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# HYDROLOGY AND NUTRIENT GRADIENTS IN NORTH CAROLINA PEATLANDS

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*Abstract:* Soil chemistry and hydrology gradients are closely associated with and have often been cited as the causative agents for changes in wetland plant community composition. We analyzed the biogeochemistry and hydrology of three freshwater peatland communities on the North Carolina Coastal Plain—short pocosins, tall pocosins, and gum swamps. We compare this community gradient to the classical bog-fen gradient of northern peatlands. Short pocosins, in the ombrotrophic center of the raised bog complex, have the highest summer water table, with a large part of the peat profile remaining anaerobic throughout the year. They are highly nutrient-deficient with low levels of total and extractable P, N, and basic cations. They additionally have the greatest peat depth, with an organic matter content of ca. 95%. Tall pocosins have a highly seasonal water table, shallower peat depth, low soil nutrient levels, and an average soil organic matter content from 76 to 93% in the top 30 cm. Gum swamp forests have a highly seasonal water table and the shallowest peat depth. They are the most minerotrophic community, based on low organic matter and high N and P content of the soil, but have low levels of exchangeable Ca and Mg and low percent base saturation. All communities had low soil pH ($< 4$). Short pocosins and tall pocosins were effectively differentiated by seasonal hydrology and peat depth but not by soil characteristics, while the pocosins and swamp forest had large differences in seasonal hydrology, peat depth, percent organic matter, and soil nutrients.

This community gradient contrasts sharply with the bog-fen gradient of northern peatlands, in which there is an increase in soil pH, basic cations, percent base saturation, and ash content, and a decrease in extractable N, P, and K. This biogeographical comparison suggests a need for further study of the nutrients likely to control plant growth in peatlands (i.e., P, N, and K), in addition to the historical emphasis on basic cations and pH.

*Key Words:* bog-fen gradient, hydrology, North Carolina, nutrients, peatlands, pocosins.

## INTRODUCTION

Many biogeochemical processes are unique in wetlands due to waterlogging and the extensive accumulation of soil organic matter. Soil chemistry gradients are closely associated with changes in wetland plant community composition (Heinselman 1970, Richardson et al. 1978, Schwintzer and Tomberlin 1982, Malmer 1986, Vitt and Chee 1990, Walbridge 1991) and in net primary production (Richardson 1978, Brinson et al. 1981, Verhoeven et al. 1988, Vitt 1990). Probably the most classic example of an association between soil chemistry and plant community gradients is the bog, poor fen, rich fen classification in northern peatlands (Moore and Bellamy 1974).

Hydrology is the dominant variable controlling ecosystem dynamics in wetlands, influencing such diverse factors as redox potential, soil oxygen content, pH, nutrient and carbon cycling, community composition, and wetland development (Moore and Bellamy 1974, Brinson et al. 1981, Carter 1986, Day et al. 1988, Bridgham et al. 1991a,b). Important attributes of the hydroperiod are the frequency, timing, depth, and duration of flooding or waterlogging.

Differences in hydrology among wetlands, and ultimately their position on the landscape, are often the underlying cause of differences in soil chemistry. The accumulation of peat is itself often the prime agent of change in the hydrology of wetlands. Peatlands develop from primary to secondary to tertiary mires in a paludification sequence, with increasing peat storage, isolation from the surrounding watershed, and dependence on precipitation for nutrient inputs (Moore and Bellamy 1974). Ombrotrophic (rain-fed) peatlands receive mineral input solely from precipitation and hence are considered nutrient-deficient, while minerotrophic peatlands receive mineral input at least partially from mineral-influenced run-off and ground water. The degree of mineral influence determines the nutrient status and soil chemistry of the peatland (Moore and Bellamy 1974).

Several freshwater peatland communities (e.g., short pocosins, tall pocosins, and swamp forests) occur on the Coastal Plain of North Carolina and are most readily distinguished by differing height and biomass of the aboveground vegetation. The postulated reason for the existence of this array of communities, often in close proximity to each other on the landscape, is differences in nutrient availability and/or hydrology (Otte 1981, Walbridge 1991). Although these peatland communities are an important component of the Coastal Plain landscape (Richardson 1983), limited knowledge exists on the biogeochemistry and hydrology of undisturbed North Carolina peatlands.

The primary objective of this study was to determine if the biogeochemistry and hydrology of these three NC peatland communities differed significantly. Also, we wanted to compare this community gradient to the bog-fen gradient of northern peatlands. Our central hypotheses were that (1) the NC peatland community gradient also reflects a nutrient (N, P) and hydrology gradient, with decreasing soil nutrient availability and soil aeration from gum swamp to tall pocosin to short pocosin and (2) soil chemical factors that are commonly associated with increasing ground-water influence (basic metal cations, percent base saturation, pH) do not effectively discriminate these communities.

## STUDY AREA

Distinct peatland communities occur in different topographic settings on the Coastal Plain, even though local relief is generally 2 m or less over several kilometers (Christensen et al. 1988, Weakley and Schafale 1991, Bridgham and Richardson 1992a, Richardson and Gibbons 1992). Short pocosins occupy the ombrotrophic center of domed bog complexes on poorly drained interstream flats and are characterized by stunted pond pine (*Pinus serotina* Michaux) and low (< 1.5-m height) broad-leaf, deciduous-to-evergreen shrubs such as *Cyrilla racemiflora* L., *Lyonia lucida* (Lam.) K. Koch, and *Zenobia pulverulenta* (Bartram) Pollard. Peat depth ranges from 1 to 5 m. Tall pocosins occur on the fringes of short pocosins, have shallower peat (< 1.5 m), and a species mixture similar to short pocosins but of taller stature and greater aboveground biomass. Gum swamps occur along the outflows of lakes and along streams. Vegetation is typical of southeastern bottomland hardwood forests, with a canopy of black gum (*Nyssa sylvatica* Marshall), sweet gum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), and bald cypress (*Taxodium distichum* (L.) Richard). Peat thickness is < 1 m.

All plots for our study were in the Croatan National Forest, Craven County, NC (34° 55′ N latitude, 77° 5′ W longitude). The area consists of a large expanse of peatlands on a broad, flat interstream divide between the Neuse and White Oak Rivers. The surface elevation varies from 9 to 13 m above sea level, with the highest elevation in the middle of the large pocosin complex west of Great Lake (Figure 1). Soils at all sites are dysic, thermic Medisaprists. Soil series are Dare for short pocosins, Dare or Croatan for tall pocosins, and Dorovan for gum swamps (SCS 1989).

Coastal NC has a warm, humid climate with an annual average temperature of 16.8°C and average temperatures of 6.7°C in January and 26.2°C in July. Average annual precipitation is 134.9 cm and is fairly evenly distributed throughout the year (1951–1980, in New Bern, NC, ca. 18 km NW of the study site) (NOAA 1988–1990).

## METHODS

### Plot Establishment

Four 0.1-ha (20 × 50 m) plots were established in each of the three communities in an area that had not burned since the 1950s (National Forest Service, personal communication). Representative stands of each community type were chosen from aerial infrared photography and ground reconnaissance. Additionally, four 2-m wide drained plots were established 8 m from primary drainage ditches, extending parallel with the ditches for 10 m (20 $m^2$). This distance is within the area of maximum drainage effect (Maki 1974). The drained plots were formerly short pocosins, but a narrow band of taller vegetation now borders the drainage ditches. Tall pocosin plots were often necessarily established near roads as a result of the impenetrability of the extremely dense vegetation. However, all tall pocosin plots were at least 100 m from the nearest road or drainage ditch to ensure unaltered hydrology (Maki 1974, Otte 1981).

### Hydrology

We inserted a water-table well in the center of each plot to monitor seasonal water-level changes. Wells were constructed from 7.5-cm dia. PVC pipe that had closely spaced holes drilled over the entire length. Wells were sunk in a pre-augered hole to 1 m and loosely capped. Uncoated steel welding rods were inserted in the soil within 1 m of water-table wells, and depth of rusting on the rods was used as an indicator of the extent of the soil aerobic zone (Bridgham et al. 1991a). Three soil samples from 0- to 10-cm depth were composited per plot, and soil moisture was determined gravimetrically after drying at 70°C; results were subsequently converted to a volumetric basis by multiplying by the respective bulk densities. Measurements of water table, depth of rusting on steel rods, and soil moisture were taken at approximately monthly intervals. Data from the New Bern, NC weather station (NOAA 1988–1990) was used to determine rainfall and potential evapotranspiration (PET) with the Thornthwaite equation (Dunne and Leopold 1978).

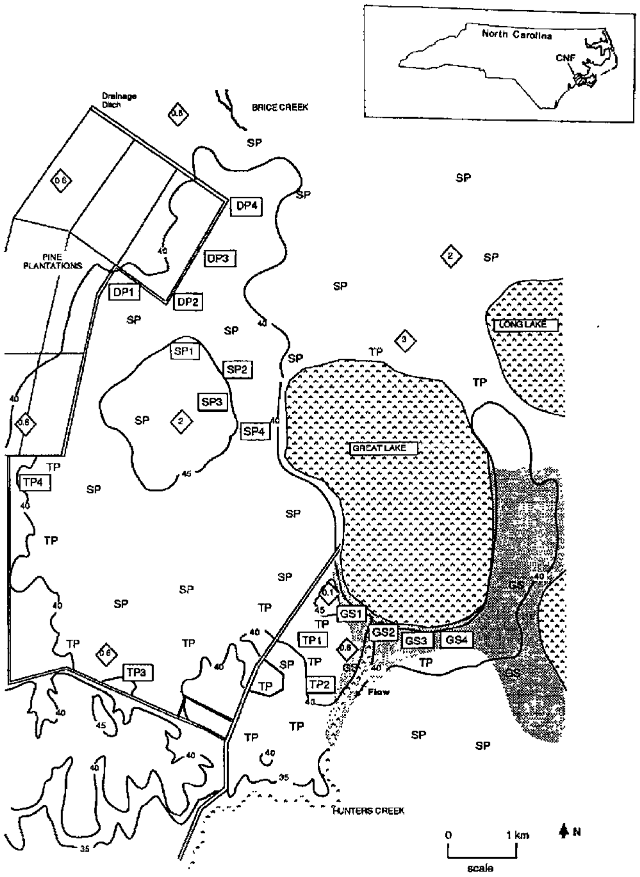

Figure 1. Map of the study area in the Croatan National Forest, NC. Individual sites are shown in boxes and peat depth (m) in diamonds (Otte 1981). Contour lines from USGS topographic maps are shown in feet. SP=short pocosin, TP=tall pocosin, GS=gum swamp (also shown in stippled area), DP=drained pocosin.

### Nutrients

Three soil samples from each plot were taken with a stainless steel box corer (Richardson, unpublished design), which caused minimal compaction of peat, and were composited. Large roots were removed from the samples by hand before further processing, and samples for bulk density and total nutrient concentrations were dried at 70°C. Organic matter was determined by loss-on-ignition after combustion at 500°C for 3 hr, and total carbon was estimated by assuming this organic matter to be 63.7% C (Otte and Ingram 1979). A 1:1 wet soil mass/water slurry was used to determine pH.

Total soil nutrients (N, P, Ca, Mg, K) were determined in dried samples after digestion with concentrated $H_2SO_4$ and 30% $H_2O_2$ (Lowther 1980). Extractable soil nutrients were determined on wet samples and adjusted to a dry-mass equivalent from oven-dried subsamples. Phosphate was extracted with a dilute double-acid solution of 0.05 M HCl and 0.0125 M $H_2SO_4$ (Olsen and Sommers 1982), while $NO_3^-$ and $NH_4^+$ were extracted with 2 M KCl (Keeney and Nelson 1982). Nitrogen and P were measured with standard autoanalyzer techniques (Orion Scientific Instruments 1984), and cations were measured with atomic absorption spectrophotometry (Perkin Elmer 1982). Due to large differences in bulk density between sites and with depth within a site, all nutrient concentrations are presented on an area or volume basis.

Several soil analyses were performed by the State Soils Laboratory of the NC Department of Agriculture. These included humic matter content based on a 0.2 M NaOH extraction (Mehlich 1984a), cation exchange capacity (CEC) based on an extractant of 0.2 M $CH_3COOH$, 0.25 M $NH_4NO_3$, 0.015 M $NH_4F$, 0.013 M $HNO_3$, and 0.001 M EDTA (Mehlich 1984b), and exchangeable acidity (Mehlich 1976). Base saturation of CEC was determined by (CEC- exchangeable acidity) / CEC.

### Statistics

Variables were log transformed before statistical tests when it was necessary to ensure equality of variances (Steel and Torrie 1980). Statistical differences between communities were determined with a one-way ANOVA, while differences in variables measured at several depths were determined with a two-way ANOVA with site and depth as the independent variables . A repeated measure ANOVA was used to compare seasonal differences in water-table depth, depth of rusting on steel rods, and soil moisture content. We used Fisher's Protected Least Significant Difference for pairwise comparisons with statistical significance assigned for $P < 0.05$.

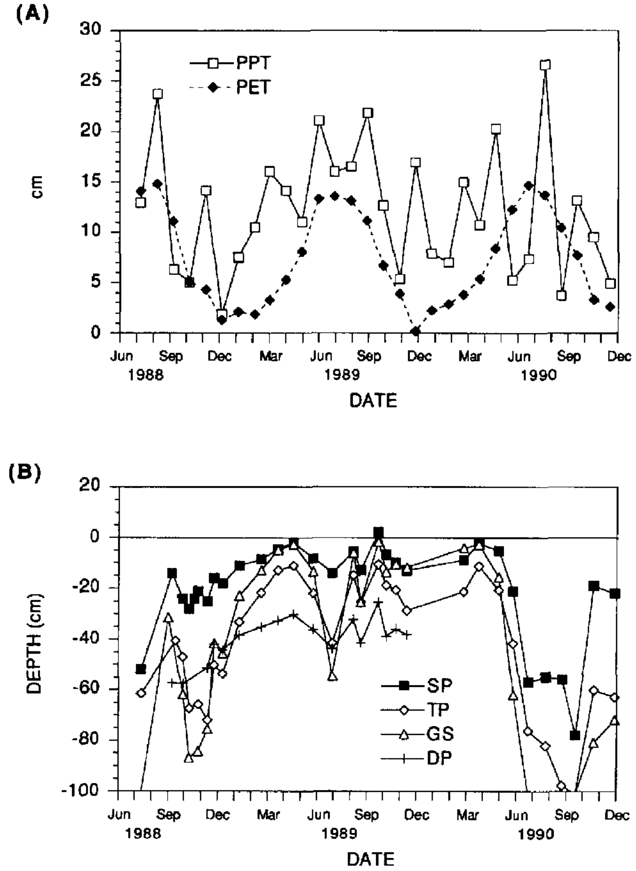

Figure 2. (A) Precipitation (PPT) and potential evapotranspiration (PET) from New Bern, NC. (B) Water-table depth averaged over four plots for short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP) in the Croatan National Forest, NC. The minimum depth measured was −100 cm.

## RESULTS

### Hydrology

The period of measurement included two years with relatively average rainfall, 1988 and 1990, and a relatively wet year, 1989 (Figure 2A). Rainfall was 133.1 cm in 1988, 169.6 cm in 1989, and 131.5 cm in 1990, departing −1.8 cm in 1988, +34.7 cm in 1989, and −3.4 cm in 1990 from long-term mean precipitation (1951–1980). Annual rainfall exceeded potential evapotranspiration (PET) (81 to 91 cm) in all 3 years (Figure 2A). Monthly PET exceeded rainfall only in July and September in 1988 and June, July, and September in 1990.

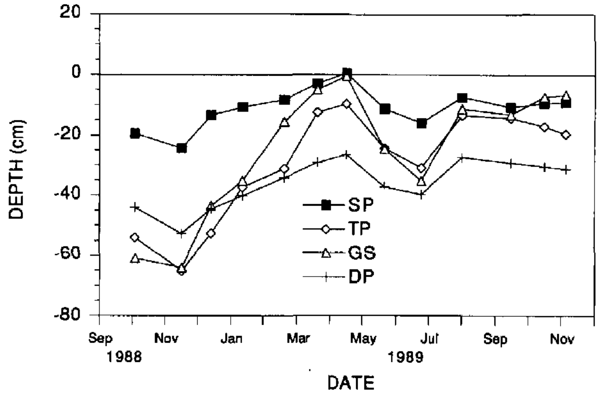

Figure 3. Steel-rod rusting depth averaged over four plots for short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP).

Distinct differences in seasonal hydrology existed between the three communities. Water-table level differed significantly ($P < 0.01$) among sites, dates, and the interaction term. The water table was lowest in the late summer and early autumn, and rose through the winter and spring until it approached the soil surface (Figure 2B). Relatively high water tables were maintained throughout 1989 due to high precipitation during the growing season. Water-table levels generally tracked the monthly surplus/deficit of precipitation over PET.

The water table in the short pocosin dropped 40 cm below the surface only after extended dry periods during the growing season, while the water tables in the tall pocosin and gum swamp dropped more than 100 cm below the surface (e.g., the summer of 1990). The gum swamp tended to have even lower water-table levels than the tall pocosin during the growing season. During winter and spring, the water table approached the surface in the short pocosin and gum swamp, although surface flow was never observed in either community. The tall pocosin tended to have a somewhat lower water table than the short pocosin and gum swamp during the wettest periods of the year. The effectiveness of drainage is shown in the drained pocosin plots, where the water table was relatively constant at −30 to −60 cm and never approached the soil surface.

Site, date, and the interaction term were all significant ($P < 0.01$) in determining the depth of rusting on steel rods. During the period measured from the autumn of 1988 through 1989, the aerobic zone ranged from 0 to 25 cm in depth in the short pocosin (Figure 3). The tall pocosin and gum swamp showed more variable aerobic zones, with as much as 60 to 70 cm of the peat profile oxidized during extended periods in the summer and autumn. The top 30 cm remained aerobic throughout the year in the drained pocosin plots.

Soil moisture in the surface 10 cm did not show the distinct seasonal differences found with water-table and steel-rod rusting depth, except the short pocosin had peaks in soil moisture in May 1989 and April/May 1990 with greater than 50% moisture by volume (Figure 4). Site, date, and the interaction term all significantly ($P < 0.01$) affected soil moisture levels. The short pocosin and gum swamp had the greatest soil moisture on most sampling dates. Soil moisture in the gum swamp ranged from 17 to 37%, while in the tall pocosin, it ranged from 8 to 22%. The drained pocosin plots were driest, with average soil moisture content always less than 10%.

### Bulk Density

Significant differences ($P < 0.0001$) in soil bulk density existed between sites, depths, and in the interaction term (Table 1). Gum swamp peat had a greater bulk density than pocosin peat at all measured depth increments. Short pocosin, tall pocosin, and drained pocosin peats had similar bulk densities, except the bulk density in short pocosin peat was significantly less than in tall pocosin peat from 20 to 30-cm depth. Bulk density increased with soil depth at each site.

The relatively high percent soil moisture content in the gum swamp compared to the other sites during periods of low water-table levels (Figures 2B, 4) was likely due to its higher bulk density. Soil water-holding capacity increases with greater bulk density and smaller soil pores that are not as easily drained.

### Soil Chemistry

The short pocosin and drained pocosin peats contained from 95 to 97% organic matter, and no depth gradients in organic matter content existed over the top 30 cm (Table 1). The decrease in mean organic matter content with depth in the tall pocosin peats was not statistically significant due to the large variability between plots from 10 to 30 cm; for example, organic matter content varied from 35 to over 90% in the 20 to 30-cm depth increments. There was no apparent relationship between height of the aboveground vegetation and organic matter content of the peat in the tall pocosin plots. The gum swamp was much more minerotrophic than the other communities, with mean organic matter content decreasing from 81% at 0- to 5-cm depth to 50% at 20-to 30-cm depth.

Nutrient concentrations on a volume basis increased with depth in all communities for total N, P, and Mg and for total K in the tall pocosin and gum swamp (Table 1), but this increase with depth was largely due to increasing bulk density. On a dry-mass basis, only the total K concentration in the gum swamp increased with depth, while all other total nutrient concentrations either decreased with depth or remained unchanged. This indicates the importance of translocation of elements by biotic and hydrologic processes in these peatlands, as decomposition without removal of an element will lead to an increase in concentration on a dry-mass basis with depth and time.

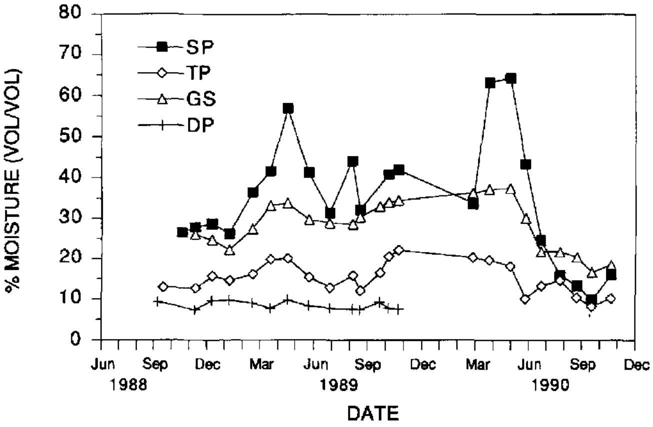

Figure 4. Percent soil moisture expressed on a volume basis from 0–10 cm averaged over four plots for short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP).

The gum swamp generally had the greatest total soil nutrient concentrations at individual depths increments (Tables 1) and integrated to 30 cm (Table 2), while the short pocosin generally had a similar soil chemistry to the drained sites, which it bordered. Total N was approximately twice as great in gum swamp peat as in pocosin peats (Table 2). Total P was approximately ten times greater in the gum swamp than in the pocosins and was significantly greater in the tall pocosin than in the short pocosin and the drained sites. The N:P ratio decreased with increasing total nutrient concentrations. Total soil Mg, Ca, and K were significantly greater in the gum swamp than in the pocosins, although the drained pocosin sites had high Ca concentrations, likely due to contamination from road dust. The short pocosin and drained pocosin sites also had less than half the total K found in the tall pocosin.

Total soil C integrated to 30 cm was slightly lower in the tall pocosin than in the other communities (Table 2), but this does not consider differences in peat depth. Average peat depths in the Croatan National Forest have been estimated to be 200, 108, and 97 cm for short pocosins, tall pocosins, and gum swamps respectively (Otte 1981, Walbridge 1991). If we additionally assume a constant bulk density and organic matter content below 20 cm (cf. Otte 1981, Clymo 1983), then total soil C pools are 152,000 g $m^{-2}$ in the short pocosin, 86,000 g $m^{-2}$ in the tall pocosin, and 101,000 g $m^{-2}$ in the gum swamp. Thus these communities, as with other peatlands, are locally massive soil C reservoirs.

Extractable nutrients and pH from 0- to 10-cm soil depth were measured in May 1989 and March 1990 (Table 3). The peat in all communities was very acidic

Table 1. Total nutrient and carbon concentrations, root-free bulk density (BD), and organic matter content (OM) at four depth intervals for short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP). Significant differences ($P < 0.05$) between sites within a depth interval are shown by different small letters, while significant differences between depths within a site are shown by different numbers. Mean ± (SE), n = 4.

| Site | Depth (cm) | BD (g/cm$^3$) | OM (%) | C (mg/cm$^3$) | N (mg/cm$^3$) | P ($\mu$g/cm$^3$) | Mg ($\mu$g/cm$^3$) | Ca ($\mu$g/cm$^3$) | K ($\mu$g/cm$^3$) |
|---|---|---|---|---|---|---|---|---|---|
| SP | 0–5 | 0.027 (0.001)$^{b3}$ | 95.3 (0.3)$^{a1}$ | 16.5 (0.6)$^{b3}$ | 0.393 (0.009)$^{b3}$ | 9.63 (0.10)$^{b3}$ | 32.5 (1.1)$^{a3}$ | 22.6 (6.6)$^{a1}$ | 16.1 (1.4)$^{b3}$ |
|  | 5–10 | 0.049 (0.008)$^{b2}$ | 95.0 (0.9)$^{a1}$ | 29.2 (4.6)$^{ab2}$ | 0.793 (0.133)$^{b2}$ | 16.2 (2.7)$^{b2}$ | 52.9 (8.3)$^{a3}$ | 19.0 (2.0)$^{a1}$ | 19.3 (1.9)$^{b3}$ |
|  | 10–20 | 0.115 (0.009)$^{b1}$ | 95.5 (1.3)$^{a1}$ | 69.7 (5.1)$^{b1}$ | 1.74 (0.14)$^{b1}$ | 36.1 (1.7)$^{b1}$ | 117 (8)$^{b2}$ | 25.2 (1.8)$^{b1}$ | 27.5 (1.6)$^{b1}$ |
|  | 20–30 | 0.129 (0.003)$^{c1}$ | 96.7 (0.4)$^{a1}$ | 79.6 (2.0)$^{b1}$ | 1.67 (0.06)$^{b1}$ | 36.5 (2.8)$^{b1}$ | 141 (6)$^{b1}$ | 22.5 (2.1)$^{b1}$ | 18.5 (1.1)$^{b2,3}$ |
| DP | 0–5 | 0.021 (0.001)$^{b4}$ | 95.8 (0.5)$^{a1}$ | 12.7 (0.8)$^{b4}$ | 0.296 (0.017)$^{b3}$ | 8.82 (0.42)$^{b3}$ | 24.1 (1.6)$^{a4}$ | 59.8 (3.9)$^{a1}$ | 13.4 (1.7)$^{b3}$ |
|  | 5–10 | 0.041 (0.004)$^{b3}$ | 95.1 (0.3)$^{a1}$ | 24.7 (2.6)$^{b3}$ | 0.641 (0.080)$^{b2}$ | 13.3 (0.7)$^{b2}$ | 51.1 (7.5)$^{a3}$ | 52.2 (11.7)$^{a1}$ | 19.1 (2.6)$^{b2,3}$ |
|  | 10–20 | 0.103 (0.006)$^{b2}$ | 95.7 (1.2)$^{a1}$ | 62.8 (3.3)$^{b2}$ | 1.51 (0.06)$^{b1}$ | 32.7 (0.5)$^{b1}$ | 127 (12)$^{ab2}$ | 54.2 (13.2)$^{ab1}$ | 29.8 (0.4)$^{b1}$ |
|  | 20–30 | 0.130 (0.005)$^{bc1}$ | 96.7 (1.2)$^{a1}$ | 80.0 (2.3)$^{b1}$ | 1.70 (0.08)$^{b1}$ | 33.2 (2.4)$^{b1}$ | 167 (8)$^{b1}$ | 39.2 (9.8)$^{b1}$ | 23.8 (4.4)$^{b1,2}$ |
| TP | 0–5 | 0.028 (0.002)$^{b3}$ | 93.2 (3.1)$^{a1}$ | 15.4 (1.5)$^{b3}$ | 0.345 (0.034)$^{b2}$ | 12.5 (1.1)$^{b2}$ | 32.8 (3.9)$^{a2}$ | 50.2 (10.1)$^{a1}$ | 12.1 (3.2)$^{b2}$ |
|  | 5–10 | 0.042 (0.002)$^{b3}$ | 89.7 (5.0)$^{a1}$ | 21.1 (1.3)$^{b3}$ | 0.520 (0.061)$^{b2}$ | 17.2 (1.6)$^{b2}$ | 42.1 (5.0)$^{a2}$ | 26.0 (8.0)$^{a1}$ | 15.0 (3.7)$^{b2}$ |
|  | 10–20 | 0.132 (0.008)$^{b2}$ | 79.1 (11.0)$^{ab1}$ | 56.0 (6.8)$^{b2}$ | 1.57 (0.27)$^{b1}$ | 48.0 (4.1)$^{b1}$ | 94.2 (17.6)$^{b1}$ | 27.2 (12.2)$^{b1}$ | 54.9 (6.5)$^{b1}$ |
|  | 20–30 | 0.181 (0.017)$^{b1}$ | 75.9 (14.0)$^{a1}$ | 76.0 (7.4)$^{b1}$ | 1.76 (0.15)$^{b1}$ | 55.2 (1.8)$^{b1}$ | 125 (24.9)$^{b1}$ | 18.8 (4.2)$^{b1}$ | 74.4 (13.2)$^{b1}$ |
| GS | 0–5 | 0.047 (0.007)$^{a3}$ | 81.2 (6.2)$^{b1}$ | 23.3 (2.4)$^{a3}$ | 0.923 (0.117)$^{a2}$ | 71.2 (15.7)$^{a2}$ | 28.3 (6.1)$^{a3}$ | 43.9 (18.9)$^{a1}$ | 53.3 (15.1)$^{a3}$ |
|  | 5–10 | 0.095 (0.025)$^{a3}$ | 70.4 (8.0)$^{b1}$ | 38.9 (5.5)$^{a3}$ | 1.54 (0.26)$^{a2}$ | 151 (41)$^{a2}$ | 62.8 (20.6)$^{a3}$ | 35.5 (7.4)$^{a1}$ | 147 (54)$^{a3}$ |
|  | 10–20 | 0.265 (0.042)$^{a2}$ | 57.4 (9.1)$^{b1}$ | 89.7 (5.8)$^{a2}$ | 3.35 (0.05)$^{a1}$ | 347 (41)$^{a1}$ | 190 (35)$^{a2}$ | 69.7 (10.8)$^{a1}$ | 475 (99)$^{a2}$ |
|  | 20–30 | 0.359 (0.034)$^{a1}$ | 49.9 (7.2)$^{b1}$ | 109 (10)$^{a1}$ | 3.44 (0.32)$^{a1}$ | 371 (36)$^{a1}$ | 281 (32)$^{a1}$ | 78.9 (19.2)$^{a1}$ | 708 (84)$^{a1}$ |

Table 2. Total soil nutrient concentrations integrated to 30-cm depth, mean ± (SE). Significant differences between sites ($P < 0.05$) for a nutrient are shown by different letters.

| Site | C | N | P | Mg | Ca | K | N:P |
|---|---|---|---|---|---|---|---|
| | g/m$^2$ | | | | | | |
| Short pocosin | 17200 (700)$^{a}$ | 401 (17)$^{b}$ | 8.56 (0.26)$^{c}$ | 30.1 (0.7)$^{b}$ | 6.86 (0.64)$^{b}$ | 6.38 (0.31)$^{c}$ | 46.9 (1.8)$^{a}$ |
| Drained pocosin | 16200 (600)$^{a}$ | 367 (12)$^{b}$ | 7.69 (0.23)$^{c}$ | 33.1 (2.4)$^{b}$ | 14.9 (2.7)$^{a}$ | 6.98 (0.58)$^{c}$ | 47.9 (1.9)$^{a}$ |
| Tall pocosin | 15000 (1400)$^{b}$ | 376 (42)$^{b}$ | 11.8 (0.4)$^{b}$ | 25.7 (4.5)$^{b}$ | 8.41 (2.32)$^{b}$ | 14.3 (1.8)$^{b}$ | 31.8 (3.2)$^{b}$ |
| Gum swamp | 23000 (1500)$^{a}$ | 802 (40)$^{a}$ | 82.9 (10.1)$^{a}$ | 51.7 (7.3)$^{a}$ | 18.8 (3.3)$^{a}$ | 128 (19)$^{a}$ | 10.1 (1.2)$^{c}$ |

with a pH $< 4$. Extractable $PO_4^{-3}$ was more than an order of magnitude greater in the gum swamp than in the pocosins on both sampling dates, but this difference was not statistically significant in March 1990 due to the large variation. No trend in extractable $NH_4^+$ concentrations was apparent between communities. Extractable $NO_3^-$ was much higher in the gum swamp than in the pocosins, but again the differences in March 1990 were not statistically significant because of the large variance in the gum swamp data. In May 1989, extractable $NO_3^-$ concentrations in the tall pocosin were very low and were below the detection limit in the drained pocosin.

Percent humic matter was 42 to 79% higher in the surface 10 cm of the gum swamp peat than in the pocosin peats (Table 4). The high cation exchange capacity (CEC) was similar in all communities. Percent base saturation was greatest in the drained pocosin, intermediate in the short pocosin and tall pocosin, and lowest in the gum swamp. Exchangeable Ca was less than half as great in the undrained sites as in the drained sites, likely due to contamination from road dust in the drained sites. No significant differences in exchangeable Ca occurred between the natural communities, while exchangeable Mg was significantly lower in the gum swamp than in the pocosins.

## DISCUSSION

### Hydrology

Although all three communities are classified as seasonally flooded or saturated palustrine wetlands, there were distinct differences in seasonal hydrology among them (Figure 2B, Table 5), with the gum swamp having the greatest seasonal change in water-table level and the short pocosin the smallest change. A similar highly seasonal water table was found in four forested communities in the Dismal Swamp in Virginia (Day et al. 1988), although those sites had extensive surface flooding in the winter and early spring.

Seasonal water-table levels are governed by net differences in water inflows and outflows from the system. The large, seasonal water-table fluctuations in the gum swamp likely occurred due to reduced lateral seepage from Great Lake during low water periods and high evapotranspiration because of its large aboveground biomass. Similarly, the tall pocosin likely had greater seasonal water-table fluctuations than the short pocosin due to its greater aboveground biomass and, hence, greater evapotranspiration.

Potential evapotranspiration accounted for approximately two-thirds of annual water loss from these peatlands (Figure 2). Richardson and Gibbons (1992) simulated actual evapotranspiration and run-off from a typical pocosin for a 20-year period and similarly found that evapotranspiration was 66% of annual precipitation. Run-off was highest during the winter and lowest during the summer due to increased evapotranspiration (Richardson and Gibbons 1992). Daniel (1981) found that nearly 70% of water output in a pocosin was through evapotranspiration if rainfall was in the summer and fall, but water output shifted to run-off if precipitation occurred in winter and spring. Our water-table data (Figure 2B) indicate that pocosins have a large residual (or unused) water storage capacity in summer and fall but a limited residual storage capacity in winter and spring. Seasonal changes in storage capacity and associated changes in run-off of fresh water from pocosins may, in turn, affect seasonal dynamics in adjacent estuaries (Brinson 1991).

Depth of rusting on steel rods is an indicator of the extent of the aerobic zone in wetlands, and close correspondence between steel-rod rusting depth and water-table depth has been found in peatlands (Bridgham et al. 1991a). Both the water-table and steel-rod data (Figures 2B, 3, Table 5) indicate a significant portion of the peat profile is aerobic during the warmest period of the year in all three communities, particularly in the tall pocosin and gum swamp. The warm-temperate climate and pronounced water-table drawdown during the growing season when decay rates are rapid result in the highly decomposed hemic-sapric peat of pocosins. The highly recalcitrant soil organic matter is the likely reason these peatlands can exist under this climate (Bridgham 1991, Bridgham and Richardson 1992b). However, anaerobic conditions remain important in depressing soil carbon cycling rates in po-

Table 3. Extractable soil nutirent concentrations and pH from 0–10 cm depth on 2 dates, mean ± (SE). Significant differences between sites at each sampling date ($P < 0.05$) are shown by different letters.

| Site | pH | $PO_4$-P | $NH_4$-N | $NO_3$-N |
|---|---|---|---|---|
| | | µg/cm$^3$ | | |
| May 3, 1989 | | | | |
| Short pocosin | 3.94 (0.01)$^{a}$ | 0.075 (0.013)$^{b}$ | 0.610 (0.442)$^{a}$ | 0.042 (0.013)$^{b}$ |
| Drained pocosin | 3.89 (0.10)$^{a}$ | 0.031 (0.005)$^{b}$ | 0.159 (0.039)$^{a}$ | 0.000 (0.000)$^{b}$ |
| Tall pocosin | 3.71 (0.04)$^{b}$ | 0.053 (0.012)$^{b}$ | 0.100 (0.063)$^{a}$ | 0.005 (0.002)$^{b}$ |
| Gum swamp | 3.92 (0.05)$^{a}$ | 0.865 (0.243)$^{a}$ | 0.440 (0.349)$^{a}$ | 0.449 (0.136)$^{a}$ |
| March 19, 1990 | | | | |
| Short pocosin | 3.74 (0.05)$^{a}$ | 0.073 (0.004)$^{a}$ | 0.186 (0.144)$^{a}$ | 0.078 (0.014)$^{a}$ |
| Tall pocosin | 3.64 (0.12)$^{a}$ | 0.072 (0.003)$^{a}$ | 0.241 (0.156)$^{a}$ | 0.033 (0.012)$^{a}$ |
| Gum swamp | 3.99 (0.12)$^{a}$ | 1.14 (0.72)$^{a}$ | 0.256 (0.129)$^{a}$ | 0.390 (0.213)$^{a}$ |

cosins, as drained pocosins have much higher decomposition rates than those with unaltered hydrology (Bridgham et al. 1991b).

## Biogeochemistry

The biogeochemical data demonstrate large nutrient differences between the pocosins and the gum swamp (Table 5). This result agrees with the classical concept developed in northern peatlands that ombrotrophic peatlands, such as the pocosins, are nutrient-poor, while minerotrophic peatlands, such as the gum swamp, are relatively nutrient-rich (Moore and Bellamy 1974, Mitsch and Gosselink 1986). Gum swamp peat had a significantly lower N:P ratio and organic matter content and greater total soil nutrients and extractable $PO_4^{-3}$ and $NO_3^-$ in May 1989 than the pocosins (Table 5). Nutrient differences between the short pocosin and tall pocosin are more difficult to demonstrate, with only total soil P, K, and N:P ratios being significantly different and no significant differences in extractable nutrients.

Thus, our soil data support the hypothesis that nutrients, possibly in conjunction with hydrology, are responsible for the community gradient between pocosins and swamp forests, but the data provide only weak support for soil nutrients differentiating short and tall pocosins (Table 5). The very large differences in seasonal hydrology observed between short and tall pocosins may be of primary importance in differentiating these communities. Nevertheless, a study by Walbridge (1991) supports the hypothesis that this community gradient is at least partially the result of differences in nutrient availability. He found significant increases from short pocosin to tall pocosin to bay forest (a community similar to our gum swamp designation) in total soil P, annual $PO_4^{3-}$ supply to anion-exchange resin bags, and microbial biomass P. Changes in nutrient availability between short and tall pocosins were smaller than between pocosins and the bay forest, as in our study.

Pocosin vegetation may be responding to subtle soil nutrient differences not readily discerned by traditional methods. Significant differences do occur between all three communities in nutrient concentrations and annual nutrient return in litterfall, nutrient-use efficiency, and belowground-aboveground C allocation dynamics (Table 5, Bridgham 1991, Walbridge 1991). For example, P return in litterfall was 32, 174, and 626 mg m$^{-2}$ yr$^{-1}$ in the short pocosin, tall pocosin, and gum swamp, respectively, reflecting differences in both mass and P concentration of litter (Bridgham 1991). Several investigators have found pocosin vegetation to be P-limited, with N occasionally co-limiting growth

Table 4. Percent humic matter (%HM), cation exchange capacity (CEC), percent base saturation of CEC (%BS), exchangeable Ca and Mg concentrations, and Ca:Mg molar ratio from 0–10 cm soil depth for short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP), mean ± (SE). Significant differences between sites ($P < 0.05$) are shown by different letters.

| Site | %HM | CEC (cmol 100/cm$^3$) | %BS | Ca (µg/cm$^3$) | Mg (µg/cm$^3$) | Ca:Mg |
|---|---|---|---|---|---|---|
| SP | 1.7 (0.1)$^{b}$ | 1.17 (0.10)$^{a}$ | 22 (2)$^{b}$ | 32.4 (6.5)$^{b}$ | 32.5 (6.6)$^{a}$ | 0.61 (0.02)$^{c}$ |
| DP | 1.2 (0.2)$^{b}$ | 1.37 (0.03)$^{a}$ | 36 (2)$^{a}$ | 86.2 (13.8)$^{a}$ | 32.8 (4.9)$^{a}$ | 1.70 (0.34)$^{a}$ |
| TP | 0.9 (0.1)$^{b}$ | 1.21 (0.06)$^{a}$ | 20 (1)$^{b}$ | 30.8 (3.6)$^{b}$ | 26.0 (1.0)$^{a}$ | 0.72 (0.07)$^{bc}$ |
| GS | 7.1 (1.7)$^{a}$ | 1.13 (0.08)$^{a}$ | 16 (1)$^{c}$ | 25.9 (5.2)$^{b}$ | 13.7 (2.1)$^{b}$ | 1.14 (0.15)$^{ab}$ |

Table 5. A summary of the hydrologic and biogeochemical differences between three peatland communities on the North Carolina Coastal Plain. See text for details.

| Variable | Short Pocosin | Tall Pocosin | Gum Swamp |
|---|---|---|---|
| Hydrology | | | |
| Trophic status | Ombrotrophic | Weakly Minerotrophic? | Minerotrophic |
| Water table | Perched | Not perched? | Not perched |
| Seasonal water table change | Smallest | Large | Largest |
| Surface soil moisture | Highest | Lowest | Intermediate |
| Soil oxidation zone | Smallest | Large in growing season | Large in growing season |
| Groundwater loss | Low | Low | Low |
| Evapotranspiration | Smallest | Intermediate | Largest |
| Biogeochemistry | | | |
| Peat depth | 1 to 5 m | $\leq 1.5$ m | $\leq 1$ m |
| Soil | Medisaprist | Medisaprist | Medisaprist |
| Bulk density | Lowest | Low | Highest |
| % Organic matter (0–30 cm) | 95 to 97% | 76 to 93% | 50 to 81% |
| Soil pH | $<4$ | $<4$ | $<4$ |
| Total nutrient concs. | Lowest P & K; low N, Mg, Ca | Low N, P, Mg, Ca, K | Highest N, P, Mg, Ca, K |
| N:P ratio | Highest | Intermediate | Lowest |
| Extractable nutrient concs. | Low $PO_4$ & $NO_3$, avg. $NH_4$ | Low $PO_4$ & $NO_3$, avg. $NH_4$ | High $PO_4$ & $NO_3$, avg. $NH_4$ |
| % Humic matter | Low | Low | High |
| CEC | High | High | High |
| % Base saturation | Low | Low | Lowest |
| Ca:Mg ratio | $<1$ | $<1$ | $>1$ |
| % Exchangeable nutrients | Low N & P; high Mg & Ca | Low N & P; high Mg & Ca | Low N; higher P; high Ca; lowest Mg |
| P mineralization[1] | Low | Low | High |
| Anion exchange resin-P[1] | Lowest | Low | Highest |
| Nutrient return in litterfall[2] | Lowest | Intermediate | Highest |
| Nutrient use efficiency[2] | High N; highest P | High N; intermediate P | Lowest N and P |
| Below-/aboveground C allocation[2] | High | Low | Low |

[1] From Walbridge 1991.
[2] From Bridgham 1991.

(Woodwell 1958, Maki 1974, MacCarthy and Davey 1976, Wilbur and Christensen 1983, Simms 1987). High N:P ratios also indicate that P is likely to be the major limiting nutrient in pocosins.

The Ca:Mg molar ratio has been used as an indicator of the importance of the influence of mineral soil water, with a ratio of approximately 1 proposed as the minerotrophic/ombrotrophic boundary ( cf. Waughman 1980, Clymo 1983, Shotyk 1988). The gum swamp had an exchangeable Ca:Mg ratio slightly greater than 1, while the short and tall pocosins had ratios less than 1 (Tables 4, 5), indicating a weak gradient of increasing mineral influence from the pocosins to the gum swamp. The drained pocosins were likely influenced by dust from adjacent dirt roads with greater percent base saturation, exchangeable Ca, and exchangeable Ca:Mg ratio from 0- to 10-cm soil depth.

Exchangeable base metal cations did not effectively differentiate the natural communities (Tables 4, 5), despite the distinct differences in total cations (Table 2). This lack of correspondence between the two fractions is at least partially explained by the lower percentage of base cations in exchangeable form in the more minerotrophic sites. From 0- to 10-cm depth, 73–76% of the Mg was exchangeable in the pocosins, but only 34% was exchangeable in the gum swamp. The majority of Ca (> 76%) was exchangeable in all communities. Less than 1% of N and P were in the extractable form in all communities.

Community-oriented studies have often employed factorial analyses of species assemblages and related environmental variables. Christensen et al. (1988) used detrended correspondence analysis on plant communities in the Croatan National Forest occurring on peat and hydric mineral soils. Pocosin stands had greater peat depth, exchangeable Mg and K, and CEC and lower bulk density, extractable P, Ca:Mg ratios, and pH. The age of the oldest trees on the stands was also significant, reflecting the high fire frequency in pocosins. Bridgham et al. (1991b) used a principal components analysis to differentiate physiochemical soil variables among short pocosin, tall pocosin, gum swamp and several disturbed NC peatland communities. They found that the first axis ($R^2 = 0.52$) was correlated with the N:P ratios, extractable $PO_4^{-3}$ and $NO_3^-$, total N and P, organic matter content, pH, soil moisture, and water-table depth.

Hydrology could also influence differences in nutrient supply, either through enhanced nutrient cycling in aerated soil or by supplying tall pocosins and gum swamps with diffuse nutrients from upslope short pocosins. Greater productivity and nutrient cycling have been found in downslope areas due to the transfer of nutrients in water from upslope ecosystems in tundra (Chapin et al. 1988) and in northern peat bogs (Damman 1986). The importance of the depth of the soil aeration zone is indicated by the band of taller vegetation immediately adjacent to drainage ditches in short pocosin (e.g., the drained plots in this study).

### A Comparison with the Bog-Fen Gradient

The classical bog-fen gradient of northern peatlands provides an interesting contrast to the shrub-swamp forest gradient in North Carolina peatlands. The decreasing percent organic matter and N:P ratios and increasing total soil nutrients and extractable $PO_4^{-3}$ concentrations from the pocosins to the gum swamp strongly indicate an ombrotrophic to minerotrophic gradient (Table 5).

Most investigations into the bog-fen gradient have focused on water chemistry; however, several studies do report soil nutrient values (Richardson et al. 1978, Waughman 1980, Clymo 1983, Mitsch and Gosselink, 1986 p. 296, National Wetlands Working Group 1988, Faulkner and Richardson 1989, Vitt and Chee 1990). Gorham (1967) indicated that along the bog-poor fen-rich fen gradient, soil pH increases from < 4 to circumneutral, organic matter content decreases, and percent acid-soluble Ca increases. Exchangeable Ca, and to a lesser extent exchangeable Mg, increases along the bog-fen gradient (Richardson et al. 1978, Waughman 1980, Clymo 1983, Faulkner and Richardson 1989). Total soil K and Ca often show large increases along the gradient, with Mg increasing somewhat less (Richardson et al. 1978, Waughman 1980, Clymo 1983). Gorham et al. (1985) stated that as the organic matter content exceeds 85% dry mass in peatlands, $H^+$ ions begin to dominate cation exchange reactions. Base saturation drops from greater than 50% in fens to between 2 to 25% in bogs. Northern minerotrophic swamp forests often have soil and water chemistry similar to fens (Schwintzer and Tomberlin 1982, Shotyk 1988).

By contrast, all the natural communities in our study had a pH < 4 and similar exchangeable Ca concentrations, and the lowest percent base saturation and exchangeable Mg concentration occurred in the minerotrophic gum swamp (Tables 3–5). These results indicate that pH and exchangeable base cations, so often used to discriminate the trophic status of northern peatlands, do not effectively differentiate peatland community gradients on the NC Coastal Plain, where the N and P status are much better predictors of community-type, especially between pocosins and swamp forests (Table 5, Walbridge 1991). A probable explanation for low base cation availability in minerotrophic NC peatlands is the nature of the underlying mineral strata. Many northern peatlands are underlain by glacial till or ancient glacial lake sediments. The Lower Coastal Plain of North Carolina is formed from a series of ancient marine terraces, and the soils have a high proportion of sand with low cation availability (Otte 1981, Daniels et al. 1984, SCS 1989). Shotyk (1988) noted the importance of mineral substrata in determining the chemistry of soil and water in peatlands. Minerotrophic peatlands underlain by calcareous rock will have relatively high pH and Ca concentrations, while those in siliceous terrains will have low pH and low Ca concentrations.

The close correlation often found between basic cations and pH and northern peatland plant community composition may not reflect nutrient limitation of the plants. These plant communities have generally been found to be P, N, or K limited (Heilman 1966, 1968, Waughman 1980, Mitsch and Gosselink 1986, and refs. therein). Vitt and Chee (1990) found that vascular plant occurrence in western Canadian fens was primarily associated with nutrient levels (i.e., N and P), while bryophyte occurrence was associated with alkalinity-acidity factors. High $Ca^{2+}$ concentrations and high pH inhibit many *Sphagnum* species (Clymo and Hayward 1982), and, thus, the close correspondence between bryophyte communities and alkalinity-acidity factors likely reflect a toxicity rather than a nutrient gradient. As bryophytes are a minor component of the vegetation of these southern peatlands, this may provide a taxonomic basis for the differences observed in biogeochemical/community relationships between northern and southern peatlands. This biogeographical comparison suggests a need for further study of the nutrients likely to control plant growth in peatlands in addition to the historical emphasis on basic cations and pH.

## CONCLUSIONS

Soil chemistry data indicate an ombrotrophic to minerotrophic gradient between pocosins (short and tall) and swamp forests, with the gum swamp forest having lower organic matter content and higher nutrient concentrations (total and extractable N and P, total base cations). Soil chemistry poorly differentiated short and tall pocosins, with only total soil P, K, and N:P ratios being significantly different. However, large differences in hydrology existed among all three communities, with the short pocosin having the least seasonally variable water table. Differences in the hydrology and biogeochemistry of the three communities are summarized in Table 5.

Bogs and fens in northern peatlands are usually most successfully differentiated in terms of water and soil chemistry by exchangeable basic cations and pH. These variables did not successfully differentiate peatlands on the NC Coastal Plain, where N and P dynamics were much better descriptors of community-type.

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