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Patterns of phosphorus, nitrogen and δ^{15}N along a peat development gradient in a coastal mire, Panama

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Abstract: Differentiation of limiting nutrients within small spatial scales has been observed in coastal mangrove forests, but research on other tropical peatlands suggests it is a more widespread phenomenon. In the Changuinola mire of coastal Panama, oligotrophy was hypothesized to increase along a gradient of peat development (peat doming). Nutrient and carbon concentration of leaf tissue, soil, and soil porewater were characterised over a successive sequence of plant communities along the gradient. Soil phosphorus (P) and nitrogen (N) concentrations decreased from 1200 μg P g^{-1} and 27 mg N g^{-1} to 377 μg P g^{-1} and 22 mg N g^{-1} within 2.7 km into the mire interior. These changes coincided with an increase in soil and average leaf N:P molar ratios from 52–128 and 24–41, respectively. Soil P was strongly related to leaf P and soil N:P to foliar N:P. There was a wide range in δ^{15}N values for canopy (4.0 to −9.4‰), *Campnosperma panamense* (4.0 to −7.8‰) and understorey (4.8 to −3.1‰) species. Foliar δ^{15}N values of canopy species were strongly related to soil N:P, soil P and leaf P. The depleted foliar δ^{15}N values appeared to be an effect of both the N atmospheric source and P limitation. Here, P limitation is likely associated with ombrotrophic conditions that developed as hydrologic inputs became dominated by precipitation.

Key Words: biological-physical feedbacks, isotopes, N:P ratios, nutrient limitation, ombrotrophy

INTRODUCTION

Nutrient gradients are a common feature of many wetland ecosystems (Bragazza *et al.* 2005a, Feller *et al.* 2002, Paludan & Morris 1999, Walbridge 1991). Specifically, differentiation of limiting nutrients on small spatial scales has been observed throughout temperate latitudes where minerotrophic fens grade into ombrotrophic bogs in mire systems (Bridgham & Richardson 1993, Clarkson *et al.* 2004, Heinselman 1970). In undisturbed systems, late-successional bogs are often P-limited (Verhoeven *et al.* 1996). In tropical regions, mire systems are less well understood, but are likely as complex, and highly susceptible to anthropogenic activities related to agricultural expansion into remote areas.

Extensive research on coastal tropical peatlands of Holocene origin suggests decreasing fertility with distance into the interior peat bog that often correlates with decreasing aboveground biomass (Anderson 1983, Morley 1981, Phillips *et al.* 1997). This phenomenon has been linked to the development of coastal tropical peatlands as is described by Anderson's model of domed peat development. Here, a colonizing halophytic plant community stabilizes a developing shoreline, and with deposition and accumulation of terrigenous sediments and organic debris, leads to the progressive colonization of less salt-tolerant plants (Anderson 1964, 1983; Hughes & Barber 2003). With rainfall in excess of evaporation, thick peat develops, the surface becomes elevated above the influence of tidal and riverine flood waters that are relatively higher in nutrients, leading to oligotrophy in the most developed coastal peat deposits (Anderson 1964, 1983). Sequential development of more specialized plant associations resulting from a shortage of nutrients thus occurs. These specialized plant associations develop into differentiable 'phasic communities' that successively replace each other with increasing nutrient limitation, resulting in concentric rings around the most developed (domed) peat deposit (Anderson 1983, Morley 1981, Phillips *et al.* 1997). However, this pattern has not been investigated by evaluation of plant and soil nutrient characteristics in ways that have been done for many wetlands worldwide (Bedford *et al.* 1999, Clarkson *et al.*

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2004, Güsewell *et al.* 2003, Koerselman & Mueleman 1996). Yet their susceptibility to nutrient loading and growing evidence for their importance in global C sequestration merit such an investigation.

Nutrient limitation patterns have long been discerned by plant growth responses to nutrient additions (Güsewell 2004, Vitousek & Howarth 1991). Due to limitations of these methods, Koerselman & Meuleman (1996) proposed the use of the N:P ratio as an index to assess the nutrient limitation status of plant communities. Despite inconsistent indications of nutrient limitation (Güsewell 2004, Güsewell *et al.* 2003), many studies demonstrate how N:P ratios can be useful in determining the relative nutrient limitation in natural, unamended plant communities (Bedford *et al.* 1999, Güsewell *et al.* 2003, Morse *et al.* 2004). Leaf δ^{15}N analyses have advanced the use of the N:P ratio as a tool for assessing the degree of N and P deficiency in plant communities (Clarkson *et al.* 2005, Fry *et al.* 2000, McKee *et al.* 2002). Specifically, when plants are P limited, plant fractionation discriminates against the heavier ^{15}N isotope when plant demand for N is low and δ^{15}N values are consequently depleted in ^{15}N. The nitrogen isotopic signature of plants is also dependent on source of available N, especially where atmospheric N sources dominate, and as a function of rooting depth (Bragazza *et al.* 2005b, Kohzu *et al.* 2003).

In a coastal mire of Bocas del Toro Province, Panama, Anderson's model has been similarly applied to characterize the development of the peat deposit, and the vegetation, peat depth and peat age have been described for each 'phasic community' (Phillips *et al.* 1997). While several studies have demonstrated P limitation of bog plants and associated nutrient gradients (Bragazza & Gerdol 2002, Clarkson *et al.* 2005), the hypothesis that the sequential development of an ombrotrophic peat bog leads to differentiation of limiting nutrients in tropical coastal mires has not been investigated. Specifically, I hypothesized that soil P and N, foliar P and N, and foliar ^{15}N would decrease with distance into the interior bog-plain. As such, soil and foliar P and N would be positively related to and N:P negatively related to foliar ^{15}N. Thus, this paper identifies the relationships between peat development and patterns of nutrients and N isotopes to quantify changes in limiting nutrients leading to the development of ombrotrophy in a coastal mire of Panama.

METHODS

Study site

In the province of Bocas del Toro, Panama, the Changuinola mire is a 90-km^2 wetland area which developed on the western bank of Almirante Bay. A large portion of this wetland, the San San-Pond Sak, is a designated Ramsar site (Figure 1). This region of the Caribbean coast, predominantly from the southern coast of Costa Rica to the Chiriqui Lagoon of Panama encompasses an alluvial floodplain that drains numerous rivers from the Talamanca mountains (Phillips *et al.* 1997). This wetland assemblage type represents less than 0.5%, and the tropical bog therein, only 0.02% or 1300 ha of natural vegetation cover in the country of Panama, and is therefore a geographically unique resource (Correa *et al.* 2004).

Aerial maps, vegetation composition describing each community (Phillips *et al.* 1997) and a GPS were used to identify and delineate four freshwater phasic communities along a 2.7-km transect from the swamp coastal exterior to the interior bog-plain. These plant community zones were differentiated by identifying the unique associations of species present at each 300-m location along the transect as described by Phillips et al. (1997). These species included *Campnosperma panamense* Standl., *Symphonia globulifera* L.f., *Chrysobalanus icaco* L., *Raphia taedigera* (Mart.) Mart., *Euterpe precatoria* (Mart.) Mart., *Cyrilla racemiflora* L., *Myrica mexicana* Humb. & Bonpl. ex Willd., *Dieffenbachia longispatha* Engl. & K. Krause, *Cyperus* sp. and *Nephrolepis* sp. The coastal margin of the deposit was located at N 9°25′40.1″ and W 82°24′00.6″ and the terminus of the transect in the domed, interior portion of the mire was located at N 9°24′43.2″ and W 82°24′47.7″. These locations correspond to ages of approximately 4000 and <800 y BP, respectively, based on radiocarbon dates and peat palyno-stratigraphy of the peat deposit (maximum peat elevation = 6.7 m; Phillips *et al.* 1997). This work also showed that *Raphia taedigera*, a large palm with a wide tropical distribution, served as the colonizer initiating the peat development sequence in this coastal freshwater swamp. The average temperature is 26 °C with annual rainfall of 3–5 m (Lovelock *et al.* 2004).

Samples of live leaf tissue, senesced leaves (collected from live plants), soil porewater and soils were collected every 0.3 km along the transect, and samples were pre-processed at the Smithsonian Tropical Research Institute's Bocas del Toro laboratory facility. Tissue samples were dried at 70 °C and sealed in plastic bags. Tissue was then transported to Florida International University, ground to a homogeneous powder (<500 μm), and analysed for total N, total P and total carbon (C) concentration. Leaf tissue samples were also sent to the University of California, Davis Stable Isotope Facility for ^{15}N analyses.

Soil was extracted with a 2.5-cm-diameter serrated plastic coring tube. Roots were removed from the top 15 cm of soil of each core and two subsamples were dried to a constant weight at 70 °C for soil moisture (wet-dry/dry). One subsample was then ashed at 500 °C for 4 h to determine organic matter content. The other subsample was analysed as leaf tissue for N, P and C concentration.

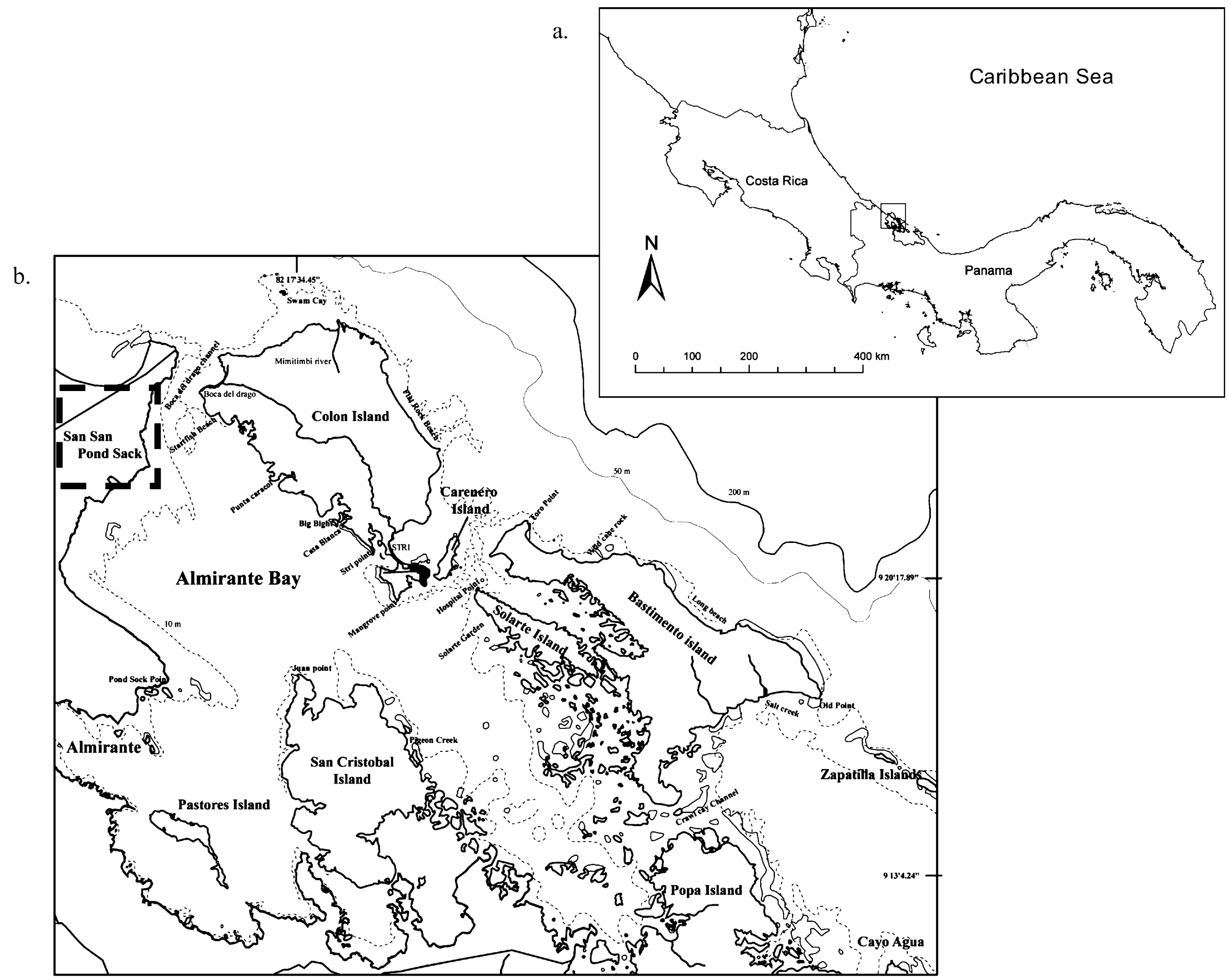

Figure 1. Central America showing Caribbean coast of Panama and Costa Rica with box outlining the Bocas del Toro archipelago and sections of mainland Bocas (a). Study site of the San San Pond Sak wetland outlined with dashed box (also Changuinola mire) (b).

Porewater was extracted with a 120-mL syringe from porewater 'sippers' (aquarium air stones equipped with fine Tygon® tubing and sealed with teflon tape; Dailey 2000) placed 15 cm into the soil. Water samples were filtered (GF/F) within 24 h and frozen until analyses at Florida International University.

Leaf and soil samples were analysed for TC and TN with a Carlo Erba elemental analyser. The modified Solorzano & Sharp (1980) method was used to analyse leaf and soil TP. Leaf tissue samples were analysed for ^{15}N on a continuous-flow isotope-ratio mass spectrometer with atmospheric air as the reference standard (Europa Hydra 20/20, PDZ Europa, Sundbach, England, UK). Water samples were analysed for soluble reactive phosphorus (SRP), ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and dissolved organic carbon (DOC). Analyses of water samples for SRP, NH_4^+, NO_3^- and NO_2^- concentrations were determined on a four-channel auto-analyser (Alpkem model RFA 300, OI Corporation, College Station, TX, USA). DOC concentration was determined using a hot platinum catalyst, direct injection analyser (Shimadzu model TOC-5000, Shimadzu Corportation, Kyoto, Japan).

Nutrient status at each 0.3-km location along the 2.7-km transect was assessed utilizing leaf nutrient indices of dominant species (concentrations, nutrient ratios) and soil N and P concentrations and soil N:P molar ratio. Linear regression was used to determine variation explained in leaf tissue and soil nutrient concentration, leaf δ^{15}N values and porewater nutrient and C concentration using distance into the interior bog plain as the independent variable. Linear regression was also used to determine relationships between soil nutrients and leaf nutrient concentrations, leaf molar ratios and leaf δ^{15}N values as well as relationships between leaf nutrient concentrations and leaf δ^{15}N values. All data followed a normal distribution. The statistical software JMP© was used for data analyses.

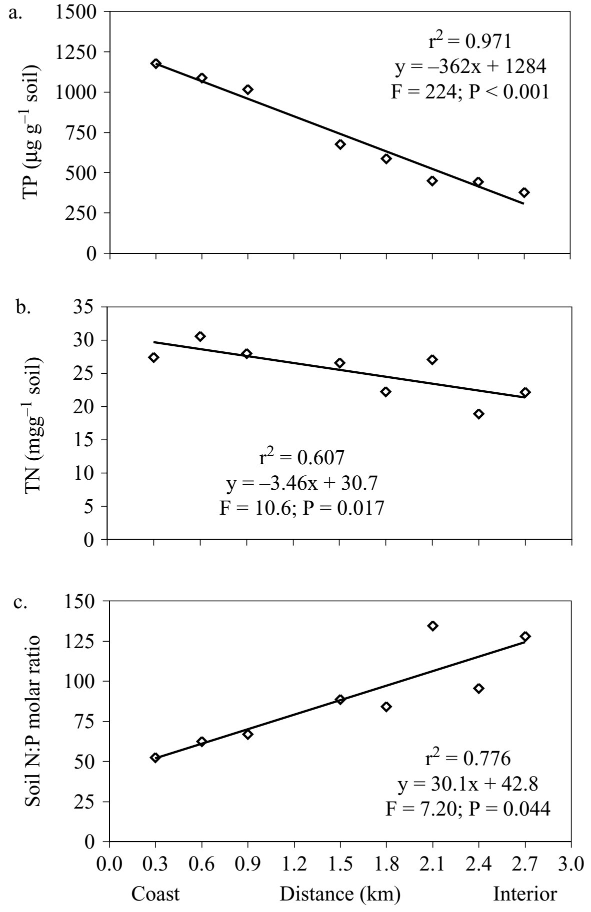

Figure 2. Soil nutrient concentrations along a 2.7-km transect from wetland exterior to interior bog-plain. Soil total phosphorus (μg P g^{-1} soil) (a); soil total nitrogen (mg N g^{-1} soil) (b); soil N:P molar ratio (c).

RESULTS

Patterns of soil P and N along the gradient

Soil P and N concentrations declined with distance from the coast inland along the transect (Figure 2a, b). As there was a greater decline in P concentrations than N concentrations, soil N:P ratio declined along this gradient, suggesting increasing P limitation with distance from the coast (Figure 2c). In general, dissolved nutrient concentrations revealed low availability of inorganic nutrients in soils. Dissolved nutrient concentrations averaged over the transect locations were $3.09 \pm 0.70\ \mu$M N, $1.79 \pm 0.55\ \mu$M N, and $0.11 \pm 0.04\ \mu$M P for NH_4^+, $NO_3^- + NO_2^-$, and SRP, respectively. Dissolved OC concentrations were $1081 \pm 110\ \mu$M. Only soil porewater $NO_3^- + NO_2^-$ concentrations exhibited a significant decline where distance from the coast explained 47% of the variation found in $NO_3^- + NO_2^-$ concentrations ($r^2 = 0.471$; $y = -2.22x + 5.56$; $F = 14.3$; $P = 0.0017$). Average organic matter content and soil moisture were 88 ± 3% and 92 ± 1%, respectively, and did not vary along the transect.

Patterns of foliar N and P

The range in P and N for canopy species was 0.040–0.161 %P and 0.817–1.85 %N. Distance along the gradient explained 68% of the variation in leaf tissue P concentrations and 20% of the variation in leaf N concentrations (Figure 3a, b). In *Campnosperma panamense*, the species occurring with the greatest frequency along the gradient, the range was 0.063–0.144 %P and 0.787–1.40 %N. *Campnosperma panamense* exhibited a decline in both P and N leaf tissue concentrations toward the interior of the wetland. Distance explained 82% and 46% of variation in leaf P and N concentrations along the transect, respectively (Figure 3c, d). The range in P and N for understorey species was 0.029–0.183 %P and 0.493–2.15 %N. Understorey species exhibited strong declines in leaf tissue P and N, and distance explained 93% and 73% of variation along transect, respectively (Figure 3e, f).

Patterns of foliar N:P ratio and δ^{15}N

The range in N:P molar ratio for canopy species, *Campnosperma panamense*, and understorey species was 17–74, 19–37, and 26–38, respectively. Despite a low coefficient of determination between transect distance and leaf N concentrations, there was a significant increase in canopy N:P values along the transect (Figure 4a). In general, a transition from N to P limitation occurred in canopy species found 1.8-km into the wetland. In *Campnosperma panamense*, N:P also generally increased with P, N limitation and co-limitation expressed at different locations along the transect (Figure 4b). No other single canopy species exhibited clear gradients in N:P ratios. Foliar N:P ratios of understorey species exhibited a trend of intraspecific expression of either N or P limitation that emerged in zones that were indicated to be either N (0.3–0.9 km) or P (2.1–2.7 km) limited by N:P ratios of canopy species and soil (Figure 4c). A general replacement of understorey species was observed along the gradient i.e. *Nephrolepis* sp. and *D. longispatha* were noted only in the 0.3–0.9-km subsection with *Cyperus* sp. found along the 1.2–2.7-km subsection of the transect.

The range of δ^{15}N values for canopy, *Campnosperma panamense* and understorey species was 4.03 to −9.37‰, 4.03 to −7.77‰, and 4.84 to −3.14‰, respectively. Leaf tissue δ^{15}N values declined significantly with distance from the coast into the bog interior in all three species groups (Figure 4d, e, f). Distance from the coast explained greater than 60% of the variation in canopy species

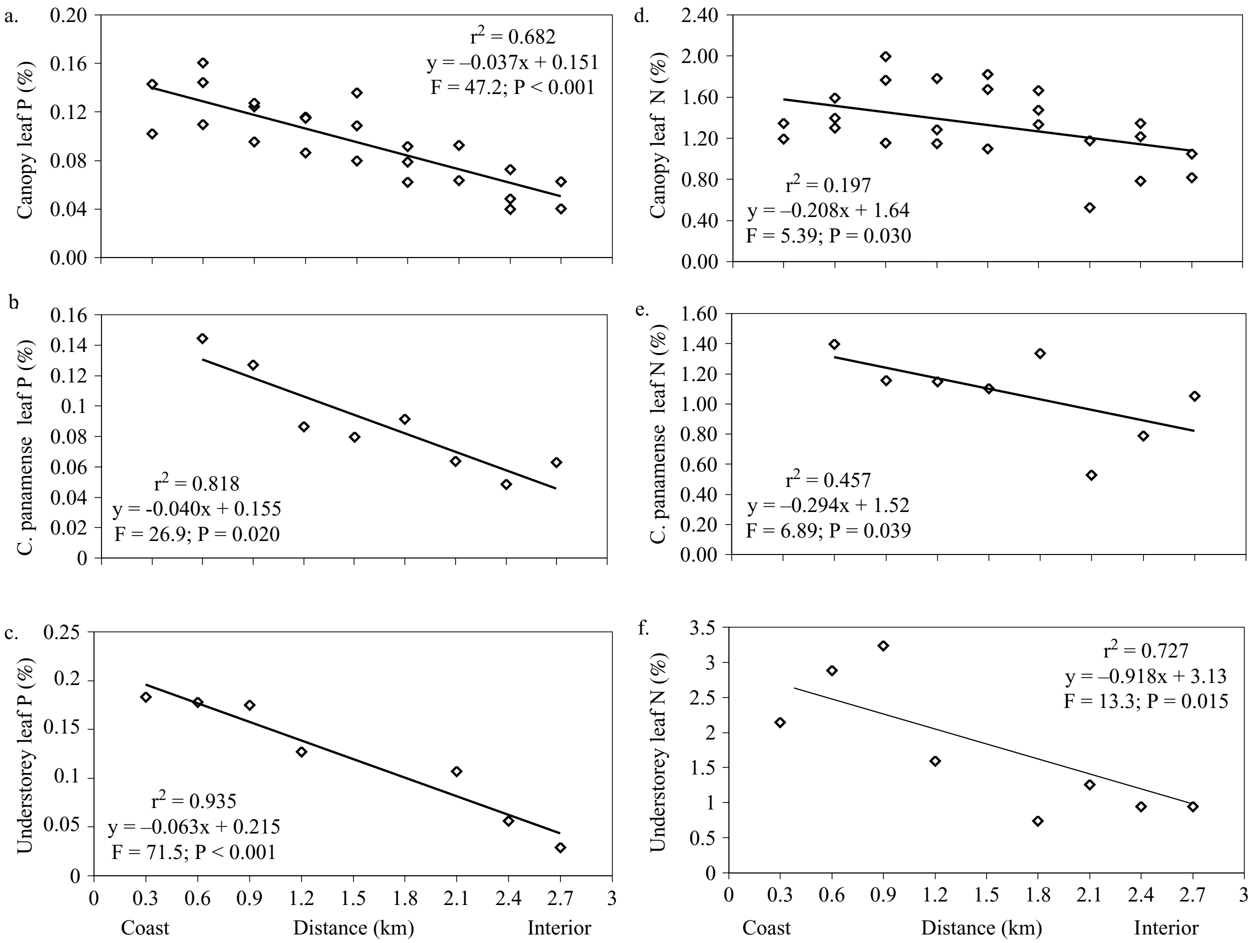

Figure 3. Leaf tissue phosphorus and nitrogen along a 2.7-km transect from wetland exterior to interior bog-plain. Leaf tissue phosphorus (% P) in canopy species (data points are individual species) (a); leaf tissue nitrogen (% N) in canopy species (data points are individual species) (b); leaf tissue phosphorus (% P) in *Campnosperma panamense* (c); leaf tissue nitrogen (% N) in *Campnosperma panamense* (d); leaf tissue phosphorus (% P) in understorey species (e); leaf tissue nitrogen (% N) in understorey species (f).

leaf δ^{15}N values (Figure 4d). However, interspecific variation likely led to lower explanatory power in canopy species when compared to relationships for *Campnosperma panamense* and understorey species (Figure 4e, f).

Predicting foliar N, P, N:P and δ^{15}N with soil N and P

The single best predictor of canopy foliar δ^{15}N values and N:P ratio was soil N:P that described 83% and 81% of the variation, respectively (Table 1). Soil P was a better predictor of foliar P concentration than soil N:P, but soil P explained slightly less variability in canopy δ^{15}N values. Both soil N and soil P were good predictors of leaf tissue P and C:P ratio, but soil P described slightly more variation in these two parameters (71 and 63%, respectively; Table 1). Variation in leaf N concentration was not related to soil N, P or N:P, but soil N was important in describing variation in foliar C:N ratio.

Predicting δ^{15}N with foliar N, P and molar ratios

Linear regression analyses revealed strong relationships between canopy leaf nutrients and leaf δ^{15}N values. Leaf tissue P and N concentration were positively related to and explained 71% and 28% of the variation in leaf δ^{15}N values, respectively (Table 2). Leaf N:P molar ratio was negatively related to leaf δ^{15}N values, explaining 26% of the variation in this relationship (Table 2). Along the transect, C:N and C:P explained more variation in leaf δ^{15}N values than leaf N concentration or N:P ratio, and both were negative relationships (Table 2).

DISCUSSION

N:P ratios and patterns of nutrient limitation

In this study, coupling patterns of leaf N:P ratios and δ^{15}N values was an effective means of assessing relative

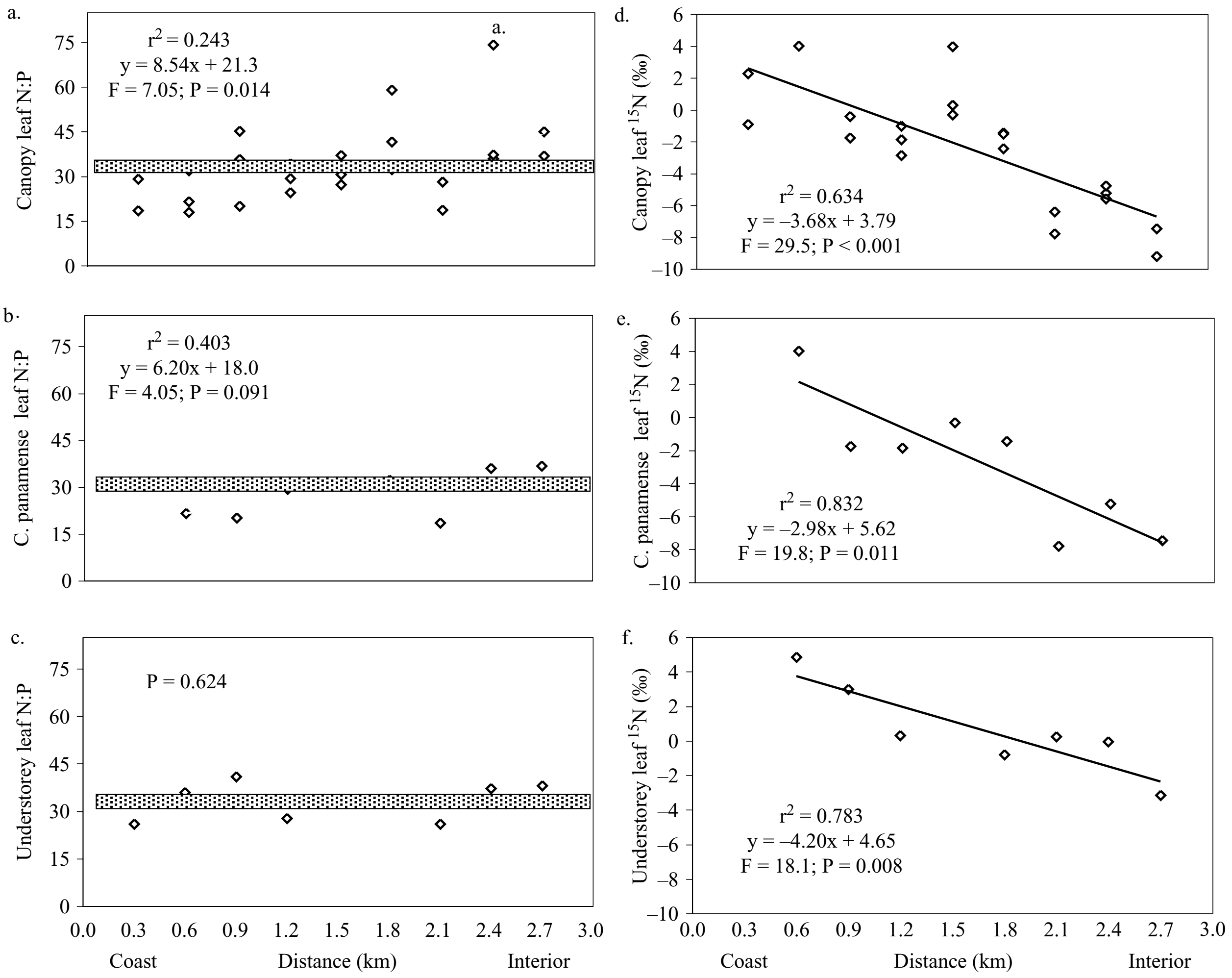

Figure 4. Leaf N:P ratio and zone of co-limitation of N and P (shaded black box) along a 2.7-km transect from wetland exterior to interior bog-plain. Canopy (data points are individual species) (a); *Campnosperma panamense* (b); understorey species (c). Leaf tissue δ^{15}N values along a 2.7-km transect from wetland exterior to interior bog-plain. Canopy (data points are individual species) (d); *Campnosperma panamense* (e); understorey (f).

nutrient limitation patterns to plants. A dramatic decline in leaf δ^{15}N values for canopy species was observed from the coastal zone into the interior bog zone. These values coincided with a strong linear decrease in soil P concentrations, a decrease in soil N concentrations, and an increase in soil N:P values. There was also a concurrent increase in N:P values for canopy species that coincided with a shift from large canopy trees that became stunted as herbaceous species dominated vegetation structure. Collectively, these data show a shift to low nutrient

Table 1. Relationships between soil nutrients and leaf tissue P, N and δ^{15}N of canopy species averaged for each transect location along the 2.7-km transect from wetland exterior (0.3 km) to interior bog-plain (2.7 km) in canopy species.

Soil (X)	Leaf (Y)	slope	intercept	r²	n	F	P
Soil P	% P	0.0001	0.046	0.753	7	15.3	0.013
	N:P	−0.018	46.3	0.621	7	8.18	0.035
	C:P	−1.07	2105	0.621	7	8.18	0.035
	δ^{15}N	0.011	−10.8	0.784	8	21.7	0.004
Soil N	% P	0.006	−0.059	0.592	8	8.70	0.026
	C:N	−1.8	90.1	0.513	8	6.33	0.046
	C:P	−109	4255	0.547	8	7.24	0.036
Soil N:P	% P	−0.001	0.167	0.593	7	7.29	0.043
	N:P	0.240	11.9	0.810	7	21.3	0.006
	δ^{15}N	−0.126	8.62	0.830	8	29.4	0.002

Table 2. Predicting δ^{15}N with foliar N, P and nutrient ratios along the 2.7-km transect from wetland exterior (0.3 km) to interior bog-plain (2.7 km) in canopy species.

Leaf (X)	Leaf (Y)	slope	intercept	r^2	n	F	P
P	δ^{15}N	88.8	−10.0	0.709	8	41.4	< 0.001
N		6.08	−9.97	0.282	8	6.68	0.019
N:P		−0.132	2.87	0.262	8	6.03	0.025
C:N		−0.183	6.25	0.360	8	9.58	0.007
C:P		−0.004	4.28	0.637	8	29.9	< 0.001

status within a short distance into the interior bog plain.

Values of δ^{15}N have also been successfully employed to indicate differential nutrient limitation to plants in a coastal mangrove system of Belize (McKee *et al.* 2002). In that study, a strong negative relationship between leaf δ^{15}N values and N:P ratios of leaf tissue was found. This was concluded to be a result of high N demand by plants that were N-limited and low N demand by plants that were P-limited. Interestingly, the range of values in that study was +1‰ in the N-limited, fringe zone to −5.38‰ in the P-limited, dwarf zone, as compared with nearly a 12‰ difference between N- and P-limited zones of this study. Studies of plants across nutrient gradients of restiad (dominated by Restionaceae) raised bogs in New Zealand demonstrate similarly depleted leaf δ^{15}N values with P limitation and a similar range in values as was found in this study (12‰, Clarkson *et al.* 2005). Given that both bogs likely depend on atmospheric deposition as the primary nutrient (N) source and are P-limited, these factors working in concert would drive ^{15}N values of plants growing on the bog surface to be more depleted when compared with plants in the Belize mangrove wetlands. However, the Clarkson *et al.* (2005) study did not conclude that N source influenced foliar δ^{15}N values.

Rooting depth, mycorrhizal associations and nutrient conservation strategies have also been cited as important factors influencing foliar δ^{15}N values (Kohzu *et al.* 2003, McKee *et al.* 2002, Michelsen *et al.* 1996). Interspecific differences among canopy species in nutrient acquisition strategies may in part explain the weak relationship with leaf N. Rooting depth is probably not a factor influencing N availability for understorey species as canopy species have more depleted ^{15}N values when growing on the bog surface (deeper rooting depth causes mire plants to be more enriched in ^{15}N; Kohzu *et al.* 2003). Thus, replacement of species along the gradient, and adaptations to their respective high- or low-nutrient environments, probably explains the close relationship between ^{15}N and N concentration in understorey species. Overall, for canopy species growing on the bog surface, more depleted values may thus be attributed to higher demand for P when compared with *Cyperus* sp., a species that is likely highly adapted to the low-nutrient conditions of the bog surface. This contention is supported by the dominance of *Cyperus* sp. and the stunted canopy trees present in the mire interior.

Synchronous nutrient patterns and evidence for biological-physical feedbacks

Mechanisms for differentiation of limiting nutrients in wetland systems include direct and indirect effects on soil biogeochemistry associated with underlying substrate, hydrologic source, sediment deposition and salinity (Anderson 1983, Bridgham & Richardson 1993, Chen & Twilley 1999, McKee *et al.* 2002, Paludan & Morris 1999). Evidence suggests similar gradients in tropical peatlands (Page *et al.* 1999), but to date have only been demonstrated for mangrove wetlands (Boto & Wellington 1983, 1984; Chen & Twilley 1999, Feller *et al.* 2002). Considering suggestions made by previous palaeoecological work on the development of this coastal peatland (Phillips *et al.* 1997), it appears that as the degree of nutrient deficiency increased over time, plant community associations typified by low phosphorus and nitrogen status developed. Ombrotrophy, or the status of isolation from groundwater sources, is a defining characteristic of peat bogs of both temperate and tropical latitudes. Ombrotrophic nutrient status apparently developed in the Changuinola mire within the last 800 y (Phillips *et al.* 1997). While a more extensive, hydrogeochemical study is needed, these results suggest that the shift towards P limitation found here was a developmental characteristic associated with ombrotrophic conditions that developed as hydrologic inputs became dominated by precipitation (Anderson 1964, 1983). Thus, this study shows that differentiation of limiting nutrients within geologically short temporal (~1000–4000 y) and small spatial (<1 km) scales, and thus biological-physical feedbacks structuring resource availability, is a more widespread ecological phenomenon, especially with respect to tropical wetlands.

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