# Forms and Amounts of Soil Nitrogen and Phosphorus Across a Longleaf Pine–Depressional Wetland Landscape

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## ABSTRACT

**Forms and amounts of soil N and P were measured across transects from freshwater depressional wetlands into longleaf pine–wiregrass forests of southwestern Georgia to evaluate changes in labile vs. recalcitrant N and P and C:N:P ratios across drainage gradients. Plant-available $NO_3^-$–N (3.7 $\mu$g cm$^{-3}$) and organic N (2000 $\mu$g cm$^{-3}$) were significantly greater in wetland than upland soils ($NO_3$–N = 0.03 $\mu$g cm$^{-3}$, organic N = 890 $\mu$g cm$^{-3}$) and C:N increased from wetlands (17:1) into uplands (43:1). Forms and amounts of P were not as strongly related to landscape position as N. Labile organic P ($P_o$, 2.6 $\mu$g cm$^{-3}$) was significantly greater in wetland than upland soils (0.88 $\mu$g cm$^{-3}$). Recalcitrant organic compounds accounted for 95 to 97% of the N and 50 to 82% of the P stored in wetland and upland soils. Wetland soils stored a disproportionately large share of N as compared with upland soils even though soil organic matter (C) content was uniform across the landscape. Landscape position (drainage, degree of wetness) is an important determinant of nutrient retention in sandy soils of the southeastern coastal plain. Periodic waterlogging favors sequestration of biological (organic) forms of N and P with proportionally greater storage of N relative to P. Soil waterlogging by promoting accumulation of N more than P favors a shift from N limitation in upland soils towards P limitation in wetland soils of the southeastern coastal plain.**

Drainage is an important determinant of nutrient (N, P) storage in soils. When drainage is impeded, as in wetland soils, anaerobic respiration dominates, decomposition slows, and organic matter and nutrients accumulate in soil (Ponnamperuma, 1972; Craft, 2001). Upland soils, in contrast, usually are well drained, most litter and organic matter decompose aerobically to $CO_2$ and, as a result, soil organic matter is low as compared with wetlands (Schlesinger, 1997). In terrestrial ecosystems, plant growth is often limited by low N availability (Hunt et al., 1988; Vitousek and Howarth, 1991; Schelsinger, 1997) caused, in part, by limited storage in soil and litter. In freshwater wetlands where organic matter and N accumulate in soil, plant growth often is limited by P (Brown, 1981; Bridgham et al., 1996; Chiang et al., 2000) or co-limited by N and P (Shaver and Chapin, 1995; Shaver et al., 1998).

Because the source (N vs. P) of nutrient limitation often differs between uplands and wetlands, their interface may represent a transition zone as N limitation of upland ecosystems shifts to P limitation or co-limitation with N in freshwater wetlands. Nitrogen and P cycling may be especially dynamic at the boundary between uplands and wetlands because episodic inundation results in alternating cycles of oxidation and reduction. When soils are flooded or inundated, decomposition slows so that organic matter and organic forms of N and P accumulate (Ponnamperuma, 1972; Craft, 1997). During dry down, aerobic soil conditions prevail and organic N compounds are mineralized (Bridgham et al., 1998), releasing inorganic nutrients ($NH_4^+$, $NO_3^-$) that can be assimilated by plants. In contrast to N, P availability usually increases in response to inundation as Fe-bound P is chemically reduced and $Fe^{2+}$ and soluble phosphate are released into the soil solution (Ponnamperuma, 1972; Bridgham et al., 1998; Vepraskas and Faulkner, 2001). Although much research has been devoted to understanding nutrient dynamics of discrete terrestrial and wetland ecosystems, few studies evaluated N and P storage and partitioning across drainage gradients from wetlands to uplands (Axt and Walbridge, 1999; Darke and Walbridge, 2000).

We measured forms and amounts of N and P along transects across three depressional wetland soils (Paleaquults) into terrestrial forest soils (Kandiudults) to quantify changes in bioavailable and recalcitrant N and P across a drainage gradient. We hypothesized that soil organic matter (organic C), bioavailable N, and recalcitrant N decreased from wetlands to uplands because periodic inundation in wetlands slows the rate of decomposition and enhances organic matter and N accumulation. We expected biological (organic) P to be the dominant fraction in wetland soils, because of higher organic matter content, whereas geochemical P (Fe and Al-P) would be the largest fraction in upland soils. Carbon:N:P ratios were used to infer patterns and intensity of N vs. P limitation along the drainage gradient.

## MATERIALS AND METHODS

### Site Description

Forms and amounts of soil N and P were measured at the Joseph W. Jones Ecological Research Center (Ichauway, Inc.) (31°13′ N, 84°29′ W) in Baker County, Southwest Georgia, USA. Ichauway is a 29 000-ha coastal plain reserve consisting of longleaf pine–wiregrass forest interspersed with freshwater depressional wetlands. Since the 1930s, the terrestrial landscape has been managed using prescribed fire every 1 to 3 yr and other tools to maintain longleaf pine–wiregrass vegetation against encroachment by hardwood vegetation. The geology of the study site, in the Dougherty Plain, consists of marine sands overlying fractured Ocala limestone, with resultant karst topography, numerous shallow depressions, and limited surface drainage. The soils of our study sites are classified as fine, kaolinitic, thermic Typic Paleaquults (Grady series) in the wetlands and loamy, kaolinitic, thermic Arenic Kandiudults

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**Abbreviations:** $P_i$, inorganic phosphorus; $P_o$, organic phosphorus.

(Wagram series) and fine-loamy, kaolinitic, thermic Plinthic Kandiudults (Tifton series) in the adjacent uplands (USDA, 1986). Ecotone soils are classified as fine, kaolinitic, thermic Aquic Paleudults (Duplin series).

Depressional wetland vegetation consisted of pond cypress {*Taxodium ascendens* Brongn. [= *T. distichum* var. *imbricarium* (Nutt.) H.B. Croom]}, with a well developed herbaceous layer of sedges (*Rhynchospora* spp.) and wetland grasses *Panicum hemitomon* Schult., *P. hians* Elliott, and *P. wrightianum* Scribner.) (Kirkman et al., 1998, 2000). Longleaf pine (*Pinus palustris* Mill.) was the dominant tree in the uplands, with a ground cover consisting of wiregrass (*Aristida stricta* Michx.) and other terrestrial grasses (*Andropogon virginicus* L., *Panicum angustifolia* Ell.) (Kirkman et al., 1998). Ecotones had an open canopy of slash pine (*Pinus elliottii* Engelm.) with both wetland and upland herbaceous species. There is no record of agricultural cultivation (e.g., tillage) of our wetland, ecotone, and upland soils during the past 70 yr, nor is there any evidence that they were tilled in the past.

Soil samples were collected in March 1998 from three replicate sites, each consisting of a freshwater depressional wetland, an ecotone area, and a longleaf pine–wiregrass upland area. The study sites exist along a gradient of decreasing water table from the depressional wetland to the upland. The depressional wetlands primarily are rainfall fed as evidenced by the absence of surface drainage as well as surface water alkalinity that is similar to rainfall rather than carbonate-rich groundwater of the underlying Floridan aquifer (Battle and Golladay, 2001). In 1998, when the samples were collected, the depressional wetlands were inundated for ≈6 mo, from December 1997 through May 1998 (Craft and Casey, 2000). At the time of sampling (March), the water table in the wetlands was 20 to 40 cm above the soil surface in the wetland interior. The water table in the ecotone was at or near the soil surface. At upland transect points, the water table was >30 cm below the surface.

## Soil Sampling and Analysis

At each site, three transects, each ≈50 m in length, were established from the wetland interior to the longleaf pine–wiregrass upland. Each transect consisted of two samples from the wetland, one from the ecotone, and two from the upland. At each transect point, soils were sampled using a 8.5-cm diameter by 30-cm deep stainless steel cylindrical soil corer. Samples were collected from two depths, 0 to 5 cm and 20 to 25 cm, and transported to the lab on ice. Samples were refrigerated at 4 °C except when being processed and analyzed. Each field-moist sample was weighed to determine bulk density, then separated into six homogenous subsamples of 20 g wet soil each (three sets for N, two for P, and one for bulk density, total organic C, and N analyses).

Nitrogen fractionation consisted of nonsequential analyses of plant-available, microbial, and organic N (Table 1). Soils were extracted with 2 *M* potassium chloride to estimate $NO_3^-$ and exchangeable (plant-available) $NH_4^+$ (Keeney and Nelson, 1982). Microbial-bound N was determined using the chloroform extraction procedure of Davidson et al. (1989) then microwave digested with potassium persulfate in a 1:1 sample:reagent ratio (modified from Cabrera and Beare, 1993). A replicate set of soils was extracted as above, but without exposure to chloroform. Microbial-bound N was calculated as the amount of N from the chloroform extraction minus the nonchloroformed soils. A 5-μg $g^{-1}$ urea solution was digested as a standard for comparison of recovery results. We obtained a 90% recovery of the urea standard with a mean of 4.5 μg $g^{-1}$ ($n = 10$).

Phosphorus fractionation consisted of sequential extraction of labile and recalcitrant forms of inorganic P ($P_i$) and $P_o$ (Hedley et al., 1982; Qualls and Richardson, 1995) (Table 1). Labile forms consist of $P_i$ and $P_o$ extracted with sodium bicarbonate (Cross and Schlesinger, 1995). Recalcitrant forms of P include mineral P (Fe, Al, Ca-P) and $P_o$ extracted with strong acids or bases (Cross and Schlesinger, 1995).

A subsample from each bicarbonate extract was microwave digested with potassium persulfate in a 1:2 sample:reagent ratio to determine amounts of easily exchangeable (labile) total P. Labile $P_o$ was calculated by subtracting labile $P_i$ from labile total P (Hedley and Stewart, 1982). A 2-μg $g^{-1}$ phytic acid solution was digested as a standard for comparison of recovery results. We obtained 89% recovery of the phytic acid standard with a mean of 1.77 μg $g^{-1}$ ($n = 9$).

A separate set of soils was exposed to chloroform, extracted with 0.5 *M* sodium bicarbonate, and digested with potassium persulfate. Microbial-bound P was calculated as the amount of phosphate from the chloroform extracted soils minus that from labile $P_o$. Following chloroform treatment, soils were extracted with 0.1 *M* NaOH followed by NaOH + sonication and analyzed for surface and occluded Al- and Fe-bound $P_i$ (Qualls and Richardson, 1995). Humic acids were precipitated from the sonicated and unsonicated NaOH extractions and analyzed for humic acid-bound $P_o$ after digestion in nitric-perchloric acid (Sommers and Nelson, 1972). Calcium-bound $P_i$ was extracted with 1 *M* HCl. The soil residue was dried at 70 °C, ground and sieved, and digested with nitric and perchloric acid to estimate residual $P_o$. All extracts were determined colorimetrically using a Lachat Flow Injection autoanalyzer (Lachat Instruments, Milwaukee, WI).

**Table 1. Operational definitions for forms of N and P extracted sequentially.**

| Operational definition | Targeted fraction |
|---|---|
| **N (nonsequential extractions):** | |
| **2 *M* KCl extraction** | **Plant available $NO_3^-$ and $NH_4^+$** |
| **0.5 *M* $K_2SO_4$ extraction + $CHCl_3$ + potassium persulfate digestion** | **Microbial-bound N** |
| **Total N less above 2 fractions** | **Organic N** |
| **Combustion in CHN analyzer** | **Total N** |
| **P (sequential extractions):** | |
| **0.5 *M* $NaHCO_3$ extraction** | **Labile (plant available) inorganic P** |
| **0.5 *M* $NaHCO_3$ extraction + K persulfate digestion** | **Labile total P** |
| **0.5 *M* $NaHCO_3$ total P less 0.5 *M* $NaHCO_3$ inorganic P** | **Labile organic P** |
| **$CHCl_3$ + 0.5 *M* $NaHCO_3$ + persulfate digestion** | **Microbial-bound P** |
| **0.1 *M* NaOH extraction** | **Surface Al- and Fe-bound inorganic P** |
| **0.1 *M* NaOH extraction + sonication** | **Occluded Al- and Fe-bound inorganic P** |
| **Residual NaOH fraction + nitric/perchloric acid digestion** | **Humic acid-bound organic P** |
| **1 *M* HCl extraction** | **Calcium-bound inorganic P** |
| **Nitric and perchloric acid digestion** | **Residual organic P** |
| **Sum of above P fractions** | **Total P** |

A final set of soils was dried at 70°C, and the oven-dried weight recorded to determine bulk density. The dried sample was sieved through a ball mill grinder with a 0.125-mm mesh diameter screen, and analyzed for total N and organic C (Perkin-Elmer 2400 CHN Analyzer). Dried subsamples also were analyzed for total P (Sommers and Nelson, 1972). Comparison of total P with summed P fractions revealed that the fractionation recovered 67 to 80% of total P.

### Statistical Analysis

Analysis of variance was used to test for differences among landscape position (wetland, ecotone, and upland) and sample depth (0–5 and 20–25 cm) (SAS Institute, 1996). Means were separated using the Ryan-Einot-Gabriel-Welsh multiple range test (SAS Institute, 1996). All tests of significance were made at $P = 0.05$.

## RESULTS AND DISCUSSION

### Soil Bulk Density, Organic Carbon, Total Nitrogen, and Phosphorus

At the time of sample collection, wetlands were inundated with surface water, ecotone soils were saturated but not inundated, and upland soils were unsaturated (Table 2). There was no difference in soil bulk density, organic C, and total P (volume basis) across the wetland to upland continuum (Table 2). There was, however, a gradient of decreasing soil N along the wetland to upland continuum as the wetland interior contained significantly more N ($P < 0.05$) than upland soils (Table 2). The observed gradient of increasing N, but not C, from the upland into the wetland was somewhat surprising because both elements are strongly correlated with soil organic matter content (Craft et al., 1991) that oftentimes is greater in wetlands than uplands. Wetland soils typically contain more organic matter and N than upland soils (Schlesinger, 1997; Axt and Walbridge, 1999; Collins and Kuehl, 2001) because anaerobic conditions caused by inundation and soil saturation slow the rate of decomposition (Craft, 2001).

Similar to other mineral soils, bulk density increased with depth and organic C, total N, and P exhibited a significant decrease with depth ($P < 0.05$) regardless of landscape position (Table 2). On a volume basis, surface soils (0–5 cm) contained 3 to 4 times more organic C than subsurface soils (20–25 cm) and total N and P were two times greater in surface vs. subsurface soils. Bulk density and nutrient content of our wetland soils were similar to values reported for cypress-savanna depressions (Craft and Casey, 2000) and other depressional wetlands such as prairie potholes (Richardson and Bigler, 1984; Arndt and Richardson, 1988; Freeland et al., 1999). Bulk density (1.09–1.64 g $\text{cm}^{-3}$) and organic C (0.5–3.4% C) of our upland soils were comparable with bulk density of never cultivated, second growth longleaf pine forest at Ichauway (1.2–1.6 g $\text{cm}^{-3}$, 1–2.5% C, respectively) (Markewitz et al., 2002). Total N content (0.03–0.10%) of our upland soils was higher and total P (18–48 μg $\text{g}^{-1}$) was lower as compared with soils of never cultivated longleaf pine forest (N = 0.02–0.06%, P = 75–125 μg $\text{g}^{-1}$) that occupy higher, drier parts of the landscape as compared with our upland sites (Markewitz et al., 2002).

### Forms of Soil Nitrogen and Phosphorus

Nearly all soil N existed in recalcitrant organic form, regardless of landscape position or sampling depth (Fig. 1). Organic N accounted for 97 to 98% of total N, a value that is comparable with 95% reported for other wetland soils (Craft et al., 1991). Microbial-bound N was the second largest fraction, accounting for 1 to 3% of total N. Plant-available (KCl-extractable) $NH_4$-N and $NO_3$-N accounted for <1% of total soil N. Like total N, organic

**Table 2. Water level, bulk density soil organic C, total N, and total P along a depressional wetlands:ecotone:upland continuum at Ichauway, in southwestern Georgia, USA. Three wetland:upland gradients were sampled, each containing three transects. Except for water levels, numbers represent mean values ±1 SE.**

| | Wetland | | Ecotone | Upland | |
|---|---|---|---|---|---|
| **Water level, cm†** | **20–40** | **10–30** | **Saturated** | **<−30** | **<−30** |
| **Bulk density, g $\text{cm}^{-3}$** | | | | | |
| **0–5 cm:** | **0.91 ± 0.07** | **1.00 ± 0.09** | **1.06 ± 0.08** | **1.09 ± 0.08** | **1.09 ± 0.09** |
| **20–25 cm:** | **1.61 ± 0.05** | **1.57 ± 0.03** | **1.53 ± 0.03** | **1.62 ± 0.06** | **1.64 ± 0.07** |
| **Organic C, mg $\text{cm}^{-3}$** | | | | | |
| **0–5 cm:** | **28.0 ± 2.3** | **24.9 ± 3.9** | **35.9 ± 5.4** | **37.5 ± 3.8** | **31.7 ± 7.2** |
| **20–25 cm:** | **6.4 ± 0.6a‡** | **6.2 ± 0.9a** | **11.0 ± 1.6a,b** | **13.3 ± 0.7b** | **8.3 ± 0.7a** |
| **Organic C, %** | | | | | |
| **0–5 cm:** | **3.1 ± 0.3** | **2.5 ± 0.4** | **3.4 ± 0.5** | **3.4 ± 0.3** | **2.9 ± 0.7** |
| **20–25 cm:** | **1.0 ± 0.04a** | **0.4 ± 0.06c** | **0.7 ± 0.1b,c** | **0.8 ± 0.04a,b** | **0.5 ± 0.04c** |
| **Total N, mg $\text{cm}^{-3}$** | | | | | |
| **0–5 cm:** | **2.06 ± 0.20a** | **1.58 ± 0.24a,b** | **1.41 ± 0.23a,b** | **1.11 ± 0.09b** | **0.86 ± 0.14b** |
| **20–25 cm:** | **0.64 ± 0.08** | **0.50 ± 0.05** | **0.49 ± 0.06** | **0.46 ± 0.07** | **0.42 ± 0.10** |
| **Total N, %** | | | | | |
| **0–5 cm:** | **0.23 ± 0.02a** | **0.16 ± 0.02a,b** | **0.13 ± 0.02a,b** | **0.10 ± 0.01b** | **0.08 ± 0.01b** |
| **20–25 cm:** | **0.04 ± 0.01** | **0.03 ± 0.01** | **0.03 ± 0.01** | **0.03 ± 0.01** | **0.03 ± 0.01** |
| **Total P, μg $\text{cm}^{-3}$** | | | | | |
| **0–5 cm:** | **72 ± 12** | **53 ± 11** | **54 ± 12** | **52 ± 3** | **40 ± 4** |
| **20–25 cm:** | **31 ± 4** | **22 ± 4** | **25 ± 4** | **30 ± 3** | **29 ± 4** |
| **Total P μg $\text{g}^{-1}$** | | | | | |
| **0–5 cm:** | **79 ± 13a** | **53 ± 11a,b** | **51 ± 11a,b** | **48 ± 3a,b** | **37 ± 4b** |
| **20–25 cm:** | **19 ± 2** | **14 ± 2** | **16 ± 3** | **19 ± 2** | **18 ± 2** |

**† Water levels are measured relative to the soil surface.**

**‡ Means within the same row followed by the same letter are not significantly different ($P \leq 0.05$) the Ryan-Einot-Gabriel-Welsh multiple range test.**

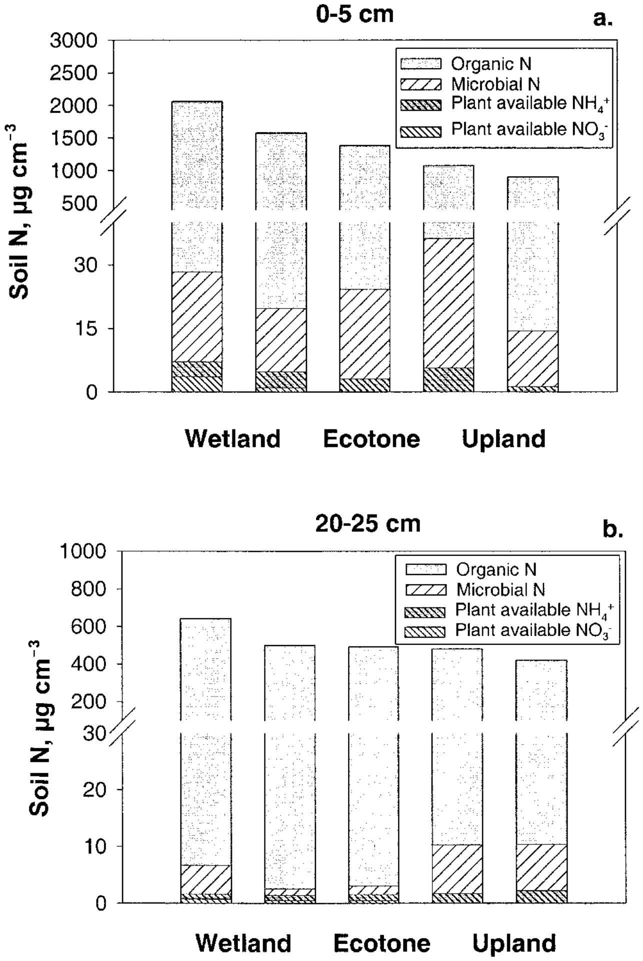

**Fig. 1. Soil N fractions expressed on a volume basis at (a) 0–5 cm and (b) 20–25 cm across the wetland-ecotone-upland transect at Ichauway. Plant-available $NH_4^+$ and $NO_3^-$ refers to 2M KCl extraction fraction.**

and microbial N were significantly higher in surface than subsurface soil (Fig. 1). Surface (0–5 cm) soil microbial N ranged from 13 to 31 $\mu g\ cm^{-3}$ as compared with 0.5 to 2.0 $\mu g\ cm^{-3}$ in subsurface (20–25 cm) soil. Plant-available N ($NH_4$-N, $NO_3$-N) also was significantly greater in surface than subsurface soils (Fig. 1). Plant-available $NO_3$-N and microbial-bound N were significantly correlated with total N ($r = 0.67$–$0.74$, $P < 0.001$, $n = 90$). Plant-available $NH_4$-N was not as strongly correlated with total N ($r = 0.35$, $P < 0.001$) as $NO_3$-N.

Like N, most soil P existed in recalcitrant organic form (Fig. 2). Fifty to 82 % of the P was bound to humic acids. Phosphorus-bound to Fe and Al was the second largest fraction, consisting of 5 to 31% of the total. Microbial P accounted for 4 to 6% of the total in surface soil and 2 to 5% in subsurface soil. Labile (bicarbonate-extractable) $P_o$ and $P_i$ and Ca-bound P accounted for 2 to 4%, 0 to 1.5% and 0 to 2%, respectively. Essentially no P (residual P) was recovered from the terminal step of the fractionation.

Our reported values are comparable with a variety of mineral soils where recalcitrant P accounts 86% of total P (Tiessen et al., 1984; Cross and Schlesinger, 1995). Phosphorus fractions of the Kandiudults (uplands) and Paleaquults (wetlands) reported herein are dominated by humic acid-bound $P_o$ and Fe- and Al-bound P with essentially no Ca-bound $P_i$, similar to other Ultisols (Tiessen et al., 1984; Cross and Schlesinger, 1995).

Phosphorus pools of our Ultisols and other low P ($<100\ \mu g\ g^{-1}$) Ultisols are dominated by humic acid and residual $P_o$ and Fe- or Al-$P_i$ (Sharpley et al., 1985; Lee et al., 1990). In our soils, humic-bound $P_o$ was the largest fraction, accounting for 50 to 82% of total P. Our values are similar to a low P (78 $\mu g\ g^{-1}$) Typic Paleudult (Ruston series: fine-loamy, siliceous, semiactive, thermic Typic Paleudults) in Louisiana where humic acid plus residual $P_o$ accounted for 78% of total P (Sharpley et al., 1985). The predominance of humic-bound $P_o$ over mineral P probably reflects the coarse texture (75–78% sand) and low clay (4–9%), Fe, Al, and P sorption of our soils as compared with high clay content (42% clay) Ultisols where Fe- and Al-$P_i$ is largest P fraction (Lee et al., 1990).

Forms and amounts of soil P in our depressional wetlands differed somewhat from alluvial floodplains of the southeastern coastal plain. Similar to our soils, P pools of Inceptisols (Chastain series: fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts; and Tawcaw series: fine, kaolinitic, thermic Fluvaquentic Dystrudepts) along the Ogeechee River in Georgia (total P = 375 $\mu g\ g^{-1}$) were dominated by recalcitrant organic (humic acid plus residual) P that accounted for 37% of the total (Wright et al., 2001). In alluvial soils, however, microbial P contributed 31% of total P as compared with 4 to 6% in our soils. Greater microbial P in alluvial wetland soils probably reflected environmental conditions that are more conducive to microbial activity. For example, soil organic matter (which fuels heterotrophic microbial activity) was greater in alluvial (9%) than depressional wetland soils (5–6%). Alluvial soils also contained more silt plus clay (38%, which retains moisture) than depressional wetland soils (25%) although Wright et al. (2001) reported that flooding alluvial soils reduced microbial P as compared with unflooded soils. In our study, however, microbial P was low (4–6%) in both wetland and upland soils regardless of flooding. Finally, fires that periodically burn across depressional wetlands may affect microbial populations and microbial P, although the nature of such effects is unknown. Similar to microbial P, labile $P_i$ (5%) and $P_o$ (10%) were much greater in alluvial soils than in depressional wetland soils ($P_i$ = 1%, $P_o$ = 2–4%). Alluvial (16%) and depressional (5–31%) wetland soils contained comparable amounts of Fe- or Al-bound $P_i$. Neither alluvial nor depressional wetland soil contained much Ca-bound P (<1%).

As with N, the surface soil was enriched in all forms of P as compared with subsurface soil (Fig. 2). Microbial-bound P in surface soil (5–8 $\mu g\ cm^{-3}$) was four to eight times greater than in subsurface soil (0.5–2.3 $\mu g\ cm^{-3}$), which was not surprising since biological activity and biological forms of P tend to be concentrated at the soil surface (Walbridge et al., 1991). Five to eight times more labile $P_i$ was present in surface soil (0.46–0.77 $\mu g\ cm^{-3}$) than subsurface soil (0.04–0.10 $\mu g\ cm^{-3}$). Labile $P_o$, hu-

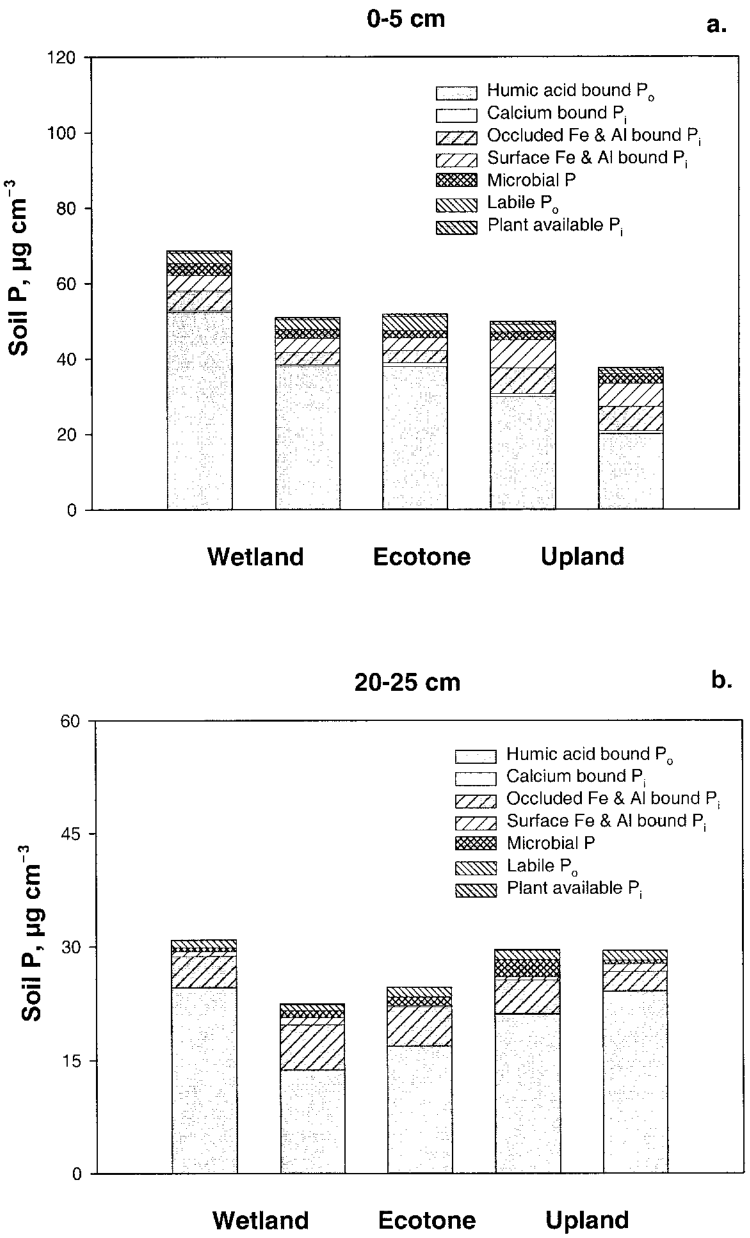

**Fig. 2. Soil P fractions expressed on a volume basis at (a) 0–5 cm and (b) 20–25 cm across the wetland-ecotone-upland transect at Ichauway.**

mic acid $P_o$, and Fe- and Al-$P_i$ were greater in surface vs. subsurface soil (Fig. 2).

Labile $P_i$ was significantly correlated ($P < 0.001$) with surface Fe- and Al-bound $P_i$ ($r = 0.69$) ($n = 90$). Tiessen et al. (1984) reported a similar association between labile $P_i$ and surface ($r = 0.76$) and occluded ($r = 0.62$) Fe- and Al-bound $P_i$ of a variety of soils ranging from Entisols to Oxisols. Labile $P_o$ was highly correlated ($P <$ 0.001) with various fractions associated with soil organic matter, including humic acid $P_o$ ($r = 0.83$) and total N ($r = 0.86$) and organic C ($r = 0.75$) ($n = 90$).

## Variation in Nitrogen and Phosphorus Across the Drainage Gradient

Soil organic N and $NO_3$-N decreased from wetland into upland soils (Fig. 3). In surface soils, $NO_3$-N was significantly greater ($P < 0.05$) in the interior of the wetland (3.7 $\mu$g cm$^{-3}$) than at all other transect (0.03–1.0 $\mu$g cm$^{-3}$) points (Fig. 3a). Plant-available $NO_3$-N in subsurface soil also was significantly greater ($P < 0.05$) in the wetland and ecotone (0.50–0.80 $\mu$g cm$^{-3}$) as compared with upland locations (0.07–0.08 $\mu$g cm$^{-3}$). Like plant-available $NO_3$-N, surface soil organic N was significantly greater ($P < 0.05$) in the wetland interior (2030 $\mu$g cm$^{-3}$) as compared with the upland locations (890–1040 $\mu$g cm$^{-3}$) (Fig. 3b). No trend in microbial N or plant-available $NH_4$-N was observed across the wetland to upland continuum.

The percentage of N stored in labile forms (KCl-extractable $NH_4$-N and $NO_3$-N plus microbial N) increased from wetland into upland soils (Table 3). In surface and subsurface soil, the percentage stored as labile N was significantly greater in upland soils (1.9–4.4%)

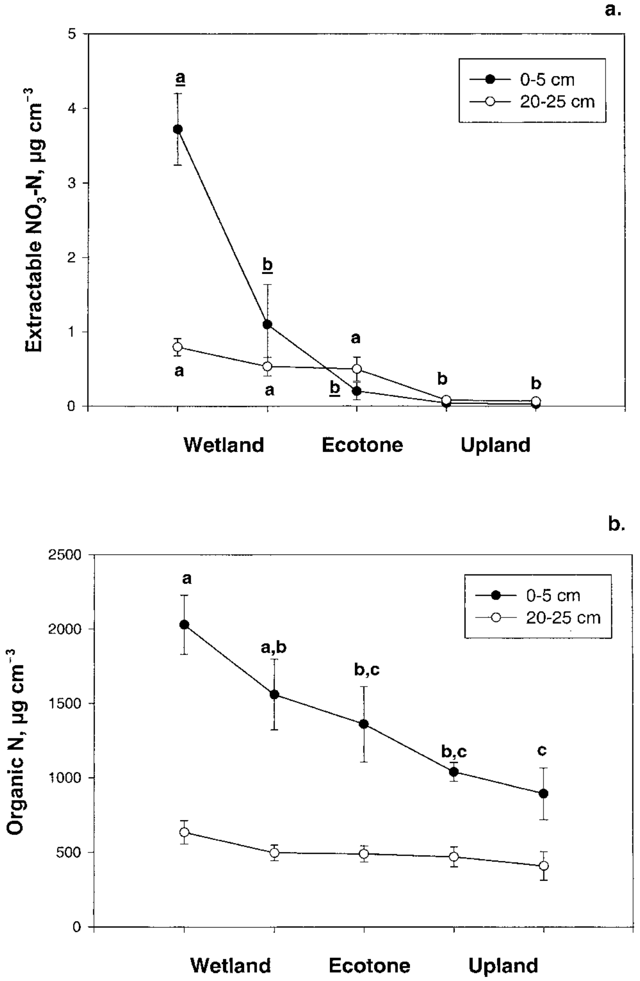

Fig. 3. (a) Plant-available (KCl-extractable) $NO_3$-N and (b) organic N across the wetland-ecotone-upland transect at Ichauway. Means at transect points within the same depth followed by the same letter are not significantly different ($P < 0.05$) according to the Ryan-Einot-Gabriel-Welsh multiple range test.

than in wetlands (0.6–1.5%). Even though upland soils contained less total N than wetlands, a greater proportion existed in labile forms in upland soils.

Like N, there was a general decrease in surface soil P from wetland to upland although the trends were less pronounced than with N. Total P (mass basis, 0–5 cm) was significantly greater in the wetland interior than in the upland (Table 2). Similarly, Labile $P_o$ was significantly greater in the wetland and ecotone as compared with the upland (Fig. 4a). Humic acid-bound $P_o$ and total P (volume basis) were greater in wetland than upland soils (Fig. 4b and d), although the differences were not significant. Other forms of P, including labile $P_i$, Ca-bound $P_i$, and Fe- and Al-bound $P_i$ (Fig. 4c) did not differ between wetland and upland soils. Mineral P-bound to Fe and Al often increases with clay content (Cooper and Gilliam, 1987). However, in our soils, Fe- and Al-$P_i$ were constant across the landscape even though clay content of our soils doubled from 4% in uplands to 9% in wetlands (C.B. Craft, 2000, unpublished data). Similarly, other studies in Georgia and Virginia found no difference in oxalate-extractable Al (which sorbs P) along drainage gradients from wetland to upland soils (Axt and Walbridge, 1999; Darke and Walbridge, 2000).

Table 3. Percentage of total N and P stored in labile† vs. recalcitrant‡ forms across the wetland-ecotone-upland continuum at Ichauway. Percentage of total P stored in biological vs. geochemical form also are shown.

| | Wetland | | Ecotone | Upland | |
|---|---|---|---|---|---|
| Transect Point | 1 | 2 | 3 | 4 | 5 |
| | | 0- to 5-cm depth | | | |
| Labile N | 1.5a§ | 1.3a | 1.9a,b | 3.4b | 1.9a,b |
| Recalcitrant N | 98.5a | 98.7a | 98.1a,b | 96.6b | 98.1a,b |
| Labile P¶ | 11 | 12 | 14 | 10 | 11 |
| Recalcitrant P# | 89 | 88 | 86 | 90 | 89 |
| Biological P | 83a | 80a | 82a | 71a,b | 67b |
| Geochemical P | 17a | 20a | 18a | 29a,b | 33b |
| | | 20- to 25-cm depth | | | |
| Labile N | 1.1a | 0.6a | 0.7a | 2.3a,b | 4.4b |
| Recalcitrant N | 98.9a | 99.4a | 99.3a | 97.7a,b | 95.6b |
| Labile P | 5 | 7 | 8 | 8 | 6 |
| Recalcitrant P | 95 | 93 | 92 | 92 | 94 |
| Biological P | 88 | 67 | 78 | 85 | 88 |
| Geochemical P | 12 | 33 | 22 | 15 | 12 |

† Labile N = KCl-extractable $NH_4$-N/$NO_3$-N + microbial N. Labile P = bicarbonate-extractable inorganic and organic P + microbial P.

‡ Biological P = bicarbonate-extractable organic P + microbial P + humic acid-bound $P_o$. Geochemical P = bicarbonate extractable inorganic P + Fe, Al- and Ca-bound $P_i$.

§ Means within the same row separated by the same letter are not significantly different ($P \leq 0.05$) according to the Ryan-Einot-Gabriel-Welsh multiple range test.

¶ Percentage stored in the 0- to 5-cm depth is significantly greater than in the 20- to 25-cm depth according to ANOVA.

# Percentage stored in the 0- to 5-cm depth is significantly less than in the 20- to 25-cm depth according to ANOVA.

There was no difference in labile vs. recalcitrant P along the wetland to upland continuum (Table 3). Labile P (bicarbonate-extractable $P_i$ and $P_o$ plus microbial P) accounted for 10 to 14% of total P in surface soil and 5 to 8% in subsurface soil. The percentage of total P stored as labile forms in our soils was similar to values reported for other Ultisols where labile P accounted for <14% of the total (Cross and Schlesinger, 1995).

Biological (organic) and geochemical (inorganic) P, however, varied significantly along the wetland to upland continuum (Table 3). Biological P (0–5 cm) was significantly greater in wetland (80–83%) than upland soils (67–71%). Upland soils contained more geochemical P (29–33%) than wetland soils (17–20%). Fe- and Al-bound $P_i$, the primary component of geochemical P, also increased from wetlands (13%) where the soils periodically are saturated, to uplands (31%) where the soils are seldom saturated and highly leached. In our soils, biological P accounted for a higher percentage of the total (67–83%) as compared with other Ultisols where biological P contributed ≈30 to 35% (Cross and Schlesinger, 1995).

Wetland soils stored more N than upland soils even though organic C content was uniform (0- to 5-cm depth) or increased (20- to 25-cm depth) across the wetland to upland continuum (Table 2). Reduced N storage in upland soils may be the result of periodic fire that volatilizes N in soil organic matter. Prescribed fire, with a frequency of 1 to 3 yr, is used to maintain longleaf pine-wiregrass vegetation against encroachment from hardwoods (Kirkman et al., 1998). Fire sometimes burns

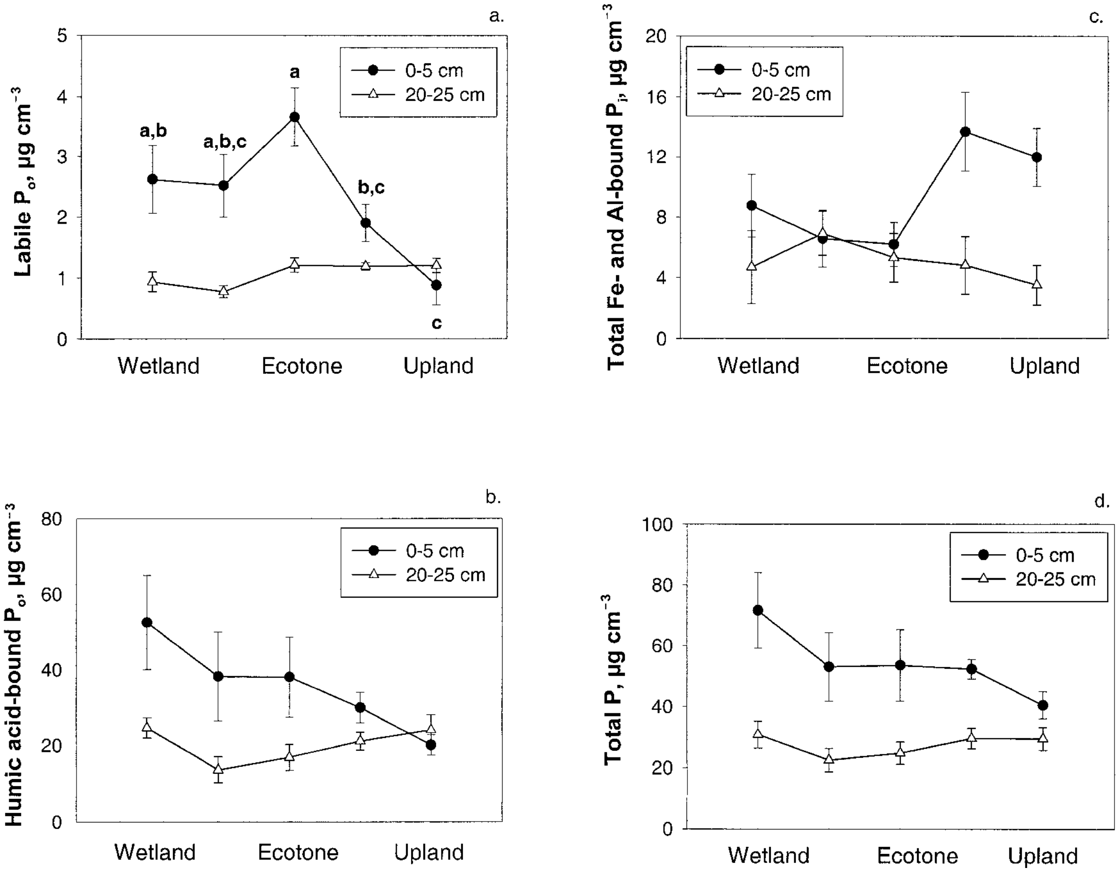

**Fig. 4. Phosphorus fractions across the wetland-ecotone-upland transect at Ichauway. (a) Labile ($NaHCO_3$–extractable) organic P, (b) humic acid-bound organic P, (c) total Fe- and Al-bound inorganic P and (d) total P. Means at transect points within the same depth followed by the same letter are not significantly different ($P < 0.05$) the Ryan-Einot-Gabriel-Welsh multiple range test.**

the depressional wetlands but with less frequency than adjacent upland forests (Kirkman et al., 1998). It has been estimated that 30 to 70% of N in longleaf pine-wiregrass litter is lost to volatilization during fires (DeBell and Ralston, 1970; Christensen, 1987, 1993). One would also expect a proportional amount of organic C to be lost (as $CO_2$) during combustion (Raison et al., 1985). This is not the case for our soils, where C is uniformly distributed across the landscape (Table 2). The discrepancy in soil C vs. N pools may be due to differences in C vs. N volatility or to differences in humification in upland vs. wetland soils. For example, in upland soils, fires often result in substantial carbon input to soils as charcoal that accumulates, whereas N is volatilized or oxidized to nitrate that is leached from the soil (Richter et al., 1982). An alternate hypothesis is that, in wetlands soils, humification processes lead to greater retention of N over C in soil, with a resultant decrease in C:N (Stevenson, 1994). In either case, in the coastal plain landscape, depressional wetland soils are islands of N in a N-poor landscape.

## Carbon:Nitrogen:Phosphorus Ratios

Surface and subsurface soil C:N increased along the continuum from wetland to upland (Fig. 5a). Carbon: nitrogen was significantly lower in the wetland than in upland soil at both the 0- to 5-cm and 20- to 25-cm depths. Using 20:1 as the critical ratio (Tisdale et al., 1985), our high C:N ratio (35:1 to 42:1) in the upland indicates that N limits plant productivity in the longleaf pine–wiregrass whereas the C:N ratio in the wetland (12–18) indicates that sufficient N is available to meet microbial needs. High litter (118:1) (Wilson et al., 1999) and soil C:N and low soil $NO_3$-N and total N support the notion that our upland soils are limited or co-limited by N (Vitousek and Howarth, 1991).

Plant-available (KCl-extractable $NH_4$-N + $NO_3$-N: bicarbonate-extractable $P_i$) and total N:P of surface soils decreased from wetlands to uplands (Fig. 5b). Plant-available N:P was significantly greater in the wetland interior (33:1) as compared with the upland interior (5:1). Similarly, total soil N:P in the 0- to 5-cm depth varied from 76:1 to 81:1 in wetlands to 48:1 to 52:1 in upland soils. Total N:P was significantly lower in subsurface than in surface soil because N decreased with depth more than P (Table 2). Walbridge (1991) evaluated P cycling across a hydrology gradient of pocosin peatland to bay forest wetland, that represents a gradient of increasing mineral soil content and P availability, and reported that soil N:P ratios decreased from 57:1 in organic soils of pocosin to 19:1 in mineral soils of bay forest.

Nitrogen:phosphorus ratios in plant tissue and soil have been employed to assess for N vs. P limitation of freshwater wetlands (Koerselman and Mueleman, 1996;

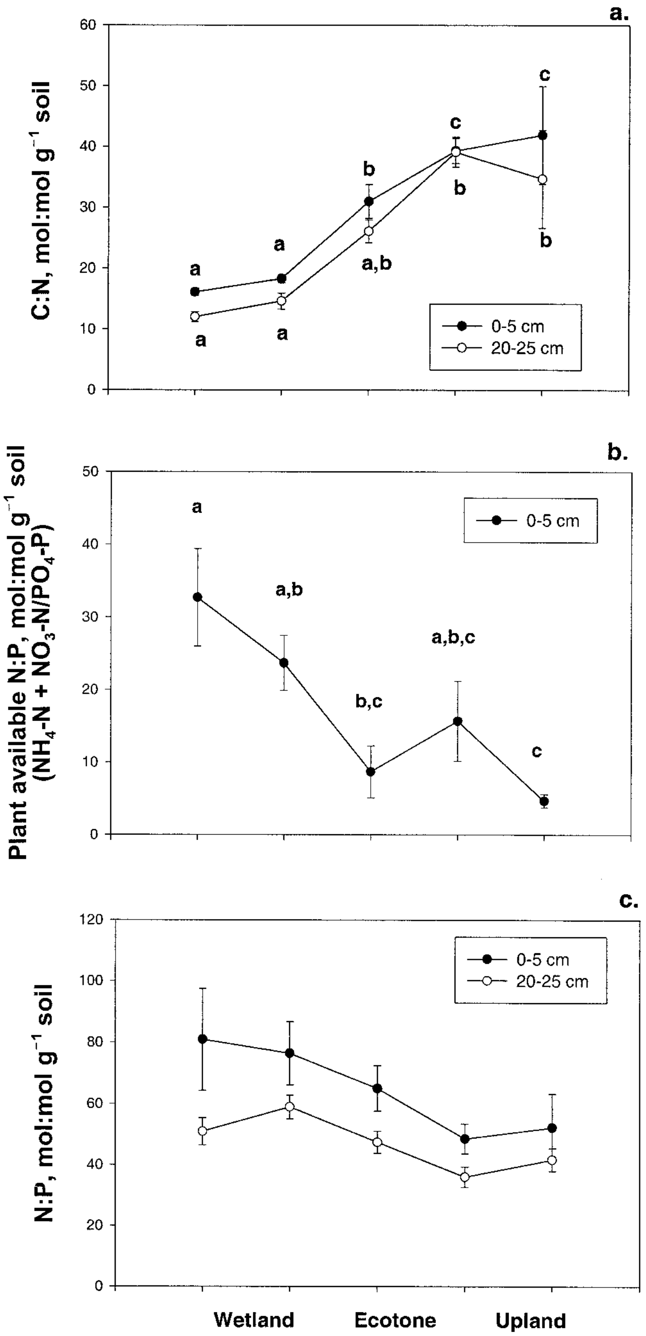

**Fig. 5. (a) Soil C:N, (b) plant-available N:P and (c) total N:P across the wetland-ecotone-upland transect at Ichauway. Plant-available N:P is the ratio of KCl-extractable $NH_4$-N $+NO_3$-N/bicarbonate extractactable inorganic P. Means at transect points within the same depth followed by the same letter are not significantly different ($P < 0.05$) the Ryan-Einot-Gabriel-Welsh multiple range test.**

Verhoeven, 1996; Bedford et al., 1999). In vegetation, N:P $> 16$ is indicative of P limitation, whereas N:P $< 14$ suggests that N is the primary limiting nutrient (Koerselman and Mueleman, 1996). The shift in labile N:P from 5:1 in upland soils to 20:1 in wetlands suggests a pattern of decreasing P availability relative to N and, possibly, a shift from N limitation on drier to parts of the landscape to P limitation or co-limitation in the wetlands.

## CONCLUSIONS

Plant-available ($NO_3$-N), organic, and total N decreased and C:N increased from wetland to upland soils. Total P, labile $P_o$, and recalcitrant (humic acid) $P_o$ also were greater in wetland than upland soils. Nearly all N (97–98%) and most P (50–82%) existed in recalcitrant organic forms, regardless of landscape position. Recalcitrant $P_i$ (Fe- and Al-bound $P_i$) accounted for 5 to 31% of total P. Surface soil (0–5 cm) contained 1.5 to 3 times more N and P than subsurface soil (20–25 cm). Wetland soils concentrated N at higher levels than upland soils even though organic matter (C) content was uniform across the drainage gradient.

Periodic waterlogging favors sequestration of biological (organic) forms of N and P in soil. Wetness also favors N retention more than P with a resultant increase in labile and total N:P from drier to wetter parts of the landscape. In upland soils, high C:N (35–42) and low plant-available N:P (5) indicate N limitation of plant growth. Low C:N (12–18) and high labile N:P (33) of wetland soils suggests a shift towards P limitation or N and P co-limitation in wetlands. Soil N and P pools and N:P ratios may be useful for inferring patterns and intensity of N vs. P limitation across ecosystems of the southeastern coastal plain.

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