sediment and nutrient retention but occur infrequently. It is the fluxes, however, rather than the storage compartments, that control the net effect of a wetland on water quality.

In an effort to preserve dwindling wetland resources, scientists have frequently oversold the ability of wetlands to retain sediment and nutrients, often to the ecological detriment of wetlands that are used as disposal sites for anthropogenic wastes. While this review has demonstrated that wetlands can and do benefit surface water quality, it has not discussed the impacts of sediment and nutrient retention to the wetlands themselves. While some processes (e.g., denitrification) are probably indefinitely sustainable without detriment to the wetland, others (e.g., excessive P loading) clearly are not. Hydrologic modifications associated with these loadings may be as detrimental to the wetland as nutrients are. Long-term manipulative studies are needed to determine thresholds of wetland function and response to cumulative sediment and nutrient loadings, and policy studies are needed to determine the trade-offs between improved water quality and wetland degradation.

ACKNOWLEDGMENTS

This research was partially supported by U.S. Environmental Protection Agency Cooperative Agreement CR-815482-010. Anda Bellamy is thanked for typing the manuscript.

REFERENCES

1. **Chan, E., Bursztynsky, T. A., Hantzsche, N., and Litwin, Y. J.,** *The Use of Wetlands for Water Pollution Control,* Municipal Environmental Research Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Cincinnati, OH, 1982.
2. **Stockdale, E. C.,** *Freshwater Wetlands, Urban Stormwater, and Nonpoint Pollution Control: A Literature Review and Annotated Bibliography,* Washington State Department of Ecology, Olympia, WA, 1990.
3. **Nixon, S. W. and Lee, V.,** *Wetlands and Water Quality,* Wetlands Research Program, Tech. Rep. Y-86-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 1986.
4. **Johnston, C. A., Johnson, T., Kuehl, M., Taylor, D., and Westman, J.,** *The Effects of Freshwater Wetlands on Water Quality: A Compilation of Literature Values,* Natural Resources Research Institute Report NRRI/TR-90/15, University of Minnesota, Duluth, 1990.
5. **Cowardin, L. M., Carter, V., Golet, F. C., and LaRoe, E. T.,** *Classification of Wetlands and Deepwater Habitats of the United States,* U.S. Fish and Wildlife Service, Washington, D.C., FWS/OBS-79/31, 1979.
6. Soil Survey Staff, *Soil Taxonomy,* USDA Soil Conservation Service, Argriculture Handbook No. 436, U.S. Government Printing Office, Washington, D.C., 1975.
7. **Mitsch, W. J. and Gosselink, J. G.,** *Wetlands,* Reinhold, New York, 1986.
8. **Gosselink, J. G. and Turner, R. E.,** The role of hydrology in freshwater wetland ecosystems, in *Freshwater Wetlands,* Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 63.
9. **Carter, V.,** An overview of the hydrologic concerns related to wetlands in the United States, *Can. J. Bot.,* 64, 364, 1986.
10. **Richardson, C. J.,** Freshwater wetlands: transformers, filters, or sinks?, in *Freshwater Wetlands and Wildlife,* Sharitz, R. R. and Gibbons, J. W., Eds., U.S. Department of Energy, Oak Ridge, TN, 1989, 25.
11. **Kadlec, R. H.,** The Bellaire wetland: wastewater alteration and recovery, *Wetlands,* 3, 44, 1983.
12. **Nichols, D. S.,** Capacity of natural wetlands to remove nutrients from wastewater, *J. Water Pollut. Control Fed.,* 55, 495, 1983.
13. **Richardson, C. J.,** Mechanisms controlling phosphorus retention capacity in freshwater wetlands, *Science,* 228, 1424, 1985.
14. **Stall, J. B.,** Effects of sediment on water quality, *J. Environ. Qual.,* 1, 353, 1972.
15. **Carper, G. L. and Bachmann, R. W.,** Wind resuspension of sediments in a prairie lake, *Can. J. Fish. Aquat. Sci.,* 41, 1763, 1984.
16. **Boto, K. G. and Patrick, W. H., Jr.,** Role of wetlands in the removal of suspended sediments, in *Wetland Functions and Values: The State of Our Understanding,* Greeson, P. E., Clark, J. R., and Clark, J. E., Eds., American Water Resources Association, Minneapolis, 1979, 479.
17. **Hjulström, F.,** Transportation of detritus by moving water, in *Recent Marine Sediments; A Symposium,* Trask, P. D., Ed., American Association of Petrology and Geology, 1939, 5.
18. **Rust, B. R.,** Sedimentation in fluvial and lacustrine environments, *Hydrobiologia,* 91, 59, 1982.
19. **Akhurst, E. G. J. and Breen, C. M.,** Ionic content as a factor influencing turbidity in two floodplain lakes after a flood, *Hydrobiologia,* 160, 19, 1988.
20. **Lowrance, R., Sharpe, J. K., and Sheridan, J. M.,** Long-term sediment deposition in the riparian zone of a coastal plain watershed, *J. Soil Water Conserv.,* July–August, 266, 1986.

21. **Eckblad, J. W., Peterson, N. L., Ostlie, K., and Temte, A.,** The morphometry, benthos and sedimentation rates of a floodplain lake in Pool 9 of the upper Mississippi River, *Am. Midl. Nat.*, 97, 433, 1977.
22. **Mitsch, W. J., Dorge, C. L., and Wiemhoff, J. R.,** Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois, *Ecology*, 60, 1116, 1979.
23. **Striegl, R. G.,** Suspended sediment and metals removal from urban runoff by a small lake, *Water Res. Bull.*, 23, 985, 1987.
24. **Baumann, R. H.,** Mechanisms of Maintaining Marsh Elevation in a Subsiding Environment, M.S. thesis, Louisiana State University, Baton Rouge, 1980.
25. **Baumann, R. H. and Day, J. W., Jr.,** Mississippi deltaic wetland survival: sedimentation versus coastal submergence, *Science*, 224, 1093, 1984.
26. **DeLaune, R. D., Whitcomb, J. H., Patrick, W. H., Jr., Pardue, J. H., and Pezeshki, S. R.,** Accretion and canal impacts in a rapidly subsiding wetland. I. ^{137}Cs and ^{210}Pb techniques, *Estuaries*, 12, 247, 1989.
27. **Feijtel, T. C., DeLaune, R. D., and Patrick, W. H., Jr.,** Biogeochemical control on metal distribution and accumulation in Louisiana sediments, *J. Environ. Qual.*, 17, 88, 1988.
28. **Stow, C. A., DeLaune, R. D., and Patrick, W. H., Jr.,** Nutrient fluxes in a eutrophic coastal Louisiana freshwater lake, *Environ. Manage.*, 9, 243, 1985.
29. **Kadlec, R. H. and Robbins, J. A.,** Sedimentation and sediment accretion in Michigan coastal wetlands (U.S.A.), *Chem. Geol.*, 44, 119, 1984.
30. **Cooper, J. R., Gilliam, J. W., Daniels, R. B., and Robarge, W. P.,** Riparian areas as filters for agricultural sediment, *Soil Sci. Soc. Am. J.*, 51, 416, 1987.
31. **Kuenzler, E. J., Mulholland, P. J., Yarbro, L. A., and Smock, L. A.,** *Distributions and Budgets of Carbon, Phosphorus, Iron and Manganese in a Floodplain Swamp Ecosystem*, Water Resources Research Institute, University of North Carolina, Raleigh, Report No. 157, 1980.
32. **Martin, D. B. and Hartman, W. A.,** Correlations between selected trace elements and organic matter and texture in sediments of northern prairie wetlands, *J. Assoc. Off. Anal. Chem.*, 70, 916, 1987.
33. **Johnston, C. A., Bubenzer, G. D., Lee, G. B., Madison, F. W., and McHenry, J. R.,** Nutrient trapping by sediment deposition in a seasonally flooded lakeside wetland, *J. Environ. Qual.*, 13, 283, 1984a.
34. **Novitzki, R. P.,** *Hydrology of the Nevin Wetland near Madison, Wisconsin*, U.S. Geological Survey, Water Resources Investigation 78-48, 1978.
35. **Hupp, C. R. and Morris, E. E.,** A dendrogeomorphic approach to measurement of sedimentation in a forested wetland, Black Swamp, Arkansas, *Wetlands*, 10, 107, 1990.
36. **Molinas, A., Auble, G. T., Segelquist, C. A., and Ischinger, L. S.,** *Assessment of the Role of Bottomland Hardwoods in Sediment and Erosion Control*, U.S. Fish and Wildlife Service, National Ecology Research Center, Ft. Collins, CO, Report No. NERC-88/11, 1988.
37. **Korschgen, C. E., Jackson, G. A., Muessig, L. F., and Southworth, D. C.,** Sedimentation in Lake Onalaska, Navigation Pool 7, upper Mississippi River, since impoundment, *Water Res. Bull.*, 23, 221, 1987.
38. **Johnston, C. A., Detenbeck, N. E., and Niemi, G. J.,** The cumulative effect of wetlands on stream water quality and quantity: a landscape approach, *Biogeochemistry*, 10, 105, 1990.
39. **Phillips, J. D.,** Fluvial sediment storage in wetlands, *Water Resourc. Bull.*, 25, 867, 1989.
40. **Lehre, A. K.,** Sediment budget of a small coast range drainage basin in north-central California, in *Sediment Budgets and Routing in Forested Drainage Basins*, Swanson, F. J., Janda, R. J., Dunne, T., and Swanston, D. N., Eds., U.S. Forest Service General Technical Report PNW-141, Portland, OR, 1982, 67.
41. Soil Conservation Service, *Upper Neuse River Erosion Study*, U.S. Soil Conservation Service, Raleigh, NC, 1983.

42. **Simmons, C. E.,** *Sediment Characteristics of Streams in the Eastern Piedmont and Western Coastal Plan Regions of North Carolina,* U.S. Geological Survey Water-Supply Paper 1798-0, 1976.
43. **Spomer, R. G., Mahurin, R. L., and Piest, R. F.,** Erosion, deposition, and sediment yield from Dry Creek Basin, Nebraska, *Trans. ASAE,* 29, 484, 1986.
44. **Trimble, S. W.,** A sediment budget for Coon Creek, the Driftless Area, Wisconsin, 1853–1977, *Am. J. Sci.,* 283, 454, 1983.
45. **Melville, M. D. and Erskine, W.,** Sediment remobilization and storage by discontinuous gullying in humid southeastern Australia, *Drainage Basin Sediment Delivery,* Hadley, R. F., Ed., International Association of Hydrological Sciences Publication 159, 1986, 423.
46. **Van Hooff, P. P. M. and Jungerius, P. D.,** Sediment source and storage in small watersheds on the Keuper Maris in Luxembourg, as indicated by soil profile truncation and the deposition of colluvium, *Catena,* 11, 133, 1984.
47. **Walling, D. E., Bradley, S., and Wilkinson, C. J.,** A Cesium-137 budget approach to the study of sediment delivery from a small agricultural drainage basin in Devon, U.K., in *Drainage Basin Sediment Delivery,* Hadley, R. F., Ed., International Association of Hydrological Sciences Publication 159, 1986, 423.
48. **Waksman, S. A.,** *Humus: Origin, Chemical Composition, and Importance in Nature,* 2nd ed., Williams & Wilkins, Baltimore, 1938.
49. **Clymo, R. S.,** Peat, in *Mires: Swamp, Bog, Fen and Moor,* Gore, A. J. P., Ed., Elsevier, Amsterdam, 1983, 159.
50. **Heinselman, M. L.,** Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota, *Ecol. Monogr.,* 33, 327, 1963.
51. **Heilman, P. E.,** Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska, *Ecology,* 49, 331, 1968.
52. **Hemond, H. F.,** The nitrogen budget of Thoreau's Bog, *Ecology,* 64, 99, 1983.
53. **Heinselman, M. L.,** Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota, *Ecol. Monogr.,* 40, 236, 1970.
54. **Johnston, C. A., Lee, G. B., and Madison, F. W.,** The stratigraphy and composition of a lakeside wetland, *Soil Sci. Soc. Am. J.,* 48, 347, 1984.
55. **Flebbe, P. A.,** Biogeochemistry of Carbon, Nitrogen and Phosphorus in the Aquatic Subsystem of Selected Okefenokee Swamp Sites, Ph.D. thesis, University of Georgia, Athens, 1982.
56. **Reader, R. J. and Stewart, J. M.,** The relationship between net primary production and accumulation for a peatland in southeastern Manitoba, *Ecology,* 53, 1024, 1972.
57. **Clymo, R. S.,** A model of peat bog growth, in *Production Ecology of British Moors and Montane Grasslands,* Heal, O. W. and Perkins, D. E., Eds., Springer-Verlag, Berlin, 1978, 187.
58. **Grigal, D. F.,** *Sphagnum* production in forested bogs of northern Minnesota, *Can. J. Bot.,* 63, 1204, 1985.
59. **Leisman, G. A.,** The rate of organic matter accumulation on the sedge mat zone of bogs in the Itasca State Park region of Minnesota, *Ecology,* 34, 81, 1953.
60. **Leisman, G. A.,** Further data on the rate of organic matter accumulation in bogs, *Ecology,* 38, 361, 1957.
61. **Damman, A. W. H.,** Distribution and movement of elements in ombrotrophic peat bogs, *Oikos,* 30, 480, 1978.
62. **Clymo, R. S.,** The growth of *Sphagnum*: methods of measurement, *J. Ecol.,* 58, 13, 1970.
63. **Johnston, C. A.,** *Productivity of Wet Soils: Biomass of Cultivated and Natural Vegetation,* Oak Ridge National Laboratory, Oak Ridge, TN, Report ORNL/Sub/84-18435/1, 1988.
64. **Guntenspergen, G. R. and Stearns, F.,** Ecological perspectives on wetland systems, in *Wetlands Treatment of Municipal Wastewaters,* Godfrey, P. J., Kaynor, E. R., Pelczarski, S., and Benforado, S., Eds., Van Nostrand Reinhold, New York, 1985, 69.
65. **Hemond, H. F.,** Biogeochemistry of Thoreau's Bog, Concord, Massachusetts, *Ecol. Monogr.,* 50, 507, 1980.

66. **Urban, N. R. and Eisenreich, S. J.,** Nitrogen cycling in a forested Minnesota bog, *Can. J. Bot.*, 66, 435, 1988.
67. **Barsdate, R. J. and Alexander, V.,** The nitrogen balance of Arctic tundra: pathways, rates, and environmental implications, *J. Environ. Qual.*, 4, 111, 1975.
68. **Dowding, P., Chapin, F. S., III, Wielgolaski, F. W., and Kilfeather, P.,** Nutrients in tundra ecosystems, in *Tundra Ecosystems: A Comparative Analysis,* Bliss, L. C., Heal, O. W., and Moore, J. J., Eds., Cambridge University Press, U.K., 1981, 647.
69. **Logan, J. A.,** Nitrogen oxides in the troposphere: global and regional budgets, *J. Geophys. Res.*, 88, 10785, 1983.
70. **Graham, W. F. and Duce, R. A.,** Atmospheric pathways of the phosphorus cycle, *Geochim. Cosmochim. Acta,* 43, 1195, 1979.
71. MAP 35/RAINE Research Community, The MAP 35/RAINE precipitation chemistry network: statistical overview for the period 1976–1980, *Atmos. Environ.*, 16, 1603, 1982.
72. **Dierberg, F. E. and Brezonik, P. L.,** Nitrogen and phosphorus mass balances in a cypress dome receiving wastewater, in *Cypress Swamps,* Ewel, K. C. and Odum, H. T., Eds., University of Florida Press, Gainesville, 1984.
73. **Haines, E., Chalmers, A., Hanson, R., and Sherr, B.,** Nitrogen pools and fluxes in a Georgia salt marsh, in *Estuarine Processes,* Vol. 2, Wiley, M., Ed., Academic Press, New York, 1976, 241.
74. **Krebs, J. E. and Golley, F. B.,** *Budgets of Selected Mineral Nutrients for Two Watershed Ecosystems in the Southeastern Piedmont,* Research Paper No. ERL-03-77, Institute of Ecology, University of Georgia, Athens, 1977.
75. **Schlesinger, W. H.,** Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest, *Ecol. Monogr.*, 48, 43, 1978.
76. **Valiela, I., Teal, J. M., Volkmann, S., Shafer, D., and Carpenter, E.,** Nutrient and particulate fluxes in a salt marsh ecosystem: tidal exchanges and inputs by precipitation and groundwater, *Limnol. Oceanogr.*, 23, 798, 1978.
77. **Jordan, T. E., Correll, D. L., Peterjohn, W. T., and Weller, D. E.,** Nutrient flux in a landscape: the Rhode River watershed and receiving waters, in *Watershed Research Perspectives,* Correll, D. L., Ed., Smithsonian Institution Press, Washington, D.C., 1986, 57.
78. **Richardson, C. J., Tilton, D. L., Kadlec, J. A., Chamie, J. P. M., and Wentz, W. A.,** Nutrient dynamics of northern wetland ecosystems, in *Freshwater Wetlands: Ecological Processes and Management Potential,* Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 217.
79. **Munger, J. W.,** Chemistry of atmospheric precipitation in the north-central United States: influence of sulfate, nitrate and calcareous soil particulates, *Atmos. Environ.*, 16, 1633, 1982.
80. **Verry, E. S. and Timmons, D. R.,** Waterborne nutrient flow through an upland-peatland watershed in Minnesota, *Ecology,* 63, 1456, 1982.
81. **Brinson, M., Bradshaw, H. D., Holmes, R. N., and Elkins, J. B., Jr.,** Litterfall stemflow, and throughfall nutrient fluxes in an alluvial swamp forest, *Ecology,* 61, 827, 1980.
82. **Swank, W. T. and Douglass, J. E.,** Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina, in *Watershed Research in Eastern North America,* Vol. 1, Correll, D. L., Ed., Edgewater, MD, 1977, 343.
83. **Wells, C. A., Whigham, D., and Lieth, H.,** Investigation of mineral nutrient cycling in an upland Piedmont forest, *J. Elisha Mitchell Sci. Soc.*, 88, 66, 1972.
84. **Likens, G. E.,** Nutrient flux and cycling in freshwater ecosystems, in *Mineral Cycling in Southeastern Ecosystems,* Howell, F. G., Gentry, J. B., and Smith, M. H., Eds., U.S. ERDA Tech. Int. Off. Conf. 740513, U.S. Department of Commerce, Springfield, VA, 1975, 314.
85. **Meyer, J. L. and Likens, G. E.,** Transport and transformation of phosphorus in a forest stream ecosystem, *Ecology,* 60, 1255, 1979.
86. **Polisini, J. M., Boyd, C. E., and Pidgeon, B.,** Nutrient limiting factors in an oligotrophic South Carolina pond, *Oikos,* 21, 344, 1970.

87. **Swank, W. T. and Henderson, G. T.,** Atmospheric input of some cations and anions to forest ecosystems in North Carolina and Tennessee, *Water Resour. Res.*, 12, 541, 1976.
88. **Buresh, R. J., Casselman, M. E., and Patrick, W. H., Jr.,** Nitrogen fixation in flooded soil systems, a review, *Adv. Agron.*, 33, 149, 1980.
89. **Hardy, R. W. F., Holsten, R. D., Jackson, E. K., and Burns, R. C.,** The acetylene-ethylene assay for N_2 fixation: laboratory and field evaluation, *Plant Physiol.*, 43, 1185, 1968.
90. **Howarth, R. W., Marino, R., Lane, J., and Cole, J. J.,** Nitrogen fixation in freshwater, esuarine, and marine ecosystems. I. Rates and importance, *Limnol. Oceanogr.*, 33, 669, 1988.
91. **Reddy, K. R. and Patrick, W. H., Jr.,** Nitrogen fixation in flooded soil, *Soil Sci.*, 128, 80, 1979.
92. **Chapman, R. R. and Hemond, H. F.,** Dinitrogen fixation by surface peat and *Sphagnum* in an ombrotrophic bog, *Can. J. Bot.*, 60, 538, 1982.
93. **Reddy, K. R.,** Nitrogen fixation by *Azolla* cultured in nutrient enriched waters, *J. Aquat. Plant Manage.*, 25, 43, 1987.
94. **Smith, D. W.,** An evaluation of marsh nitrogen fixation, in *Estuarine Perspectives*, Kennedy, V. S., Ed., Academic Press, New York, 1980, 135.
95. **Alimagno, B. V. and Yoshida, T.,** In situ acetylene-ethylene assay of biological nitrogen fixation in lowland rice soils, *Plant Soil*, 47, 239, 1977.
96. **Biesboer, D. D.,** Nitrogen fixation associated with natural and cultivated stands of *Typha latifolia* (Typhaceae), *Am. J. Bot.*, 71, 505, 1984.
97. **Ogan, M. T.,** Factors affecting nitrogenase activity associated with marsh grasses and their soils from eutrophic lakes, *Aquat. Bot.*, 17, 215, 1983.
98. **Alexander, V.,** A synthesis of the International Biological Program Tundra Biome Circumpolar Study of nitrogen fixation in *Soil Organisms and Decomposition in Tundra, Proc. Workshop, Fairbanks, A. K.*, Holding, S. J., Heal, O. W., MacLean, S. F., and Flanagan, P. W., Eds., Swedish IBP Comm., Wenner-Gren Center, Stockholm, Sweden, 1974.
99. **Dierberg, F. E. and Brezonik, P. L.,** Nitrogen fixation (acetylene reduction) associated with decaying leaves of pond cypress (*Taxodium distichum* var. *nutans*) in a natural and sewage-enriched cypress dome, *Appl. Environ. Microbiol.*, 41, 1413, 1981.
100. **DeLaune, R. D., Smith, C. J., and Sarafyan, M. N.,** Nitrogen cycling in a freshwater marsh of *Panicum hemitomon* on the deltaic plain of the Mississippi River, *J. Ecol.*, 74, 249, 1986.
101. **Kana, T. M. and Tjepkema, J. D.,** Nitrogen fixation associated with *Scirpus atrovirens* and other nonnodulated plants in Massachusetts, USA, *Can. J. Bot.*, 56, 2636, 1978.
102. **Schwintzer, C. R.,** Non symbiotic and symbiotic nitrogen fixation in a weakly minerotrophic peatland, *Am. J. Bot.*, 70, 1071, 1983.
103. **Lipschultz, F.,** Nitrogen Fixation in Horn Point Marsh on the Upper Chesapeake Bay, M.S. thesis, University of Maryland, 1978.
104. **Bristow, J. M.,** Nitrogen fixation in the rhizosphere of freshwater angiosperms, *Can. J. Bot.*, 52, 217, 1974.
105. **Francis, M. M., Naiman, R. J., and Melillo, J. M.,** Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*), *Hydrobiologia*, 121, 193, 1985.
106. **Waughman, G. J. and Bellamy, D. J.,** Nitrogen fixation and the nitrogen balance in peatland ecosystems, *Ecology*, 61, 1185, 1980.
107. **Koerselman, W., De Caluwe, H., and Kieskamp, W. M.,** Denitrification and dinitrogen fixation in two quaking fens in the Vechtplassen area, The Netherlands, *Biogeochemistry*, 8, 153, 1989.
108. **Martin, N. J. and Holding, A. J.,** Nutrient availability and other factors limiting microbial activity in the blanket peat, in *Production Ecology of British Moors and Montane Grasslands*, Heal, O. W. and Perkins, D. F., Eds., Ecological Studies No. 27, Springer-Verlag, New York, 1978, 113.

109. **Varshney, C. K. and Mandhan, K.,** Estimation of nitrogen fixation associated with *Typha angustata* Bory et Chaub, *Aquat. Bot.*, 13, 351, 1982.
110. **Balandreau, J. P., Rinaudo, G., Oumaron, M. M., and Dommergue, Y. R.,** in *Proc. First Int. Symp. of N Fixation,* Vol. 2, Newton, W. E. and Nyman, C. T., Eds., Pullman, WA, 1976, 611.
111. **Viner, A. B.,** Nitrogen fixation and denitrification in sediments of two Kenyan lakes, *Biotropica,* 14, 91, 1982.
112. **Schwintzer, C. R.,** Nitrogen fixation by *Myrica gale* root nodules in a Massachusetts USA wetland, *Oecologia (Berlin),* 43, 283, 1979.
113. **Voigt, G. K. and Steucek, G. L.,** Nitrogen distribution and accretion in an alder ecosystem, *Soil Sci. Soc. Am. Proc.*, 33, 946, 1969.
114. **Daly, G. T.,** Nitrogen fixation by nodulated *Alnus rugosa, Can. J. Bot.*, 44, 1607, 1966.
115. **Goldman, C. R.,** The contribution of alder trees (*Alnus tenuifolia*) to the primary productivity of Castle Lake, California, *Ecology,* 42, 282, 1961.
116. **Chapin, F. S., III,** Field measurements of growth and phosphate absorption in *Carex-aquatilis* along a latitudinal gradient, *Arct. Alp. Res.*, 13, 83, 1981.
117. **McKendrick, J. D.,** in *Vegetation and Production Ecology of an Alaskan Arctic Tundra,* Tieszen, L. L., Ed., Ecological Studies 29, Springer-Verlag, New York, 1978.
118. **Boyt, F. L., Bayley, S. E., and Zoltek, J., Jr.,** Removal of nutrients from treated municipal waste water by wetland vegetation, *J. Water Pollut. Control Fed.*, 49, 789, 1977.
119. **Brown, S.,** A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida, *Ecol. Monogr.*, 51, 403, 1981.
120. **Dolan, T. J., Bayley, S. E., Zoltek, J., Jr., and Hermann, A. J.,** Phosphorus dynamics of a Florida freshwater marsh receiving treated wastewater, *J. Appl. Ecol.*, 18, 205, 1981.
121. **Graetz, D. A., Krottje, P. A., Erickson, N. L., Fiskell, J., and Rothwell, D. F.,** *Denitrification in Wetlands as a Means of Water Quality Improvement,* Florida Water Resources Research Center Publ. No. 48, University of Florida, Gainesville, 1980.
122. **Marois, K. C. and Ewel, K. C.,** Natural and management-related variation in cypress domes, *Forest Sci.*, 29, 627, 1983.
123. **Nessel, J. K. and Bayley, S. E.,** Distribution and dynamics of organic matter and phosphorus in a sewage-enriched cypress swamp, in *Cypress Swamps,* Ewel, K. C. and Odum, H. T., Eds., University of Florida Press, Gainesville, 1984, 262.
124. **Kemp, G. P. and Day, J. W., Jr.,** *Floodwater Nutrient Processing in a Louisiana Swamp Forest Receiving Agricultural Runoff,* Water Resources Research Institute, Louisiana State University, Baton Rouge, Report No. A-043-LA, 1981.
125. **Brinson, M. M., Bradshaw, H. D., and Kane, E. S.,** *Nitrogen Cycling and Assimilative Capacity of Nitrogen and Phosphorus by Riverine Wetland Forests,* Water Resources Research Institute, University of North Carolina, Raleigh, NC, 1981.
126. **Peterka, J. J.,** *Effects of Wetlands in Water Quality in the Devils Lake Basin, North Dakota,* National Technical Information Service, Springfield, VA, PB-80-175292, OWRT A-052-N. Dakota (1), 1979.
127. **Simpson, R. L., Good, R. E., Walker, R., and Frasco, B. R.,** The role of Delaware River freshwater tidal wetlands in the retention of nutrients and heavy metals, *J. Environ. Qual.*, 12, 41, 1983.
128. **Staneck, W. and Jeglum, J. K.,** Comparison of peatland types using macronutrient contents of peat, *Vegetation,* 33, 163, 1977.
129. **Paul, H.,** Phosphorus status of peat soils in British Guiana, *Soil Sci.*, 77, 87, 1954.
130. **Anderson, V. J. M.,** Nitrogen and phosphorus budgets and the role of sediments in six shallow Danish lakes, *Arch. Hydrobiol.*, 74, 528, 1974.
131. **Damman, A. W. H.,** *Mobilization and Accumulation of Heavy Metals in Freshwater Wetlands,* Institute of Water Resources, University of Connecticut, Storrs, Technical report, 1979.
132. **Coultas, C. L.,** Soils of the Appalachicola National Forest wetlands. I. Titiswamps and savannahs, *Proc. Soil Crop Sci. Soc. Fla.*, 36, 72, 1977.

133. **Coultas, C. L.,** Soils of the Appalachicola National Forest wetlands. II. Cypress and gum swamps, *Proc. Soil Crop Sci. Soc. Fla.*, 37, 154, 1978.
134. **Steward, K. K. and Ornes, W. H.,** The autecology of sawgrass in The Florida Everglades, *Ecology*, 56, 162, 1975.
135. **Hatton, R. S., DeLaune, R. D., and Patrick, W. H., Jr.,** Sedimentation, accretion, and subsidence in marshes of Barataria Bay, Louisiana, *Limnol. Oceanogr.*, 28, 494, 1983.
136. **Bowden, W. B.,** Nitrogen and phosphorus in the sediments of a tidal, freshwater marsh in Massachusetts, *Estuaries*, 7, 108, 1984.
137. **Whigham, D. F. and Richardson, C. J.,** Soil and plant chemistry of an Atlantic white cedar wetland on the Inner Coastal Plain of Maryland, *Can. J. Bot.*, 66, 568, 1988.
138. **Richardson, C. J., Kadlec, J. A., Wentz, W. A., Chamie, J. P. M., and Kadlec, R. H.,** Background ecology and the effects of nutrient additions on a central Michigan wetland, in *Proc. 3rd Wetlands Conf.*, Lefor, M. W., Kennard, W. C., and Helfgott, T. B., Eds., University of Connecticut, Storrs, Water Resources Report No. 26, 1976, 34.
139. **Bares, R. H. and Wali, M. K.,** Chemical relations and litter production of *Picea mariana* and *Larix laricina* stands on an alkaline peatland in northern Minnesota, *Vegetatio*, 40, 79, 1979.
140. **Ingram, R. L. and Otte, L. J.,** Peat in North Carolina wetlands, in *Pocosin Wetlands*, Richardson, C. J., Ed., Hutchinson, Ross Company, Stroudsburg, PA, 1981, 125.
141. **Gorham, E.,** Chemical studies on the soils and vegetation of waterlogged habitats in the English lake district, *J. Ecol.*, 41, 345, 1953.
142. **Klopatek, J. M.,** The role of emergent macrophytes in mineral cycling in a freshwater marsh, in *Mineral Cycling in Southeastern Ecosystems*, Howell, F. G., Gentry, J. B., and Smith, M. H., Eds., ERDA Symposium Series, CONF 740513, U.S. Government Printing Office, Washington, D.C., 1975, 367.
143. **Wilson, K. A. and Fitter, A. H.,** The role of phosphorus in vegetational differentiation in a small valley mire, *J. Ecol.*, 72, 463, 1984.
144. **Walsh, T. and Barry, T. A.,** The chemical composition of some Irish peats, *Proc. Royal Irish Acad.*, 59, 305, 1958.
145. **Verhoeven, J. T. A. and Arts, H. M. M.,** Nutrient dynamics in small mesotrophic fens surrounded by cultivated land. II. N and P accumulation in plant biomass in relation to the release of inorganic N and P in the peat soil, *Oecologia (Berlin)*, 72, 557, 1987.
146. **Malmer, N. and Sjors, H.,** Some determinations of elementary constituents in mire plants and peat, *Bot. Notiser*, 108, 46, 1955.
147. **Mehlich, A.,** Uniformity of expressing soil test results: a case for calculating results on a volume basis, *Commun. Soil Sci. Plant Anal.*, 3, 417, 1972.
148. **DeLaune, R. D., Buresh, R. J., and Patrick, W. H., Jr.,** Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh, *Estuarine Coastal Mar. Sci.*, 8, 477, 1979.
149. **Whigham, D. F. and Simpson, R. L.,** Sewage spray irrigation in a Delaware River freshwater tidal marsh, in *Freshwater Wetlands and Sewage Disposal*, Tilton, D. L., Kadlec, R. H., and Richardson, C. J., Eds., University of Michigan, Ann Arbor, 1976, 121.
150. **Boyd, C. E.,** Production, mineral nutrient adsorption, and biochemical assimilation by *Justicia americana* and *Alternanthera philoxeroides*, *Arch. Hydrobiol.*, 66, 139, 1969.
151. **Garten, C. T., Jr.,** Multivariate perspectives on the ecology of plant mineral element composition, *Am. Nat.*, 112, 534, 1978.
152. **Chapin, F. S., III, Van Cleve, K., and Tieszen, L. L.,** Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska, *Arct. Alp. Res.*, 7, 209, 1975.
153. **Ulrich, A. and Gersper, P. L.,** Plant nutrient limitations of tundra plant growth, in *Vegetation and Production Ecology of an Alaskan Arctic Tundra*, Tieszen, L. L., Ed., Ecological Studies 29, Springer-Verlag, New York, 1978, 457.
154. **Bernard, J. M. and Bernard, F. A.,** Winter standing crop and nutrient contents in five central New York wetlands, *Bull. Torrey Bot. Club*, 104, 57, 1977.

155. **Bernard, J. M. and Solsky, B. A.**, Nutrient cycling in a *Carex lacustris* wetland, *Can. J. Bot.*, 55, 630, 1977.
156. **Klopatek, J. M.**, Production of Emergent Macrophytes and Their Role in Mineral Cycling Within a Freshwater Marsh, M.S. thesis, University of Wisconsin, Milwaukee, 1974.
157. **Linn, J. G., Goodrich, R. D., Meiske, J. C., and Staba, E. J.**, Aquatic plants from Minnesota. IV. Nutrient composition, *Water Resour. Res. Cent. Univ. Minn. Bull.*, 56, 1973.
158. **Mudroch, A.**, *A Study of Selected Great Lakes Coastal Marshes*, Canada Centre for Inland Waters, Burlington, Ontario, Scientific Series No. 122, 1981.
159. **Van Dyke, G. D.**, Aspects Relating to Emergent Vegetation Dynamics in a Deep Marsh, Northcentral Iowa, Ph.D. thesis, Iowa State University, Ames, 1972.
160. **Small, E.**, Ecological significance of four critical elements in plants of raised *Sphagnum* peat bogs, *Ecology*, 53, 498, 1972.
161. **Davis, S. M. and Harris, L. A.**, Marsh plant production and phosphorus flux in Everglades conservation area 2, in *Environmental Quality Through Wetlands Utilization*, Drew, M. A., Ed., Tallahassee, FL, 1978.
162. **Boyd, C. E. and Vickers, D. H.**, Relationships between production, nutrient accumulation, and chlorophyll synthesis in an *Eleocharia quadrangulata* population, *Can. J. Bot.*, 49, 883, 1971.
163. **Chapin, F. S., III, Johnson, D. A., and McKendrick, J. D.**, Seasonal movement of nutrients in plants of differing growth form in an Alaskan USA tundra ecosystem: implications for herbivory, *J. Ecol.*, 68, 189, 1980.
164. **Shaver, G. R. and Chapin, F. S., III**, Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth, *Ecology*, 61, 622, 1980.
165. **Mudroch, A. and Capobianco, J. A.**, Effects of treated effluent on a natural marsh, *J. Water Pollut. Control Fed.*, 51, 2243, 1979.
166. **Boyd, C. E.**, The dynamics of dry matter and chemical substances in a *Juncus effusus* population, *Am. Midl. Nat.*, 86, 28, 1971.
167. **Mason, C. F. and Bryant, R. J.**, Production, nutrient content and decomposition of *Phragmites communis* trin. and *Typha angustifolia* L., *Ecology*, 63, 71, 1975.
168. **Boyd, C. E.**, Production and chemical composition of *Saururus cernuus* at sites of different fertility, *Ecology*, 53, 927, 1972.
169. **Boyd, C. E.**, Production, mineral accumulation and pigment concentrations in *Typha latifolia* and *Scirpus americanus*, *Ecology*, 51, 285, 1970.
170. **Boyd, C. E. and Hess, L. W.**, Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*, *Ecology*, 51, 296, 1970.
171. **Peverly, J. H.**, Element accumulation and release by macrophytes in a wetland stream, *J. Environ. Qual.*, 14, 137, 1985.
172. **Ehrenfeld, J. G.**, The role of woody vegetation in preventing ground water pollution by nitrogen from septic tank leachate, *Water Res.*, 21, 605, 1987.
173. **Agami, M. and Reddy, K. R.**, Inter-relationships between *Salvinia rotundifolia* and *Spirodela polyrhiza* at various interaction stages, *J. Aquat. Plant Manage.*, 27, 96, 1989.
174. **Boyd, C. E. and Vickers, D. H.**, Variations in the elemental content of *Eichhornia crassipes*, *Hydrobiologia*, 38, 409, 1971.
175. **Bernard, J. M. and Hankinson, G.**, Seasonal changes in standing crop, primary production, and nutrient levels in a *Carex rostrata* wetland, *Oikos*, 32, 328, 1979.
176. **Bandle, B. J. and Day, F. P., Jr.**, Influence of species, season, and soil on foliar macronutrients in the Great Dismal Swamp, *Bull. Torrey Bot. Club*, 112, 146, 1985.
177. **Day, F. P. and Monk, C. D.**, Seasonal nutrient dynamics in the vegetation on a southern Appalachian watershed, *Am. J. Bot.*, 64, 1126, 1977.
178. **Mitchell, H. L.**, Trends in nitrogen, phosphorus, potassium and calcium content of the leaves of some forest trees during the growing season, *Black Rock Forest Pap.*, 1, 29, 1936.

179. **Straub, P. and Post, D. M.,** Rates of growth and nutrient concentration of trees in cypress domes, in *Cypress Wetlands for Water Management, Recycling and Conservation,* Odum, H. T. and Ewel, K. C., Eds., Fourth Annual Report to National Science Foundation and the Rockefeller Foundation, Center for Wetlands, University of Florida, Gainesville, FL, Report PB-282-159, National Technical Information Service, Springfield, VA, 1977, 271.
180. **Peterjohn, W. T. and Correll, D. L.,** Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest, *Ecology,* 65, 1466, 1984.
181. **Lazar, V. A. and Beeson, K. C.,** Mineral nutrients in native vegetation on Atlantic coastal plain soil types, *J. Agric. Food Chem.,* 4, 439, 1956.
182. **Alway, F. J., Maki, T.E., and Methley, W. J.,** Composition of the leaves of some forest trees, *Am. Soil Survey Assoc. Bull.,* 15, 81, 1934.
183. **Davis, C. B. and van der Valk, A. G.,** Litter decomposition in prairie glacial marshes, in *Freshwater Wetlands: Ecological Processes and Management Potential,* Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 99.
184. **Simpson, R. L., Good, R. E., Walker, R., and Frasco, B. R.,** The role of the Delaware River freshwater tidal wetlands in the retention of nutrients and heavy metals, *J. Environ. Qual.,* 12, 41, 1983.
185. **Gomez, M. M. and Day, F. P., Jr.,** Litter nutrient content and production in the Great Dismal Swamp, *Am. J. Bot.,* 69, 1314, 1982.
186. **Day, F. P., Jr.,** Litter decomposition rates in the seasonally flooded Great Dismal Swamp, *Ecology,* 63, 670, 1982.
187. **Auble, G. T.,** Biogeochemistry of Okefenokee Swamp: Litterfall, Litter Decomposition, and Surface Water Dissolved Cation Concentrations, Ph.D. Dissertation, University of Georgia, Athens, 1982.
188. **Deghi, G. S., Ewel, K. C., and Mitsch, W. J.,** Effects of sewage effluent application on litter fall and litter decomposition in cypress swamps, *J. Appl. Ecol.,* 17, 397, 1980.
189. **Reddy, K. R. and DeBusk, W. F.,** Nutrient storage capabilities of aquatic and wetland plants, in *Aquatic Plants for Water Treatment and Resource Recovery,* Reddy, K. R. and Smith, W. H., Eds., Magnolia Publishing Inc., Orlando, FL, 1987, 337.
190. **Bernard, J. M. and Hankinson, G.,** Seasonal changes in standing crop, primary production, and nutrient levels in a *Carex rostrata* wetland, *Oikos,* 32, 328, 1979.
191. **Wentz, A. W.,** The Effects of Simulated Sewage Effluents on the Growth and Productivity of Peatland Plants, Ph.D. dissertation, University of Michigan, Ann Arbor, 1976.
192. **Bowden, W. B.,** Nitrogen Cycling in the Sediments of a Tidal Freshwater Marsh, Ph.D. dissertation, North Carolina State University, Raleigh, 1982.
193. **Whigham, D. F. and Simpson, R. L.,** Nitrogen and phosphorus movement in a freshwater tidal wetland receiving sewage effluent, in *Coastal Zone '78, The Proc. Symp.* on Technical Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management, ASCE, San Francisco, 1978, 2189.
194. **Gaudet, J. J.,** Nutrient relationships in the detritus of a tropical swamp, *Arch. Hydrobiol.,* 78, 213, 1976.
195. **Dykyjová, D. and Hradecká, D.,** Production ecology of *Phragmites communis.* I. Relations of two ecotypes to the microclimate and nutrient conditions of habitat, *Folia Geobot. Phytotaxon.,* 11, 23, 1976.
196. **Kvet, J.,** Growth and mineral nutrients in shoots of *Typha latifolia* L., in *Limnology of Shallow Waters,* Salanki, J. and Ponyi, J., Eds., Akadeniai Kiado, Budapest, 1975, 113.
197. **Zoltek, J., Bayley, S. E., Dolan, T., and Herman, A.,** *Removal of Nutrients from Treated Municipal Wastewater by Freshwater Marshes,* Center for Wetlands, University of Florida, Gainesville, 1978.
198. **Klopatek, J. M.,** Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes, in *Freshwater Wetlands: Ecological Processes and Management Potential,* Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 195.

199. **Rosswall, T. and Granhull, U.,** Nitrogen cycling in a subarctic ombrotophic mire, in *The Ecology of a Subarctic Mire*, Soresson, M., Ed., *Ecol. Bull. (Stockholm)*, 30, 209, 1980.
200. **Davis, C. B. and van der Valk, A. G.,** Uptake and release of nutrients by living and decomposing *Typha glauca* Godr. tissues at Eagle Lake, Iowa, *Aquat. Bot.*, 16, 75, 1983.
201. **Prentki, R. T., Gustafson, T. D., and Adams, M. S.,** Nutrient movements in lakeshore marshes, in *Freshwater Wetlands: Ecological Processes and Management Potential*, Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 169.
202. **Boyd, C. E. and Scarsbrook, E.,** Influence of nutrient additions and initial density of plants on production of waterhyacinth *Eichhornia crassipes*, *Aquat. Bot.*, 1, 253, 1975.
203. **Stewart, H. T. L., Hopmans, P., Flinn, D. W., Hillman, T. J., and Collopy, J.,** *Evaluation of Irrigated Tree Crops for Land Disposal of Municipal Effluent at Wodonga*, Albury-Wodonga Development Corporation, New South Wales, Australia, Technical Report No. 7, 1988.
204. **Brinson, M. M., Bradshaw, H. D., and Kane, E. S.,** Nutrient assimilative capacity of an alluvial floodplain swamp, *J. Appl. Ecol.*, 21, 1041, 1984.
205. **Grigal, D. F., Buttleman, C. G., and Kernik, L. K.,** Biomass and productivity of the woody strata of forested bogs in northern Minnesota, *Can. J. Bot.*, 63, 2416, 1985.
206. **Fetter, C. W., Jr., Sloey, W. E., and Spangler, F. L.,** Use of a natural marsh for wastewater polishing, *J. Water Pollut. Control Fed.*, 50, 290, 1978.
207. **Spangler, F. L., Sloey, W. E., and Fetter, C. W., Jr.,** *Wastewater Treatment by Natural and Artificial Marshes*, National Technical Information Service, Springfield, VA, PB-259-992, EPA-600/2-76-207, U.S. Environmental Protection Agency, 1976.
208. **Brinson, M. M. and Davis, G. I.,** *Primary Productivity and Mineral Cycling in Aquatic Macrophyte Communities of the Chowan River, North Carolina*, Water Resources Research Institute, University of North Carolina Report No. 120, 1976.
209. **Deghi, G. S. and Ewel, K. S.,** Simulated effect of wastewater application on phosphorus distribution in cypress domes, in *Cypress Swamps*, Ewel, K. C. and Odum, H. T., Eds., University of Florida Press, Gainesville, 1984, 102.
210. **Nessel, J.,** Distribution and Dynamics of Organic Matter and Phosphorus in a Sewage Enriched Cypress Strand, M.S. thesis, University of Florida, Gainesville, 1978.
211. **McNaughton, S. J.,** Ecotype function in the *Typha* community type, *Ecol. Monogr.*, 36, 297, 1966.
212. **Ho, Y. B.,** Short development and production studies of *Phragmites australis* (Cav.) Trin. ex Steudel in Scottish lochs, *Hydrobiologia*, 64, 215, 1979.
213. **Bernard, J. M., Solander, D., and Kvet, J.,** Production and nutrient dynamics in *Carex* wetlands, *Aquat. Bot.*, 30, 125, 1988.
214. **Simpson, R. L., Good, R. E., Leck, M. A., and Whigham, D. F.,** The ecology of freshwater tidal wetlands, *BioScience*, 33, 255, 1983b.
215. **Chapin, F. S., III,** Phosphate uptake and nutrient utilization by Barrow tundra vegetation, in *Vegetation and Production Ecology of an Alaskan Arctic Tundra*, Tieszen, L. L., Ed., Ecological Studies 29, Springer-Verlag, New York, 1978, 483.
216. **Richardson, C. J.,** Primary productivity values in freshwater wetlands, in *Wetland Functions and Values: The State of Our Understanding*, Greeson, P. E., Clark, J. R., and Clark, J. E., Eds., American Water Resources Association, Minneapolis, 1979, 131.
217. **Connor, W. H. and Day, J. W., Jr.,** The ecology of forested wetlands in the southeastern United States, in *Wetlands: Ecology and Management*, Gopal, B., Turner, R. E., Wetzel, R. G., and Whigham, D. F., Eds., National Institute of Ecology and International Scientific Publications, Jaipur, India, 1982, 69.
218. **Dabel, C. A. and Day, F. D.,** Structural comparisons of four plant communities in the Great Dismal Swamp, *Va. Bull. Torr. Bot. Club*, 104, 352, 1977.

219. **Dorge, C. L. and Mitsch, W. J.,** Net primary productivity and biomass of vegetation in Heron Pond, in *Forested Wetlands for Water Resource Management in Southern Illinois,* Mitsch, W. J., Dorge, C. L., and Wiemhoff, J. R., Eds., University of Illinois Water Resources Center Report No. 132, Urbana, 1977, 164.
220. **Brown, S. L.,** A Comparison of Cypress Ecosystems in the Landscape of Florida, Ph.D. dissertation, University of Florida, Gainesville, 1978.
221. **Lugo, A. E., Brown, S., and Brinson, M. M.,** Forested wetlands in freshwater and salt-water environments, *Limnol. Oceanogr.*, 33(4, part 2), 894, 1988.
222. **Dierberg, F. E. and Brezonik, P. L.,** Nitrogen and phosphorus removal by cypress swamp sediments, *Water Air Soil Pollut.*, 24, 207, 1985.
223. **DeBusk, T. A. and Reddy, K. R.,** BOD removal in floating aquatic macrophyte-based wastewater treatment systems, *Water Sci. Technol.*, 19, 273, 1987.
224. **Farnham, R. S.,** Use of organic soils for wastewater filtration, in *Histosols: Their Characteristics, Use, and Classification,* Soil Science Society of America, Inc., Madison, WI, 1974, 111.
225. **Reddy, K. R. and Graetz, D. A.,** Use of shallow reservoir and flooded organic soil systems for waste water treatment: nitrogen and phosphorus transformations, *J. Environ. Qual.*, 10, 113, 1981.
226. **Patrick, W. H., Jr. and Khalid, R. A.,** Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions, *Science,* 186, 53, 1974.
227. **Holford, I. C. R. and Patrick, W. H., Jr.,** Effects of duration of anaerobiosis and reoxidation on phosphate sorption characteristics of an acid soil, *Aust. J. Soil Res.*, 19, 69, 1981.
228. **Froelich, P. N.,** Kinetic control of dissolved phosphate in natural rivers and estuaries: a primer on the phosphate buffer mechanism, *Limnol. Oceanogr.*, 33, 649, 1988.
229. **Caraco, N., Cole, J., and Likens, G. E.,** A comparison of phosphorus immobilization in sediments of freshwater and coastal marine systems, *Biogeochemistry,* 9, 277, 1990.
230. **Burge, W. D. and Broadbent, F. E.,** Fixation of ammonia by organic soils, *Soil Sci. Soc. Proc.*, p. 199, 1961.
231. **Wetzel, R. G.,** Land-water interfaces: metabolic and limnological regulators, *Verh. Int. Verein. Limnol.*, 24, 6, 1990.
232. **Gersberg, R. M., Elkins, B. V., Lyon, S. R., and Goldman, C. R.,** Role of aquatic plants in wastewater treatment by artificial wetlands, *Water Res.*, 20, 363, 1986.
233. **Deghi, G. S.,** Effect of Sewage Effluent Application on Phosphorus Cycling in Cypress Domes, M.S. thesis, University of Florida, Gainesville, 1977.
234. **Straub, P. A.,** Effects of wastewater and inorganic fertilizer on growth rates and nutrient concentrations in dominant tree species in cypress domes, in *Cypress Swamps,* Ewel, K. C. and Odum, H. T., Eds., University of Florida Press, Gainesville, 1984, 127.
235. **Lindsley, D., Schuck, T., and Stearns, F.,** Productivity and nutrient content of emergent macrophytes in two Wisconsin marshes, in *Freshwater Wetlands and Sewage Disposal,* Tilton, D. L., Kadlec, R.H., and Richardson, C. J., Eds., University of Michigan, Ann Arbor, 1976, 51.
236. **Jenny, H., Gessel, S. P., and Bingham, F. T.,** Comparative study of decomposition of organic matter in temperate and tropical regions, *Soil Sci.*, 68, 419, 1949.
237. **Heal, O. W. and French, D. D.,** Decomposition of organic matter in tundra, in *Soil Organisms and Decomposition in Tundra, Proc. Microbiology, Decomposition and Invertebrate Working Groups Meeting,* Fairbanks, A. K., Holding, A. J., Heal, O. W., Maclean, S. F., Jr., and Flanagan, P. W., Eds., Tundra Biome Steering Committee, Stockholm, 1974, 279.
238. **Godshalk, G. L. and Wetzel, R. G.,** Decomposition in the littoral zone of lakes, in *Freshwater Wetlands: Ecological Processes and Management Potential,* Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 131.
239. **Brinson, M. M.,** Decomposition and nutrient exchange of litter in an alluvial swamp forest, *Ecology,* 58, 601, 1977.

240. **Duever, M. J., Carlson, J. E., and Riopelle, L. A.**, Ecosystem analysis at Corkscrew Swamp, in *Cypress Wetlands for Water Management, Recycling and Conservation*, Odum, H. T., Ewel, K. C., Ordway, J. W., and Johnston, M. K., Eds., 2nd Annual Rep. NSF (RANN) and Rockefeller Found, University of Florida, Gainesville, 1975.
241. **Odum, W. E. and Heywood, M. A.**, Decomposition of intertidal freshwater marsh plants, in *Freshwater Wetlands: Ecological Processes and Management Potential*, Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 89.
242. **Reddy, K. R. and Patrick, W. H., Jr.**, Effect of alternate aerobic and anerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil, *Soil Biol. Biochem.*, 7, 87, 1975.
243. **Polunin, N. V. C.**, The decomposition of emergent macrophytes in fresh water, in *Advances in Ecological Research*, Volume 14, Academic Press, New York, 1984, 115.
244. **Hodkinson, I. D.**, Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem, *J. Ecol.*, 63, 131, 1975.
245. **Gaudet, J. J.**, Uptake, accumulation, and loss of nutrients by papyrus in tropical swamps, *Ecology*, 58, 415, 1977.
246. **Chamie, J. P. M. and Richardson, C. J.**, Decomposition in northern wetlands, in *Freshwater Wetlands: Ecological Processes and Management Potential*, Good, R. E., Whigham, D. F., and Simpson, R. L., Eds., Academic Press, New York, 1978, 115.
247. **Andersen, F. O.**, Effects of nutrient level on the decomposition of *Phragmites communis* Trin., *Arch. Hydrobiol.*, 84, 42, 1978.
248. **Heal, O. W., Latter, P. M., and Howson, G.**, A study of the rates of decomposition of organic matter, in *Production Ecology of British Moors and Montane Grasslands*, Heal, O. W. and Perkins, D. F., Eds., Ecological Studies No. 27, Springer-Verlag, New York, 1978, 136.
249. **Payne, W. J.**, Reduction of nitrogenous oxides by microorganisms, *Bacteriol. Rev.*, 37, 409, 1973.
250. **Knowles, R.**, Denitrification, *Ecol. Bull.*, 33, 315, 1981.
251. **Sikora, L. J. and Keeney, D. R.**, Further aspects of soil chemistry under anaerobic conditions, in *Mires: Swamp, Bog, Fen and Moor*, Gore, A. J. P., Ed., Elsevier, Amsterdam, 1983, 247.
252. **Reddy, K. R. and Patrick, W. H.**, Nitrogen transformations and loss in flooded soils and sediments, *Crit. Rev. Environ. Control*, 13, 273, 1984.
253. **Bowden, W. B.**, The biogeochemistry of nitrogen in freshwater wetlands, *Biogeochemistry*, 4, 313, 1987.
254. **Klapwijk, A. and Snodgrass, W. J.**, Experimental measurement of sediment nitrification and denitrification in Hamilton Harbour, Canada, *Hydrobiologia*, 91, 207, 1982.
255. **Cooke, J. G. and White, R. E.**, Spatial distribution of denitrifying activity in a stream draining an agricultural catchment, *Freshwater Biol.*, 18, 509, 1987.
256. **Reddy, G. B. and Reddy, K. R.**, Nitrogen transformations in ponds receiving polluted water from nonpoint sources, *J. Environ. Qual.*, 16, 1, 1987.
257. **Engler, R. M. and Patrick, W. H.**, Nitrate removal from floodwater overlying flooded soils and sediments, *J. Environ. Qual.*, 3, 409, 1974.
258. **Reddy, K. R., Patrick, W. H., Jr., and Phillips, R. E.**, Ammonium diffusion as a factor in nitrogen loss from flooded soils, *Soil Sci. Soc. Am. J.*, 40, 528, 1976.
259. **Reddy, K. R., Sacco, P. D., and Graetz, D. A.**, Nitrate reduction in an organic soil-water system, *J. Environ. Qual.*, 9, 283, 1980.
260. **Bowden, W. B.**, Nitrification, nitrate reduction, and nitrogen immobilization in a tidal freshwater marsh sediment, *Ecology*, 67, 88, 1986.
261. **Patrick, W. H., Jr. and Reddy, K. R.**, Nitrification-denitrification reactions in flooded soils and water bottoms: dependence on oxygen supply and ammonium diffusion, *J. Environ. Qual.*, 5, 469, 1976.

262. **Lorenz, J. S. and Biesboer, D. D.,** Nitrification, denitrification, and ammonia diffusion in a cattail marsh, in *Aquatic Plants for Water Treatment and Resource Recovery,* Reddy, K. R. and Smith, W. H., Eds., Magnolia Publishing Co., Orlando, FL, 1987, 525.
263. **Lindau, C. W., Patrick, W. H., Jr., DeLaune, R. D., Reddy, K. R., and Bollich, P. K.,** Entrapment of nitrogen-15 dinitrogen during soil denitrification, *Soil Sci. Soc. Am. J.*, 52, 538, 1988.
264. **Reddy, K. R., Patrick, W. H., Jr., and Lindau, C. W.,** Redox processes and nitrogen transformations in flooded soils, in Trans. 13th Congr. Int. Soc. Soil Sci., August 13–20, 1986, Hamburg, Germany, Vol. 6, 1986, 729.
265. **DeLaune, R. D. and Smith, C. J.,** Simultaneous determination of nitrification and nitrate reduction in sediment-water columns by nitrate-15 dilution, *J. Environ. Qual.*, 16, 227, 1987.
266. **Kemp, W. M., Wetzel, R. L., Boynton, W. R., D'Elia, C. F., and Stevenson, J. C.,** Nitrogen cycling in estuarine interfaces: Some concepts and research directions, in *Estuarine Comparisons,* Academic Press, New York, 1982, 209.
267. **Smith, C. J. and Patrick, W. H., Jr.,** Nitrous oxide emission as affected by alternate anaerobic and aerobic conditions from soil suspensions enriched with ammonium sulfate, *Soil Biol. Biochem.*, 15, 693, 1983.
268. **Bartlett, M. S., Brown, L. C., Hanes, N. B., and Nickerson, N. H.,** Denitrification in freshwater wetland soil, *J. Environ. Qual.*, 8, 460, 1979.
269. **Yoshinari, T. and Knowles, R.,** Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria, *Biochem. Biophys. Commun.*, 69, 705, 1976.
270. **Tiedje, J. M.,** Denitrification, in *Methods of Soil Analysis, Part 2. Chemical and Microbiologicial Properties — Agronomy Monograph No. 9,* 2nd ed., ASA-SSSA, Madison, WI, 1982, 1011.
271. **Reddy, K. R., Rao, P. S. C., and Jessup, R. E.,** The effect of carbon mineralization on denitrification kinetics in mineral and organic soils, *Soil Sci. Soc. Am. J.*, 46, 62, 1982.
272. **Burford, J. R. and Bremner, J. M.,** Relationships between the denitrification capacities of soils and total water-soluble and readily decomposable soil organic matter, *Soil Biol. Biochem.*, 7, 389, 1975.
273. **Stanford, G., VanderPol, R. A., and Dzienia, S.,** Denitrification rates in relation to total and extractable soil carbon, *Soil Sci. Soc. Am. Proc.*, 39, 284, 1975.
274. **Tiedje, J. M., Sorensen, J., and Chang, Y.-Y. L.,** Assimilatory and dissimilatory nitrate reduction: perspectivies and methodology for simultaneous measurement of several nitrogen cycle processes, *Ecol. Bull.*, 33, 331, 1981.
275. **Graetz, D. A., Keeney, D. R., and Aspiras, R. B.,** The status of lake sediment-water systems in relation to nitrogen transformations, *Limnol. Oceanogr.*, 18, 908, 1973.
276. **Smith, C. J., Wright, M. F., and Patrick, W. H., Jr.,** The effect of soil redox potential and pH on the reduction and production of nitrous oxide, *J. Environ. Qual.*, 12, 186, 1983.
277. **Kroeckel, L. and Stolp, H.,** Influence of the water regime on denitrification and aerobic respiration in soil, *Biol. Fertil. Soils,* 2, 15, 1986.
278. **Westermann, P. and Ahring, B. K.,** Dynamics of methane production, sulfate reduction, and denitrification in a permanently waterlogged alder swamp, *Appl. Environ. Microbiol.*, October, 2554, 1987.
279. **Hemond, H. F. and Duran, A. P.,** Fluxes of N_2O at the sediment-water and water-atmosphere boundaries of a nitrogen-rich river, *Water Resour. Res.*, 25, 839, 1989.
280. **Pedrazzini, F. R. and Moore, P. A.,** N_2O emission and changings of redox potential and pH in submerged soil samples, *Z. Pflanzernaehr. Bodenk.*, 146, 660, 1983.
281. **Hussey, M. R., Skinner, Q. D., Adams, J. C., and Harvey, A. J.,** Denitrification and bacterial numbers in riparian soils of a Wyoming mountain watershed, *J. Range Manage.*, 38, 492, 1985.
282. **Cooke, J. G. and White, R. E.,** The effect of nitrate in stream water on the relationship between denitrification and nitrification in a stream-sediment microcosm, *Freshwater Biol.*, 18, 213, 1987b.

283. **Gordon, A. S., Cooper, W. J., and Scheidt, D. J.,** Denitrification in marl and peat sediments in the Florida everglades, *Appl. Environ. Microbiol.*, 52, 987, 1986.
284. **DeBusk, W. F. and Reddy, K. R.,** Removal of floodwater nitrogen in a cypress swamp receiving primary wastewater effluent, *Hydrobiologia*, 153, 79, 1987.
285. **Muller, M. M., Sundman, V., and Skujins, J.,** Denitrification in low pH spodosols and peats determined with the acetylene inhibition method, *Appl. Environ. Microbiol.*, 40, 235, 1980.
286. **Dierberg, F. E. and Brezonik, P. L.,** Nitrogen and phosphorus mass balances in natural and sewage enriched cypress domes, *J. Appl. Ecol.*, 20, 323, 1983.
287. **Hsieh, Y.-P. and Coultas, C. L.,** Nitrogen removal from freshwater wetlands: nitrification-denitrification coupling potential, in *Constructed Wetlands for Wastewater Treatment: Municipal, Industrial and Agricultural*, Hammer, D. A., Ed., Lewis Publishers, Chelsea, MI, 1989, 493.
288. **Reddy, K. R., Patrick, W. H., Jr., and Lindau, C. W.,** Nitrification denitrification at the plant root-sediment interface in wetlands, *Limnol. Oceanogr.*, 34, 1004, 1989.
289. **Engler, R. M., Antie, D. A., and Patrick, W. H., Jr.,** Effect of dissolved oxygen on redox potential and nitrate removal in flooded swamp and marsh soils, *J. Environ. Qual.*, 5, 230, 1976.
290. **Smith, C. J. and DeLaune, R. D.,** Nitrogen loss from freshwater and saline estuarine sediments, *J. Environ. Qual.*, 12, 514, 1983.
291. **Reddy, K. R., Patrick, W. H., Jr., and Phillips, R. E.,** The role of nitrate diffusion in determining the order and rate of denitrification in flooded soil. I. Experimental results, *Soil Sci. Soc. Am. J.*, 42, 268, 1978.
292. **Brodrick, S. J., Cullen, P., and Maher, W.,** Denitrification in a natural wetland receiving secondary treated effluent, *Water Res.*, 22, 431, 1988.
293. **Hill, A. R. and Sanmugadas, K.,** Denitrification rates in relation to stream sediment characteristics, *Water Res.*, 19, 1579, 1985.
294. **Warwick, J. and Hill, A. R.,** Nitrate depletion in the riparian zone of a small woodland stream, *Hydrobiologia*, 157, 231, 1988.
295. **Anderson, F. O. and Hansen, J. E.,** Nitrogen cycling and microbial decomposition in sediments with Phragmites australis (Poaceae), *Hydrobiol. Bull.*, 16, 11, 1982.
296. **Pinay, G. and Décamps, H.,** The role of riparian woods in regulating nitrogen fluxes between the alluvial aquifer and surface water: a conceptual model, *Reg. Rivers*, 2, 507, 1988.
297. **Hill, A. R.,** Nitrogen transformations in a small forested headwater wetland, in *Proc. Conf.: Wetlands: Inertia or Momentum*, Toronto, Ontario, Bardecki, M. J. and Patterson, N., Eds., 1988, 309.
298. **Anderson, F. O.,** Oxygen and nitrate respiration in a reed swamp sediment from a eutrophic lake, *Holarct. Ecol.*, 4, 66, 1981.
299. **Lindau, C. W., DeLaune, R. D., and Jones, G. L.,** Fate of added nitrate and ammonium-nitrogen entering a Louisiana gulf coast swamp forest, *J. Water Pollut. Control Fed.*, 60, 386, 1988.
300. **Rhodes, J., Skau, C. M., Greenlee, D., and Brown, D. L.,** Quantification of nitrate uptake by riparian forests and wetlands in an undisturbed headwaters watershed, in *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*, First North American Riparian Conference, April 16–18, 1985, Tucson, AZ, USDA Forest Service General Technical Report RM-120, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO, 1985, 175.
301. **Goodroad, L. L. and Keeney, D. R.,** Nitrous oxide emission from forest, marsh, and prairie ecosystems, *J. Environ. Qual.*, 13, 448, 1984.
302. **Murphy, T. P. and Brownlee, B. G.,** Ammonia volatilization in a hypertrophic prairie lake, *Can. J. Fish. Aquat. Sci.*, 38, 1035, 1981.

303. **Blood, E. R.,** *Environmental Impact of Upland Streams on the Okefenokee Swamp,* University of Georgia Institute of Ecology Rep. No. ERC 06-81, Athens, GA, 1981.
304. **Day, J. W., Jr., Butler, T. J., and Connor, W. H.,** Productivity and nutrient export studies in a cypress swamp and lake system in Louisiana, in *Estuarine Processes,* Vol. 2, Wiley, M., Ed., Academic Press, New York, 1976, 255.
305. **Lowrance, R., Todd, R., Fail, J., Jr., Hendrickson, O., Jr., Leonard, R., and Asmussen, L.,** Riparian forests as nutrient filters in agricultural watersheds, *BioScience,* 34, 374, 1984.
306. **Wharton, C. H. and Hopkins, H. P., Jr.,** *In situ Evaluation of the Filtering Function of a Piedmont Creek Swamp,* Environmental Resources Center, Georgia Institute of Technology, Atlanta, GA, Rep. ERC 02-80, National Technical Information Service, Springfield, VA, PB81-142234, 1980.
307. **Knight, R. L., McKim, T. W., and Kohl, H. R.,** Performance of a natural wetland treatment system for wastewater management, *J. Water Pollut. Control Fed.,* 59, 746, 1987.
308. **Velga, A. and Ewel, K. C.,** Wastewater effects on a waterhyacinth marsh and adjacent impoundment, *Environ. Manage.,* 5, 537, 1981.
309. **Knight, R. L. and Ferda, K. A.,** Performance of the Boggy Gut wetland treatment system, Hilton Head, South Carolina, in *Wetlands: Concerns and Successes,* American Water Resources Association, Bethesda, MD, 1989, 439.
310. **Kemp, G. P., Conner, W. H., and Day, J. W., Jr.,** Effects of flooding on decomposition and nutrient cycling in a Louisiana swamp forest, *Wetlands,* 5, 35, 1985.