**DIVISION S-4—SOIL FERTILITY & PLANT NUTRITION**

**Distribution of Soil and Plant Nutrients along a Trophic Gradient in the Florida Everglades**

M. S. Koch* and K. R. Reddy

**ABSTRACT**

Historically, atmospheric precipitation has been the primary source of N and P to the Florida Everglades. Alterations to the natural hydrology, surface water runoff from agricultural lands, and controlled releases from Lake Okeechobee have increased nutrient loading to the Everglades. A nutrient front encompassing approximately 8000 ha has developed in a northern Everglades marsh, Water Conservation Area 2A (WCA-2A; 44 684 ha), during the last three decades from surface water P and N loading, in addition to atmospheric inputs. Soil cores (0-60 cm) and plant tissue were collected from sawgrass, *Cladium jamaicense* Crantz, and cattail, *Typha domingensis* Pers., stands at a distance of 1.6, 5.6, and 9.3 km south of major surface water inflows in WCA-2A: Site N (northern), Site C (central), and Site S (southern), respectively. Although N loading was approximately 10-fold greater at Site N compared with Sites C and S, no significant difference in total N was found between sites at any soil depth. In contrast, P accumulated threefold in soils at Site N compared with Site S (P < 0.05). Organic P accounted for approximately 79% of the total P. Acid-extractable inorganic P (HCl-P), as an indicator of Ca-bound P, accounted for 80% of the inorganic P and was significantly correlated to dissolved P concentrations of the soil pore water (r = 0.89). Alkali-extractable inorganic P (NaOH-P), as an indicator of the Fe- and Al-bound P, comprised 20% of the total inorganic P. High pH values (>8.0) were measured from pore water associated with benthic algal mats. Interstitial P concentrations were 2 to 3 orders of magnitude higher at Site N (>1000 μg L⁻¹) than at Site S (<4 μg L⁻¹) and plant tissue N/P ratios at Site N and C were lower, 11:1 compared with 40:1 at Site S. These data suggest P may be an important nutrient limiting primary productivity in the Everglades and that Ca-P precipitation, catalyzed by algal photosynthesis, may be an important mechanism for soil P assimilation.

The Florida Everglades historically comprised approximately 1 million ha (Davis, 1943), and today represents the largest and most important freshwater subtropical peatland in North America. This ecosystem provides habitat for a high diversity of species including large populations of wading birds, and several threatened and endangered species: wood storks, snail kites, bald eagles, Florida panthers, and American crocodiles.

The Everglades is unique when compared with other extensive wetland systems of the southern USA due to its evolution from the accumulation of organic matter within a limestone depression (Davis, 1943; Gleason et al., 1984). This hydrological setting led to a lack of nutrient inputs from mineral sediment deposition, except for infrequent sheet flooding in the upper glades from Lake Okeechobee (Parker, 1974) and marine inputs in the southern regions. Thus, historically, the major source of nutrient loading to the Everglades has been in the form of atmospheric precipitation (Parker, 1974; Waller, 1975).

Low nutrient content, particularly P, in the Everglades peats support this hypothesis (Parsons, 1972; Gleason et al., 1984). Nutrient limitation has been implicated as a primary factor, in addition to hydrologic conditions, controlling the persistence of the endemic Everglades flora (Steward and Ornes, 1975; Davis, 1991). Another important ecological factor, fire, has been reported to contribute to the internal recycling of limited nutrients (Steward and Ornes, 1975) and influences vegetation community structure (Forthman, 1973; Hofstetter, 1984), an ecological strategy known to sustain high productivity of an otherwise nutrient-limited ecosystem.

Peatlands that have evolved from organic matter accumulation driven primarily by atmospheric precipitation (ombrotrophic) are characteristically nutrient poor (Pollet, 1972; Moore and Bellamy, 1974). The breadth of our understanding of nutrient cycling in these ombrotrophic peatlands is primarily based on studies from temperate regions (Pollet, 1972; Moore and Bellamy, 1974; Richardson et al., 1978). The subtropical Everglades differ from temperate peatlands in several aspects that significantly affect nutrient cycling and ecosystem productivity: (i) the majority of areas are neutral or alkaline due to peat accumulation over a limestone bedrock, with the exception of the Loxahatchee Wildlife Refuge (WCA-1) in the northern Everglades, which is characterized as acidic (Swift and Nicholas, 1987); (ii) temperatures are mild due to the subtropical environment, which would support higher rates of microbial activity; and (iii) soils are subject to periodic oxidation due to droughts and fires. There have been very few investigations on nutrient cycling in the Florida Everglades; however, available data support the hypothesis that the Everglades are nutrient limited (Steward and Ornes 1975; Swift and Nicholas, 1987; Davis, 1991).

Our objectives were to determine (i) the inorganic and organic pools of P and N in the northern Everglades peats (WCA-2A), (ii) the N and P storage in

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M.S. Koch, South Florida Water Management District, Division of Everglades Systems Research, P.O. Box 24680, West Palm Beach, FL 33416; and K.R. Reddy, Soil and Water Science Dep., Institute of Food and Agricultural Sciences, Univ. of Florida, Gainesville, FL 32611. Joint contribution of the South Florida Water Management District and the Univ. of Florida, Florida Agric. Exp. Sta. Journal Series no. R-02208. Received 23 July 1991. *Corresponding author.


Abbreviations: P<sub>n</sub>, inorganic P; P<sub>o</sub>, organic P; WCA, Water Conservation Area; ENP, Everglades National Park.
soils and plants along a range of nutrient loadings from levels approaching historical values to a 10-fold increase, and (iii) the importance of labile and non-labile pools of P as related to potential P assimilation and storage mechanisms. In addition, N/P ratios in plant tissue and interstitial pore water P and NH$_4^+$ concentrations were utilized as indicators of soil nutrient bioavailability.

**MATERIALS AND METHODS**

**Study Site**

Historically, the Florida Everglades was a contiguous wetland system but is presently fragmented into several isolated hydrological units: Water Conservation Area 1 (WCA-1; 58 900 ha), Water Conservation Area 2 (WCA-2; 54 700 ha), Water Conservation Area 3 (WCA-3; 237 000 ha), and Everglades National Park (ENP; 149 400 ha; Fig. 1). During Everglades predrainage condition, water flowed north to south by continuous sheet flow (Parker, 1974). At present, however, water flows north to south from one hydrologic unit to the next through 2400 km of canals, 18 major pump stations, and hundreds of water control structures, which are regulated by predefined water schedules.

Our research focused on WCA-2A in the northern Everglades (Fig. 1). A northeastern section (=8000 ha) of WCA-2A (44 684 ha) has been receiving surface water from drainage of agricultural lands and Lake Okeechobee for the past three decades. Phosphorus and N loads from an average 116.8 cm yr$^{-1}$ precipitation and an average total P concentration of 0.049 mg L$^{-1}$ over this 8000-ha region of WCA-2A input = 4.6 $\times$ 10$^3$ kg P yr$^{-1}$ and =1.0 $\times$ 10$^8$ kg N yr$^{-1}$ (South Florida Water Management District, 1991). An additional loading through inflow structures contributes =5.4 $\times$ 10$^3$ kg P yr$^{-1}$ and =1.6 $\times$ 10$^8$ kg N yr$^{-1}$, thus increasing the N and P loads approximately 10-fold. Mean annual loads are based on biweekly water quality samples and daily flows taken from inflow structures just north of the study sites (S-10A, C, and D) in WCA-2A for a period of record from 1979 to 1988 (South Florida Water Management District, 1991).

Sampling sites in WCA-2A for our study were located along a surface water nutrient gradient identified from biweekly surface water samples taken south of S-10 structures from 1986 to 1991 (n = 84; Fig. 2). Along this surface water nutrient gradient, shifts in microalgae have been reported (Swift and Nicholas, 1987) and macrophyte species dominance from $C.$ jamaicense (sawgrass) prairie and open water slough to extensive monotypic stands of $T.$ domingensis and mixed communities dominated by $T.$ domingensis and $C.$ jamaicense (Fig. 1). Three sites along this surface water nutrient gradient were chosen within $T.$ domingensis and $C.$ jamaicense stands: (i) Site N, a northern site 1.4 km south of the S-10 structures, (ii) Site C, a central site 5.4 km south of the structures at the leading edge of the nutrient front, and (iii) Site S, a southern control site 9.3 km south of the inflow structures (Fig. 1).

**Soil Sampling and Analysis**

Intact soil cores (6.4 by 60 cm; n = 2) were obtained in January 1990 from each of the three sites using a 1-m Plexiglas corer, which was immediately stoppered for transport to the laboratory. Soil cores were sectioned in the laboratory by 5-cm increments down to 40 cm in a glove bag under a N$_2$ atmosphere to prevent oxidation of reduced species. Sectioned soil cores were transferred into 240-mL centrifuge tubes, also under N$_2$ atmosphere, and wet weights were determined. A subsample was taken to determine dry weight and bulk densities.

Interstitial water from the soil was removed by centrifugation of a known amount of soil at 4066 $\times$ g. The soil pore water was analyzed for pH and soluble P (0.45 $\mu$m), defined as the P that reacts to form a phosphomolybdate complex (U.S. Environmental Protection Agency, 1979, Method 365.1). After the pore water was removed, the residual soil was sequentially extracted for various P forms.

![Fig. 1. The Everglades ecosystem is depicted in the upper illustration, which includes: Water Conservation Areas 1, 2, and 3, and Everglades National Park. The study area, WCA-2A, is shown with the three sampling sites: a northern site (Site N), a central site (Site C), and a southern control site (Site S). The three shaded areas in WCA-2A represent three major vegetation classes digitized from a 1987 supervised spot satellite image.](image)

**Fig. 1.** The Everglades ecosystem is depicted in the upper illustration, which includes: Water Conservation Areas 1, 2, and 3, and Everglades National Park. The study area, WCA-2A, is shown with the three sampling sites: a northern site (Site N), a central site (Site C), and a southern control site (Site S). The three shaded areas in WCA-2A represent three major vegetation classes digitized from a 1987 supervised spot satellite image.

![Fig. 2. Mean annual surface water total P (TP) concentrations as a function of distance from water inflow structure S-10C (Fig. 1). Mean of biweekly samples from 1986 to 1991 are given (n = 84) with standard errors.](image)

**Fig. 2.** Mean annual surface water total P (TP) concentrations as a function of distance from water inflow structure S-10C (Fig. 1). Mean of biweekly samples from 1986 to 1991 are given (n = 84) with standard errors.
according to a modified soil P fractionation scheme (Hieljes and Lijklema, 1980). This extraction procedure groups soil P into: (i) labile P (water soluble and KCl extractable), (ii) NaOH-P (Fe- and Al-bound P), (iii) HCl-P (Ca-bound P), (iv) NaOH-P; (alkali-extractable organic P), and (v) residual organic P.

After centrifugation, a known amount of soil (1:100 w/v) was transferred into 50-mL centrifuge tubes and treated with 1 M KCl (1:100 w/v). After 2 h of equilibration while shaking, the soil suspensions were centrifuged to 4066 x g for 15 min. The supernatant solutions were filtered through 0.45-μm filters and the filtrates were acidified to pH 2. The solutions were analyzed for soluble P and NH\(_4\) (U.S. Environmental Protection Agency, 1979, Methods 365.1 and 350.1). Residual soil was treated with 0.1 M NaOH (1:100 w/v), and the suspensions were allowed to equilibrate under continuous shaking for a period of 16 h, followed by centrifugation at 4066 x g. The filtered solutions were analyzed for soluble and total P. Inorganic P in the filtered solution indicated the amount of Fe- and Al-bound P (NaOH-P), while the difference in total P and soluble P of the NaOH extract accounted for alkali-extractable organic P (NaOH-extractable P). A NaOH extraction, the residual soil was treated with 0.5 M HCl and the suspensions were allowed to equilibrate for 24 h on a mechanical shaker. The soil suspensions were centrifuged and the filtrate analyzed for soluble P, which represented the Ca-bound P (HCl-P). Air-dried samples were digested using the Kjeldahl digestion procedure described by Brenner and Mulvaney (1982). The digested solutions were analyzed for total N and total P using an autoanalyzer (U.S. Environmental Protection Agency, 1979, Methods 351.2 and 365.4). For organic soils, Kjeldahl digestion procedure showed similar results to those measured after HNO\(_3\)–HClO\(_4\) digestion (K.R. Reddy, 1991, unpublished data). The residual P was calculated as the difference between the sum of P recovered in all extractions and the total P as determined by digestion.

**Plant Sampling and Analysis**

Three individual plants of *C. jamaicense* and *T. domin- genus* were randomly selected from each site. Above- and belowground plant materials were collected, transported back to the laboratory, and separated into live and dead leaf, belowground plant materials collected, transported back to the laboratory, and separated into live and dead leaf, stem, root, and rhizome tissue. Plant tissue was dried at 90 °C, weighed, ground, digested with H\(_2\)SO\(_4\), and analyzed for P using a Technicon Autoanalyzer II (U.S. Environmental Protection Agency, 1979, Method 365.4; Technicon/Bran-Luebbe, Elmsford, NY). Total C and N were analyzed by combustion using a 1-240 Perkin Elmer Elemental Analyzer (Perkin-Elmer Corp., Norwalk, CT).

**Interstitial and Surface Water Nutrients**

Nutrient microprofiles of the interstitial and overlying surface waters were sampled, in January 1990, utilizing Plexiglas soil pore water equilibrators (60 by 7 by 2 cm), which consisted of 30, 8-mL cells equally spaced at 1-cm intervals (Carignan, 1984). Each cell was filled with deionized water that was deoxygenated with N\(_2\) gas and covered with a 0.2-μm Nucleopore polycarbonate membrane (Nucleopore Corp., Pleasanton, CA) with a protective 1-μm Spectra mesh nylon membrane cover (Spectrum Corp., Los Angeles, CA). The entire equilibrator was then put in a storage case with deoxygenated deionized water and bubbled with N\(_2\) for 12 h. Equilibrators were transported to the field in the storage containers and quickly transferred to the sediment, leaving approximately 20 cells in the water column. One equilibrator was placed in a stand of *T. domin-genus* and one in a stand of *C. jamaicense* at each of the three sites. Cells were allowed to equilibrate with the interstitial and surface waters for 14 d, after which they were retrieved and immediately sampled in the field. Water was sampled at 2-cm intervals with a syringe and acidified (2 drops 12% H\(_2\)SO\(_4\)) to pH 2.0 in a 30-mL scintillation vial. Water samples were analyzed using a Technicon Auto Analyzer II for soluble P (U.S. Environmental Protection Agency, 1979, Method 365.1) and NH\(_4\) (U.S. Environmental Protection Agency, 1979, Method 350.1). The last 5 mL of sample was stored in the syringe stuck in a rubber stopper to prevent degassing for pH determinations with a Jenco pH/mV/Temp meter (Model 6009, Jenco electronics Corp., San Diego, CA) within 24 h of returning to the laboratory.

**Flux Calculations**

The NH\(_4\) and soluble P concentration profiles, as measured by using pore water equilibrators, were used to calculate steady-state diffusive flux using Fick's first law (Berner, 1980):

\[
F_i = -\frac{\partial D_i}{\partial z} \frac{dc}{dz} \times 86400
\]

where \(F_i\) is the flux of the dissolved species \(i\) per unit area and time, \(c_i\) = concentration of the species \(i\) in the pore water, \(z = \) depth; \(D_i =\) diffusion coefficient of species \(i\) in the electrolyte solution; \(\Theta =\) porosity of the soil (volume of water/ volume of soil at 0–5 cm); \(\Theta =\) tortuosity factor, and 86 400 is the factor to convert seconds to days. The concentration gradient \(dc/dz\) was calculated by the least square fit of the data to a linear regression between depth (4 to 4 cm). Since the bulk density of Everglades peat at sampling sites was low, ranging between 0.07 and 0.08 g cm\(^{-3}\) in the upper 5 cm, the effect of tortuosity on diffusion of dissolved species was assumed to be minimal and close to unity (Moore et al., 1991). Diffusion coefficients of 7.9 \times 10\(^{-6}\) and 19.8 \times 10\(^{-6}\) cm\(^2\) s\(^{-1}\) were used for soluble P and NH\(_4\), respectively, based on values from Li and Gregory (1974).

**Statistical Analysis**

Analysis of variance (proc GLM and ANOVA), regression (proc REG), means and standard errors (proc MEANS), and Duncan's mean range testing were determined utilizing the SAS statistical program (SAS Institute, 1988). All means are significantly different at the \(P < 0.05\) level unless otherwise stated.

**RESULTS**

**Soil Total Phosphorus and Nitrogen**

Total P (TP) decreased with soil depth (\(D\)) logarithmically at Site N [\(TP = 2.89 - 1.73 \log(D)\); \(R^2 = 0.90\)] and Site C [\(TP = 1.60 - 1.10 \log(D)\); \(R^2 = 0.90\)], but a linear decrease with depth was found at Site S [\(TP = 0.59 - 0.01(D)\); \(R^2 = 0.98\); Fig. 3]. Total P concentrations at Site N were similar to those from Site C in the upper 5 cm of the soil profile, but were three times higher than levels found at Site S (Fig. 3). Below the upper soil profile at 0 to 5 cm, total P levels at Site C were similar to Site S, but both were lower than those at Site N. Below 20 cm, however, no significant differences were found in total P between any of the three sites. In contrast to P, total soil N concentration in the soil was not significantly different between the three sites at any depth (Fig. 3). In addition, no significant trends were found for total N with depth at any of the three sites.

Bulk densities are low in Everglades peat, ranging from 0.05 (WCA-1) to 0.08 g cm\(^{-3}\) (WCA-2A), com-
Total Phosphorus (g kg$^{-1}$) 40.0
Total Nitrogen (g kg$^{-1}$)

Fig. 3. Total soil P and N concentrations with depth from Sites N (northern), C (central), and S (southern). Means are given with standard errors (n = 2).

In the past, soil N and P concentrations were expressed on a soil volume basis in Fig. 4. Total P storage in the upper 30 cm was 101 kg ha$^{-1}$ at Sites C and S and 229 kg ha$^{-1}$ at Site N.

Forms of Soil Phosphorus and Nitrogen

Although total P concentrations were significantly different in the upper soil profile between sites, the ratios of $P_0$ (0.67, 0.74, 0.78), HCl-P$_i$ (0.25, 0.20, 0.13), and NaOH-P$_i$ (0.05, 0.04, 0.08) to total P were similar (0-30 cm) in all three sites N, C, and S, respectively (Fig. 4).

Residual organic P composed approximately 75% of the total P, while NaOH-P$_i$ composed 25 to 30% of the total P pool (0-30 cm). The NaOH-P$_i$ fraction of the total organic P was low in the upper soil profile at Site N (0-20 cm) and Site C (0-10 cm), and at all soil depths at Site S (Fig. 4). In the lower soil depths of Site N and C, however, this fraction was more important, ranging from 50 to 69% of the total organic P.

Total inorganic P accounted for 30, 24, and 22% of the total P with 84, 83, and 62% as HCl-P$_i$ (Ca-bound P) at Sites N, C, and S, respectively. Thus, inorganic P storage as HCl-P$_i$ fraction was five times higher than NaOH-P$_i$ fraction at Sites N and C. At Site S, P in the HCl-P$_i$ fraction was only twice NaOH-P$_i$. The NaOH-P$_i$ may have also been overestimated due to the solubilization of humic and fulvic acids identified by colored solutions resulting from NaOH extractions. Phosphorus storage in the NaOH-P$_i$ fraction was similar at all three sites, 23, 15, and 17 $\mu$g cm$^{-3}$, but HCl-P$_i$ decreased along the trophic gradient from 159 $\mu$g cm$^{-3}$ at Site N to 40 and 29 $\mu$g cm$^{-3}$ at Sites C and S.

Water-soluble and exchangeable (KCl-extractable) P represented a small fraction, 3, 2, and <1%, of the total P for Sites N, C, and S, respectively. Similarly, water-soluble and exchangeable NH$_4^+$ were <1% of the total N stored, ranging from 0.33 to 1.81 and 4.95 to 2.69 $\mu$g N cm$^{-3}$, respectively. Although no significant differences were found in soil total N between sites, water-soluble and exchangeable NH$_4^+$ were six and two times greater at Site N than at Sites C and S.

Interstitial–Surface Water Analyses

Soluble P concentrations were one to more than two orders of magnitude higher in the surface water at Site N than at Sites C and S (Fig. 5). Although surface water soluble P levels were at the limit of detection, <0.004 mg L$^{-1}$ at Site C, P maxima of 1.20 and 0.27 mg L$^{-1}$ were found just below the soil–water interface within the detrital mats of T. domingensis and C. jamaicense, respectively (Fig. 5). In contrast to the other two sites, interstitial soluble P concentrations at Site S were low throughout the entire sediment profile (0-50 cm), ranging from 0.030 to 0.069 mg L$^{-1}$ in stands of T. domingensis and 0.006 to <0.004 mg L$^{-1}$ in stands of C. jamaicense.

Ammonium levels were low in the surface water compared with soil pore water concentrations (Fig. 5). Pore water NH$_4^+$ concentrations were 2.5 to 3.5 times higher at Site N than Sites C or S. Ammonium concentrations increased with depth at Site N but remained low through the flocculent layer of T. domingensis. At Site C, consistent with the P concentrations, NH$_4^+$ levels in pore water associated with T. domingensis peaked just below the sediment–water interface and decreased with depth. The interstitial water profiles of NH$_4^+$ from Site S showed no peak at the sediment surface, compared with the other sites, and increased with depth (Fig. 5).

Values of pH ranged from 7.3 to 8.7 in the overlying surface water with the highest values associated with benthic algae at Sites N and S (Fig. 6). Throughout the sediment profile, pH values were approximately or slightly higher than neutrality.

Nutrient Diffusive Flux

At all three sites, distinct gradients in the pore water soluble P and NH$_4^+$ profiles were found at the soil–water interface and were used as a first-order approximation of the nutrient flux rates (Table 1). At Site N, soluble P and NH$_4^+$ were in equilibrium at the soil–water interface in the T. domingensis stand, thus no
significant flux was detected. Below the *C. jamaicense* stand, soluble P had a negative flux into the flocculent detrital layer. Both soluble P and NH$_4^+$ fluxes were an order of magnitude higher at Site C than at Site S. Fluxes tended to be higher from *T. domingensis* detrital material than from *C. jamaicense* at Sites C and S.

**Plant Tissue Nitrogen and Phosphorus**

Phosphorus content in live leaf tissue was highest at Site N and lowest at Site S, with *T. domingensis* having consistently higher P levels than *C. jamaicense* (Fig. 7). Conversely, N concentrations were not significantly different at the three sites or between the two species, although *T. domingensis* tended to show higher N content in the live leaf tissue at Sites N and C than at Site S (data not shown). Nitrogen to P ratios of live leaf and root tissue were similar at each site for *T. domingensis*. In contrast, an average N/P ratio of 45:1 was found in the leaf tissue of *C. jamaicense* at Site S.

Average N/P ratios of all *C. jamaicense* tissue ranged from 3:1 to 20:1 (average = 9:1) at Site N, compared with ratios of 37:1 to 132:1 (average = 63:1) at Site S. This same comparison for *T. domingensis* depicts a smaller difference, twofold vs. sevenfold, with N/P ratios ranging from 1:1 to 12:1 (average = 6:1) at Site N, compared with 6:1 to 18:1 (average = 10:1) at Site S.

**DISCUSSION**

Although N is the most important macronutrient controlling macrophyte growth in coastal wetlands (Valiela and Teal, 1974), inland bogs and fens are reported to be limited by P or K rather than by N (Goodman and Perkins, 1968; Heilman, 1968). Total soil N levels and interstitial NH$_4^+$ concentrations in the Florida Everglades (Fig. 3 and 5) were high compared with other ombrotrophic bogs or fens (Moore and Bel-lamy, 1974). Total N storage in the upper 30 cm of WCA-2A was 6605 kg ha$^{-1}$, which is within the range reported for rich fens of North America (6830 kg ha$^{-1}$; Richardson et al., 1978), minerotrophic fens of Newfound-land (3100–8910 kg ha$^{-1}$; Pollet, 1972), but greater than floating fens of the Netherlands (3350 kg ha$^{-1}$; Verhoeven, 1986). Steward and Ornes (1975) reported soil N values in WCA-3 as high as 15 792 kg ha$^{-1}$; however, bulk densities were not given and values may have been overestimated. These maximum storage values reported by Steward and Ornes (1975) are similar to levels given for the tropical *Pavurus* swamps of Uganda (12 180 kg ha$^{-1}$; Gaudet, 1976). Nitrogen fixation by *Scytonema* spp. and other blue-green algae, which are abundant in the Everglades (Swift, 1984), may contribute to these high soil N levels. Bacterial N$_2$ fixation, shown to contribute a major input of N in minerotrophic peatlands (Verhoeven, 1986), may also be an important N source in the Everglades.

Despite surface water N loading in the northeastern area of WCA-2A, in addition to atmospheric inputs, no significant accumulation of soil N was detected along the surface water nutrient gradient (Fig. 3). Thus, northern Everglades soils under nutrient enrichment are acting as a transient sink for N, probably through high rates of denitrification, an effective N removal mechanism in wetland soils (Patrick and Tusneem, 1972; Reddy et al., 1989). In contrast, denitrification of added NO$_3^-$ (1.4 mg N L$^{-1}$) was only 10 to 34% complete in soils from ENP (Gordon et al., 1986). Addition of 2.8 mg NO$_3^-$ N L$^{-1}$ to ENP soils increased denitrification rates, resulting in an 80% NO$_3^-$ reduction efficiency. Surface water NO$_3^-$ concentrations flowing into the northern Everglades are more than two orders of magnitude (1–2 mg N L$^{-1}$) higher than at ENP (0.01 mg N L$^{-1}$; Belanger et al., 1989). Thus, NO$_3^-$ availability and other factors associated with unenriched Everglades peat may account for low denitrification potentials in ENP soils.

Phosphorus, a more persistent element in wetlands compared with N, accumulated in the northeastern region of WCA-2A (~8000 ha) due to surface water P loads. Although total P accumulation was greater at Site N, similar ratios of NaOH-P$_i$, NaOH-P$_o$, and HCl-P$_i$ to total P were found at all three sites (Fig. 4). Therefore, mechanisms controlling P assimilation and storage may be similar, even under variable P
loading rates. The largest proportion of total P was stored in the organic P form at all three sites (Fig. 4). These results suggest that a significant amount of P from surface waters can be cycled into plant and detrital material and the associated microflora. Alkali-extractable organic P accounted for approximately 25 to 50% of the total P, which includes microbial biomass P and some fraction of fulvic and humic acid bound P (Bowman and Cole, 1978). Davis (1991) found P assimilation of leaf detritus increased dramatically after being colonized by microbes during 2 yr of decomposition in the Everglades, further emphasizing the importance of the microbial P pool. The negative diffusive flux across the soil–water interface at Site N also suggests that biological uptake of P occurs from the surface water despite high soil soluble P concentrations. This phenomenon was also observed in a study by Davis (1982), where approximately three times more $^{32}$P amended to the surface water was recovered in the surface detritus at Site N than Site S (same sites as this study).

The importance of P storage in organic matter from temperate freshwater peatlands has been well documented (Moore and Bellamy, 1974; Verhoeven et al., 1990). However, very little information exists on the contribution of HCl–P, in freshwater peatlands, particularly in tropical and subtropical regions. The HCl–P fraction was found to represent a major proportion of the inorganic fraction, 62 to 84% and a significant relationship was found between P loading associated with mineral-rich agricultural drainage high in CaCO₃ (Gleason, 1974) and Ca–P storage.

These findings have very significant implications
on the processes controlling inorganic P cycling in the Everglades. If Ca precipitation is a primary mechanism for inorganic P storage, changes in pH that modify the chemical equilibria and distribution of carbonate species in solution could shift the solubility or precipitation of inorganic P. Changes in the H$^+$ ion activity in microenvironments by benthic algal photosynthesis in hard-water alkaline lakes have been shown to induce phosphate–carbonate precipitation (Otsuki and Wetzel, 1972). Wetzel (1983) reported the rate of CaCO$_3$ precipitation is slow due to the large amounts of inorganic C that can exist as carbonate and CaCO$_3$ in metastable conditions, unless catalyzed metabolically by photosynthesis. Gleason (1972) found daylight disappearances of CaCO$_3$ and pH changes in microenvironments of algal mats in the Everglades, which would cause higher calcite supersaturation than in overlying waters. An increase in available P would stimulate algal growth and production (Swift and Nicholas, 1987), lower the partial pressure of CO$_2$, and promote Ca–P precipitation (Otsuki and Wetzel, 1972).

In our study, 79% of the HCl–P$_i$ was explained by P availability in the soil pore water. The NaOH–P$_i$ was also highly correlated ($r = 0.87$) with HCl–P$_i$, suggesting Ca-phosphate precipitation was biologically mediated.

Under ambient low-nutrient conditions, Everglades benthic algae have been shown to possess high N/P ratios averaging $>$50:1, compared with 9:1 in nutrient-enriched areas (Swift and Nicholas, 1987). *Cladium jamaicense* leaf and root tissue N/P ratios were $>$40:1 at Site S. Pore water soluble P concentrations were also $<4 \mu$g L$^{-1}$ in the soil profile up to 50 cm in depth. These data lend evidence to the supposition that P may be limiting plant productivity at this site (Fig. 5 and 7). *Typha domingensis* tissue N/P ratios were consistent at all three sites (7:1–15:1; Fig. 7), similar to those measured in common cattail, *Typha latifolia* L. (5:1–11:1) at 30 sites within a wide range of environmental conditions (Boyd and Hess, 1970). *Typha domingensis* at Site S and other regions of the Everglades are primarily encircling alligator holes, which have been identified as nutrient rich due to their role as a refuge concentrating animals and their associated wastes during the dry season (Freiberger, 1972). Therefore, changes in the internal cycling of stored nutrients increasing the availability of pore water P would increase the competitive advantage of *T. domingensis* in the Everglades, which appears to have a higher requirement for P than does *C. jamaicense*.

### Table 1. Soluble P and NH$_4^+$ flux at the soil–water interface based on concentration gradients.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species†</th>
<th>Porosity</th>
<th>Soluble P (µg L$^{-1}$)</th>
<th>NH$_4^+$ (µg L$^{-1}$)</th>
<th>$\text{Gradient} \frac{(dP/dz)}{f}$</th>
<th>Diffusive flux (mg m$^{-2}$ d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern</td>
<td>T</td>
<td>0.89</td>
<td>NS§</td>
<td>NS</td>
<td>$-0.183$</td>
<td>$-0.71$</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.94</td>
<td>+0.119</td>
<td>NS</td>
<td>$0.97$</td>
<td>$+0.72$</td>
</tr>
<tr>
<td>Central</td>
<td>T</td>
<td>0.82</td>
<td>$-0.158$</td>
<td>$-0.398$</td>
<td>$0.90$</td>
<td>$+0.24$</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.99</td>
<td>$-0.036$</td>
<td>$-0.136$</td>
<td>$0.92$</td>
<td>$+2.30$</td>
</tr>
<tr>
<td>Southern</td>
<td>T</td>
<td>0.80</td>
<td>$-0.004$</td>
<td>$-0.038$</td>
<td>$0.81$</td>
<td>$+0.02$</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.73</td>
<td>NS</td>
<td>$-0.015$</td>
<td>$0.84$</td>
<td>$+0.14$</td>
</tr>
</tbody>
</table>

† T = *Typha domingensis*, C = *Cladium jamaicense*.
‡ Profile from +4 to −4 cm.
§ NS = not significant.

**Fig. 7.** Tissue P concentration and N/P ratios from live leaf and root tissue of *Typha domingensis* and *Cladium jamaicense* at Sites N (northern), C (central), and S (southern) ($n = 5$; means given with standard errors).
terial. In addition, Ca–P precipitation catalyzed by benthic algal photosynthesis may be an important mechanism for inorganic P storage in the Everglades. Pore-water soluble P, possibly regenerated by recycling of internally stored P, is more than two orders of magnitude greater at Site N under enrichment than at southern control sites. This availability of soil P could shift the competitive advantage of Everglades flora, which have adapted to a low-nutrient (particularly P) environment. However, further mechanistic studies are necessary to corroborate many of the above hypotheses generated from this investigation.

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REFERENCES


