



# $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ , carbon, nitrogen and phosphorus as indicators of plant ecophysiology and organic matter pathways in Everglades deep slough, Florida, USA

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## ABSTRACT

Historically, the Florida Everglades was characterized by a corrugated landscape of shorter hydroperiod, elevated sawgrass (*Cladium jamaicense*) ridges and longer hydroperiod, deep water slough communities. Drainage and compartmentalization of the Everglades have fundamentally altered this pattern, and sawgrass ridge communities have expanded at the expense of deep water slough communities throughout much of the landscape. In this study we provide a simple isotopic and nutrient characterization of major components of the slough ecosystem to elucidate physiological and nutrient differences among species and to suggest pathways for organic matter decomposition that contribute to peat development in deep water sloughs. We examined carbon (C) and nitrogen (N) isotopes and C, N and phosphorus (P) concentrations of the floating-leaved macrophytes *Nymphaea odorata* and *Nymphoides aquatica*, the emergent macrophyte *Eleocharis elongata*, and the submerged species *Utricularia foliosa* and *Utricularia purpurea*, as well as soil and flocculent material from the southern Water Conservation Area 3-A. Flocculent material and soils had the highest N content ( $4.5 \pm 0.2\%$ ) and *U. foliosa* and *N. odorata* had the highest P content ( $0.13 \pm 0.01\%$  to  $0.12 \pm 0.01\%$ ). The range for  $\delta^{15}\text{N}$  average  $\pm$  SE values was  $5.81 \pm 0.29\%$  (*U. foliosa*) to  $-1.84 \pm 0.63\%$  (*N. odorata*), while the range for  $\delta^{13}\text{C}$  values was  $-23.83 \pm 0.12\%$  (*N. odorata*) to  $-29.28 \pm 0.34\%$  (*U. purpurea*). Differences of up to 10‰ in C isotopic values of *U. foliosa* and *N. odorata* suggest fundamental physiological differences between these species. Along a degradation continuum, enrichment of  $^{13}\text{C}$  and  $^{15}\text{N}$  and extent of decomposition was negatively related to phosphorus concentrations. A two end-member  $^{13}\text{C}$  mixing model suggested that *Utricularia* species were the primary organic source for flocculent materials, whereas organic matter derived from root decomposition of *N. odorata* contributed to the progressively enriched  $\delta^{13}\text{C}$  values found with depth in soils. These results illustrate the fundamentally important roles of *Nymphaea* and *Utricularia* species in ecosystem dynamics of deep water sloughs.

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## 1. Introduction

Deep water sloughs in the Florida Everglades are recognized as an important pre-drainage feature of the wetland landscape. Historically, sloughs were oligotrophic, long hydroperiod, deep water habitats that dried out only on a decadal scale and were associated with deep peat soils (SCT, 2003; Ross et al., 2006). Sloughs paralleled the higher, drier sawgrass ridges to together form the patterned ridge and slough landscape that was characteristic of the historic Everglades and is a restoration target (SCT, 2003; Ross et al., 2006; Givnish et al., 2008). Dominance of the white water lily, *Nymphaea odorata*, typified this slough community (Gunderson, 1994; Olmsted and Armen-

tano, 1997; Stober et al., 2001). Drainage and compartmentalization in the last 100 years effectively reduced mean water levels and water flow rates, causing slough “infilling” and ridge expansion (SCT, 2003; Larsen et al., 2007). These hydrological changes and subsequent geomorphological “flattening” of the Everglades landscape were associated with the loss of *N. odorata* in parts of the ecosystem, so that the remaining slough habitat often lacks this species (e.g. Everglades National Park; Olmsted and Armentano, 1997; Stober et al., 2001; Ross et al., 2006; Larsen et al., 2007). Because water lilies or other slough dominants may be important in the formation and/or maintenance of the ridge and slough landscape, we need a better understanding of how slough plant ecology relates to slough geomorphology (SCT, 2003; Larsen et al., 2007).

In wetland ecosystems, studies employing natural abundance carbon (C) and nitrogen (N) isotopes have provided important insights into plant ecophysiology, organic matter cycling, and biogeochemical processes (Osmond et al., 1981; McKee et al., 2002; Ewe et al., 2007; Troxler, 2007), all of which may be

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important in understanding slough formation and maintenance. Physiologically mediated variations in C isotopic composition in wetland plants can result from a number of sources, including the photosynthetic pathway, the nature of the primary inorganic C source (atmospheric vs. dissolved), the available carbon form and subsequent mode of assimilation ( $\text{CO}_2$ ,  $\text{HCO}_3^-$ ), and the limits on diffusion imposed by plant life form or conditions of the aquatic environment (i.e. flowing vs. stagnant water; Osmond et al., 1981; Keeley and Sandquist, 1992; Keough et al., 1998). Similarly, variations in N isotopic composition can reflect differences in N source and processing (Adams and Sterner, 2000; Dai et al., 2005; McKee et al., 2002). In the Everglades, dominant species of the slough habitat exhibit very different plant life forms that potentially access different C and N sources. *Nymphaea odorata* is a floating-leaved, rooted aquatic plant, while *Utricularia* spp. are rootless, submerged and carnivorous, and *Eleocharis* species are rooted emergents. Thus, these different slough species may have very different C and N isotope signatures, which could be used to follow inputs into organic matter cycling.

Another defining feature of oligotrophic Everglades aquatic ecosystems is low surface water and soil P concentrations, with P sequestered within particular species (i.e. *Pontederia cordata*; Daoust and Childers, 1999) or in single compartments (water column particulates; Noe et al., 2007). Thus, sequestering of relatively high concentrations of P in dominant slough species or single compartments may be a historical feature of Everglades sloughs that contributed to its oligotrophic state while also supporting a historically rich avifauna (Robertson and Kushlan, 1984; Ogden, 1994). Phosphorus enrichment, however, can increase the number of ecosystem compartments with elevated levels of P (Noe et al., 2002), causing a “biogeochemical flattening” within the ecosystem.

Differentiation of C and N isotopic composition among ecosystem components, coupled with information on nutrient concentrations, can thus elucidate pathways of organic matter turnover and accumulation (Dai et al., 2005). Penton and Newman (2008) have suggested that microbial enzyme activities in Everglades sloughs cause decomposition to occur at faster rates than in ridges. Thus Rapid carbon turnover may also characterize slough habitats; submerged marsh ecosystems can exhibit bacterial production rates that exceed those of other aquatic systems, often because of shallow oxygen profiles that occur at the soil–water interface (Buesing and Gessner, 2006). In Everglades sloughs, bulk flocculent materials (floc) that sit at this interface are primarily heterotrophic (Wood, 2005). Thus, carbon turnover and peat deposition are intimately tied to plant community structure, in part, through nutrient processing and release via flocculent materials; this detrital cycling is also suggested to serve as an important base in food web structure (Moore et al., 2004).

Little is known about how slough species nutrient acquisition and decomposition contributed to slough development and ecological dynamics in the historical Everglades landscape. Mechanisms by which plant-mediated processes contribute to ecological functioning of sloughs can, however, be determined for extant sloughs. Thus, we have characterized nutrient and isotopic composition of slough ecosystem components in order to elucidate some of these mechanisms. We hypothesized that: (1) dominant slough species (*N. odorata* and *Utricularia* spp.) can be differentiated from other ecosystem components by isotopic signatures reflecting their mode of carbon acquisition and by their concentrations of limiting nutrients; and (2) organic matter of slough plant species is progressively degraded and nutrient depleted along a floc to soil depth profile and characterizes the organic matter decomposition pathway after plant senescence.

## 2. Methods

Our study was conducted at three sites in southern Water Conservation Area 3-A (WCA 3A) in the Florida Everglades. These sites were located as follows—Site 1: N25.47.402, W80.41.196; Site 2: N25.47.205, W80.41.341; Site 3: N25.47.086, W80.41.195. The Everglades WCA is a large (approximately 3000 km<sup>2</sup>) compartmentalized wetland system that spans the area south of Lake Okeechobee and north of Everglades National Park. In WCA 3A landscape structure can resemble the historical ridge and slough geomorphology (e.g. central WCA 3A; SCT, 2003; Givnish et al., 2008). We utilized this relatively intact part of the system to provide an indication of the ecosystem structure that typified the pre-drainage Everglades wetland landscape.

In October 2005 and April and July 2006, we sampled dominant vegetation of slough communities including culms of *Eleocharis elongata*, leaves of *N. odorata* and *Nymphoides aquatica*, and young photosynthetic axes of *Utricularia foliosa* and *Utricularia purpurea*. We also sampled soil and flocculent (floc) material *in situ* (“extant”) and deployed sediment traps to capture newly deposited particulate matter (“new” floc). Our sampling included three samples of each species or component collected per site. Our *in situ* soil and floc samples were collected with a 2.4 cm inner diameter PVC tube with a thin sleeve (~1 mm) affixed with a razor blade at the end to minimize peat compaction (Childers et al., 2002). We used a plunging apparatus (thin wooden dowel fitted with a 2 cm outer diameter rubber stopper) inserted into the transparent PVC tube to physically separate soil from “extant” flocculent material, recorded floc depth, and analyzed these components separately. Soil samples were extracted to ~15 cm depth, and separated into 2.5 cm sub-sections up to 5 cm depth, then into a 5 cm sub-sections to 10 cm depth. “New” floc was captured by deploying a sediment trap just above the “extant” floc surface, as determined by floc height and water depth (Leonard et al., 2006). The sediment traps were retrieved after 4–5 days. Water samples were collected with 1 L containers placed 10 cm below the water surface. Two samples were collected at each site in April and July 2006. Water depth was measured at each site to the nearest 0.5 cm with a meter stick, with one measurement per site in October 2005, and three measurements per site in April and July 2006.

Samples of live plant tissue, floc and soils were dried at 60 °C, ground to a homogeneous powder (<500 μm), and analyzed for TC and TN with a Carlo Erba elemental analyzer (Thermo Fisher Scientific Inc., Waltham, MA, USA). The modified Solorzano and Sharp (1980) method was used to analyze TP. Molar nutrient ratios were calculated from these data. Samples of plant tissue, floc and soil were also analyzed for <sup>15</sup>N and <sup>13</sup>C content using a continuous-flow isotope-ratio mass spectrometer at the Southeast Environmental Research Center’s Stable Isotope Laboratory at Florida International University (Finnigan Delta C, Thermo Fisher Scientific Inc., Waltham, MA, USA) and the University of California, Davis, CA, Stable Isotope Facility (Europa Hydra 20/20, PDZ Europa, Sundbach, England, UK). For δ<sup>15</sup>N analysis of leaves and soils, the stable isotopic ratio was calculated using standard δ notation where: δ<sup>15</sup>N = ( $R_{\text{sample}}/R_{\text{standard}} - 1$ ) × 1000 vs. atm-air.  $R$  is the ratio of <sup>15</sup>N/<sup>14</sup>N of the sample or standard (Martinelli et al., 1999). A similar equation was applied to determine isotopic composition for δ<sup>13</sup>C vs. Vienna PeeDee Belemnite.

Unfiltered water samples were analyzed for TN using an Antec 7000N Total Nitrogen analyzer and for TP using the dry ashing, acid-hydrolysis technique (Solorzano and Sharp, 1980); TOC was determined using a hot platinum catalyst, direct injection analyzer (Shimadzu model TOC-5000, Shimadzu Corporation, Kyoto, Japan). Water samples for inorganic nutrients and dissolved carbon were filtered (GF/F) within 24 h and analyzed for soluble reactive

phosphorus (SRP), ammonium ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ) + nitrite ( $\text{NO}_2^-$ ) and dissolved organic carbon (DOC). Analyses of water samples for SRP,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  +  $\text{NO}_2^-$  concentrations were determined on a four-channel auto-analyzer (Alpkem model RFA 300, OI Corporation, College Station, TX, USA). DOC concentration was determined as for TOC, after sample filtration.

We used Analysis of Variance (ANOVA) and Tukey's post hoc tests to characterize interspecific and seasonal variation in nutrient, isotopic and molar nutrient ratio values of dominant slough plant species. We examined variation among slough ecosystem components hypothesized to represent major compartments along a decomposition pathway with ANOVA and Tukey's tests. We regressed isotopic composition against nutrient content to test for correlations between plant physiological condition and nutrient status and to test explicitly our hypothesis about pathways for organic matter degradation. Our analyses were performed using nutrient concentrations, nutrient ratios and isotopic values. Data variability approximated a normal distribution. The statistical software JMP 7.0<sup>®</sup> (SAS Institute, Cary, NC, USA) was used for data analyses.

### 3. Results

#### 3.1. Site conditions

Water levels varied seasonally, being low in April ( $56 \pm 4$  cm) and July ( $50 \pm 5$  cm), which are the dry and early wet season, respectively, and twice as high in October ( $102 \pm 2$  cm), toward the end of the wet season. Water depth was similar among sampling sites. Total and dissolved N and C concentrations in surface water were twice as high in April as compared with July, but varied little among sampling sites (Table 1). Phosphorus concentrations were more similar among these sampling periods and sampling sites (Table 1).

#### 3.2. Interspecific and seasonal variation in plant isotopic and nutrient values

Analyses of  $^{15}\text{N}$  and  $^{13}\text{C}$  isotopes showed significant variation among plant species (Table 2). *U. foliosa* and *U. purpurea* had the most enriched values of  $\delta^{15}\text{N}$  and the most depleted values of  $\delta^{13}\text{C}$ . In contrast, *N. odorata* had the most depleted values of  $\delta^{15}\text{N}$  and the most enriched values of  $\delta^{13}\text{C}$ . *N. aquatica* and *E. elongata* had significantly higher values of  $\delta^{15}\text{N}$  and lower values of  $\delta^{13}\text{C}$  than *N. odorata* (Table 2).

Nutrient and C concentrations also varied significantly among species (Table 2). *N. odorata* and *N. aquatica* had the highest C values, while *U. purpurea* had the lowest. *N. odorata* and *U. foliosa* had the highest N values, and *E. elongata* had the lowest. Values for %P varied between the highest values for *U. foliosa* and *N. odorata* and significantly lower values for *N. aquatica*, *U. purpurea*, and *E. elongata*, all had approximately 50% less TP than *N. odorata* and *U. foliosa* (Table 2). Collectively, *N. odorata*, *U. purpurea*, and *U. foliosa* had significantly lower C:N ratios than both *E. elongata* and *N. aquatica*, while *E. elongata* had the highest C:N ratio. *N. odorata* and *U. foliosa* had the lowest C:P ratios, with *E. elongata* the highest. *U. purpurea* and *N. aquatica* C:P ratios were not significantly different from each other. While *N. odorata* and *U. foliosa* had the lowest values of N:P, *U. purpurea* had the highest. N:P values for *E. elongata* and *N. aquatica* were not significantly different (Table 2).

*N. odorata* showed pronounced seasonal variation in isotopic values and nutrient concentrations (Table 3). This species had significantly more enriched  $^{15}\text{N}$  in April, more enriched  $^{13}\text{C}$  in October, lower C concentration in July, lower P concentration in April, and higher %N in October than in April. C:N, C:P and N:P were all significantly higher in April for this species. *N. aquatica*, *E. elongata* and *U. purpurea* varied seasonally only in carbon concentrations, where C was approximately 2% lower in July than either October or April for each species. Like *N. odorata*, *U. foliosa* expressed intra-annual variation, most notably in  $^{15}\text{N}$  and  $^{13}\text{C}$  values (Table 3). *U. foliosa*  $^{15}\text{N}$  values were most enriched in October, while  $^{13}\text{C}$  values were most enriched in April. Values for C concentration for this species in October were significantly higher than those in July.

When we used linear regression analyses to determine how nutrient content and isotopic values varied as a function of seasonal variation in water level, *N. odorata* ( $n = 9$ ) and *U. foliosa* ( $n = 7$ ) showed different patterns of variation. Both  $\delta^{13}\text{C}$  and N concentration of *N. odorata* leaf tissue increased with increased water level ( $r^2 = 0.68$ ,  $p = 0.0065$  and  $r^2 = 0.45$ ,  $p = 0.0490$ , respectively). In contrast, C concentration and  $\delta^{15}\text{N}$  value of *U. foliosa* shoot tips increased with higher water level ( $r^2 = 0.60$ ,  $p = 0.0411$  and  $r^2 = 0.68$ ,  $p = 0.0223$ , respectively). Considering sampling periods for which we have water quality data (April and July), tissue quality of *N. odorata* (lower C:N, C:P and N:P) appeared to correspond with lower surface water TOC and TN (Table 1). Because surface water TP was similar between April and July, lower surface water TOC and TN in July resulted in lower TN:TP and TOC:TP but higher TOC:TN.

**Table 1**

Nutrient and carbon concentrations ( $\mu\text{M}$ ) of surface water averaged for each of three sampling sites. Data are averages  $\pm$  SE. Surface water samples were not collected in October 2005.

	TN	TP	TOC	$\text{NH}_4$	$\text{NO}_3 + \text{NO}_2$	SRP	DOC
April-06	$58.39 \pm 2.81$	$0.351 \pm 0.05$	$1275 \pm 12$	$1.81 \pm 0.35$	$0.22 \pm 0.10$	$0.04 \pm 0.01$	$1280 \pm 34$
July-06	$20.66 \pm 0.87$	$0.297 \pm 0.01$	$723 \pm 11$	$0.72 \pm 0.07$	$0.11 \pm 0.01$	$0.04 \pm 0.01$	$780 \pm 14$

**Table 2**

Interspecific variation in nutrient, isotopic and molar nutrient ratio values for dominant slough vegetation in WCA 3A. Data are averages  $\pm$  SE of three plants per site, three sites per sample and three sample times (October 2005, April 2006 and July 2006), except for isotopic composition for *N. aquatica* ( $n = 24$ ), all values for *U. foliosa* ( $n \geq 19$ ), and all values for *U. purpurea* ( $n \geq 25$ ). Letters indicate means that are significantly different with "a" the lowest homogeneous group.

	<i>N. odorata</i>	<i>N. aquatica</i>	<i>E. elongata</i>	<i>U. foliosa</i>	<i>U. purpurea</i>	d.f.	F	p
$\delta^{15}\text{N}$	$-1.84^a \pm 0.63$	$3.03^{bc} \pm 0.40$	$1.58^b \pm 0.70$	$5.81^d \pm 0.29$	$4.53^{cd} \pm 0.33$	123	31.20	<0.0001
$\delta^{13}\text{C}$	$-23.83^d \pm 0.12$	$-24.74^c \pm 0.13$	$-26.7^b \pm 0.18$	$-29.21^a \pm 0.31$	$-29.28^a \pm 0.34$	123	116.25	<0.0001
%C	$45.53^c \pm 0.29$	$45.36^c \pm 0.23$	$42.44^b \pm 0.28$	$42.53^b \pm 0.46$	$38.98^a \pm 0.37$	126	72.45	<0.0001
%N	$2.26^c \pm 0.06$	$1.63^b \pm 0.05$	$1.09^a \pm 0.06$	$2.26^c \pm 0.15$	$1.91^b \pm 0.07$	126	41.20	<0.0001
%P	$0.108^b \pm 0.006$	$0.063^a \pm 0.005$	$0.050^a \pm 0.004$	$0.120^b \pm 0.013$	$0.057^a \pm 0.002$	124	24.53	<0.0001
C:N	$24^a \pm 1$	$33^b \pm 1$	$48^c \pm 2$	$23^a \pm 1$	$25^a \pm 2$	126	53.08	<0.0001
C:P	$1180^a \pm 68$	$2176^{bc} \pm 198$	$2641^c \pm 252$	$1092^a \pm 104$	$1819^b \pm 71$	124	15.61	<0.0001
N:P	$49^a \pm 2$	$65^{bc} \pm 5$	$55^b \pm 4$	$45^a \pm 2$	$76^c \pm 4$	124	10.79	<0.0001

**Table 3**

Seasonal variation in isotopic, nutrient and molar ratio values for the common deep slough species *N. odorata* and *U. foliosa* in WCA 3A. Data are averages  $\pm$  SE of three plants per site for three sites per sample. Letters indicate means that are significantly different with "a" the lowest homogeneous group.

	October-05	April-06	July-06	d.f.	F	p
<i>N. odorata</i>						
$\delta^{15}\text{N}$	$-4.22^a \pm 0.32$	$0.88^b \pm 0.75$	$-2.19^a \pm 1.26$	26	8.74	0.0014
$\delta^{13}\text{C}$	$-23.09^b \pm 0.07$	$-24.37^a \pm 0.18$	$-24.05^a \pm 0.07$	26	30.65	<0.0001
%C	$46.35^b \pm 0.17$	$46.69^b \pm 0.19$	$43.56^a \pm 0.20$	26	83.88	<0.0001
%N	$2.50^b \pm 0.08$	$2.05^a \pm 0.08$	$2.23^{ab} \pm 0.10$	26	6.90	0.0043
%P	$0.125^b \pm 0.008$	$0.081^a \pm 0.007$	$0.119^b \pm 0.011$	26	7.29	0.0034
C:N	$22^a \pm 1$	$27^b \pm 1$	$23^a \pm 1$	26	8.08	0.0022
C:P	$992^a \pm 75$	$1550^b \pm 95$	$998^a \pm 68$	26	15.88	<0.0001
N:P	$45^a \pm 3$	$57^b \pm 3$	$43^a \pm 3$	26	8.33	0.0018
<i>U. foliosa</i>						
$\delta^{15}\text{N}$	$7.25^b \pm 0.29$	$5.34^a \pm 0.21$	$5.00^a \pm 0.52$	19	11.49	0.0007
$\delta^{13}\text{C}$	$-29.81^a \pm 0.38$	$-27.77^b \pm 0.20$	$-30.52^a \pm 0.24$	19	28.45	<0.0001
%C	$44.47^b \pm 0.72$	$42.35^{ab} \pm 0.56$	$40.83^a \pm 0.43$	19	8.32	0.0030
%N	$2.50 \pm 0.40$	$1.98 \pm 0.15$	$2.38 \pm 0.21$	19		ns
%P	$0.129 \pm 0.033$	$0.104 \pm 0.013$	$0.128 \pm 0.022$	19		ns
C:N	$23 \pm 3$	$26 \pm 2$	$21 \pm 2$	19		ns
C:P	$1185 \pm 268$	$1146 \pm 116$	$935 \pm 141$	19		ns
N:P	$49 \pm 6$	$42 \pm 3$	$44 \pm 3$	19		ns

### 3.3. Variation in soil and floc isotopic composition and nutrient concentrations

Soil and floc components varied significantly in nutrient concentrations and isotopic composition (Figs. 1 and 2). For  $\delta^{15}\text{N}$  values, deeper peat soils (2.5–5.0 and 5.0–10.0 cm depth) had the most enriched values, followed by shallower soil (0–2.5 cm depth). Floc, both "new" and "extant", had less enriched  $\delta^{15}\text{N}$  values than the soil (Figs. 1 and 2). Values of  $\delta^{13}\text{C}$  fell into two discrete, significantly different groups. Soils had the most enriched  $\delta^{13}\text{C}$  values, whereas floc had the least enriched values (Figs. 1 and 2). Carbon concentrations also differed significantly between soils and flocculent material, with significantly higher C concentrations for the peat soils. Most values for N concentration were similar among components with the exception of "extant" floc, which had significantly higher %N than soil at 2.5–5.0 cm depth. Like C, P concentrations varied clearly along a decomposition pathway, where flocculent materials had significantly higher values than soils (Fig. 1). Values for nutrient ratios also followed hypothesized decomposition pathways. Soils had higher C:N, C:P and N:P ratios as compared to flocculent materials, while C:P and N:P values for soils at 0–2.5 cm depth were significantly lower than values for soils at 5.0–10.0 cm depth (Fig. 2).

**Table 4**

Summary table of regression relationships between isotopic composition (x) and nutrient and molar ratio (y) values of floc and soil samples from WCA 3A. Data are shown in Figs. 1 and 2.

x	y	Intercept	Slope	$r^2$	p
$\delta^{15}\text{N}$	%C	$40.51 \pm 1.83$	$3.74 \pm 1.05$	0.81	0.0379
	%N				ns
	%P <sup>a</sup>	$-3.081 \pm 0.048$	$-0.687 \pm 0.072$	0.97	0.0025
$\delta^{13}\text{C}$	%C	$103.82 \pm 13.67$	$2.07 \pm 0.49$	0.86	0.0243
	%N				ns
	%P	$-0.284 \pm 0.012$	$-0.012 \pm 0.000$	0.99	0.0001
$\delta^{15}\text{N}$	C:N <sup>b</sup>	$0.061 \pm 0.001$	$0.011 \pm 0.001$	0.97	0.0021
	C:P	$904 \pm 644$	$1903 \pm 370$	0.90	0.0142
	N:P	$91.3 \pm 37.6$	$113.5 \pm 21.6$	0.90	0.0134
$\delta^{13}\text{C}$	C:N	$35.15 \pm 1.77$	$0.76 \pm 0.06$	0.98	0.0013
	C:P	$32,996 \pm 4,190$	$1050 \pm 150$	0.94	0.0060
	N:P	$2,003 \pm 244$	$62 \pm 9$	0.94	0.0057

<sup>a</sup>  $\log(x)$ ,  $\log(y)$ .

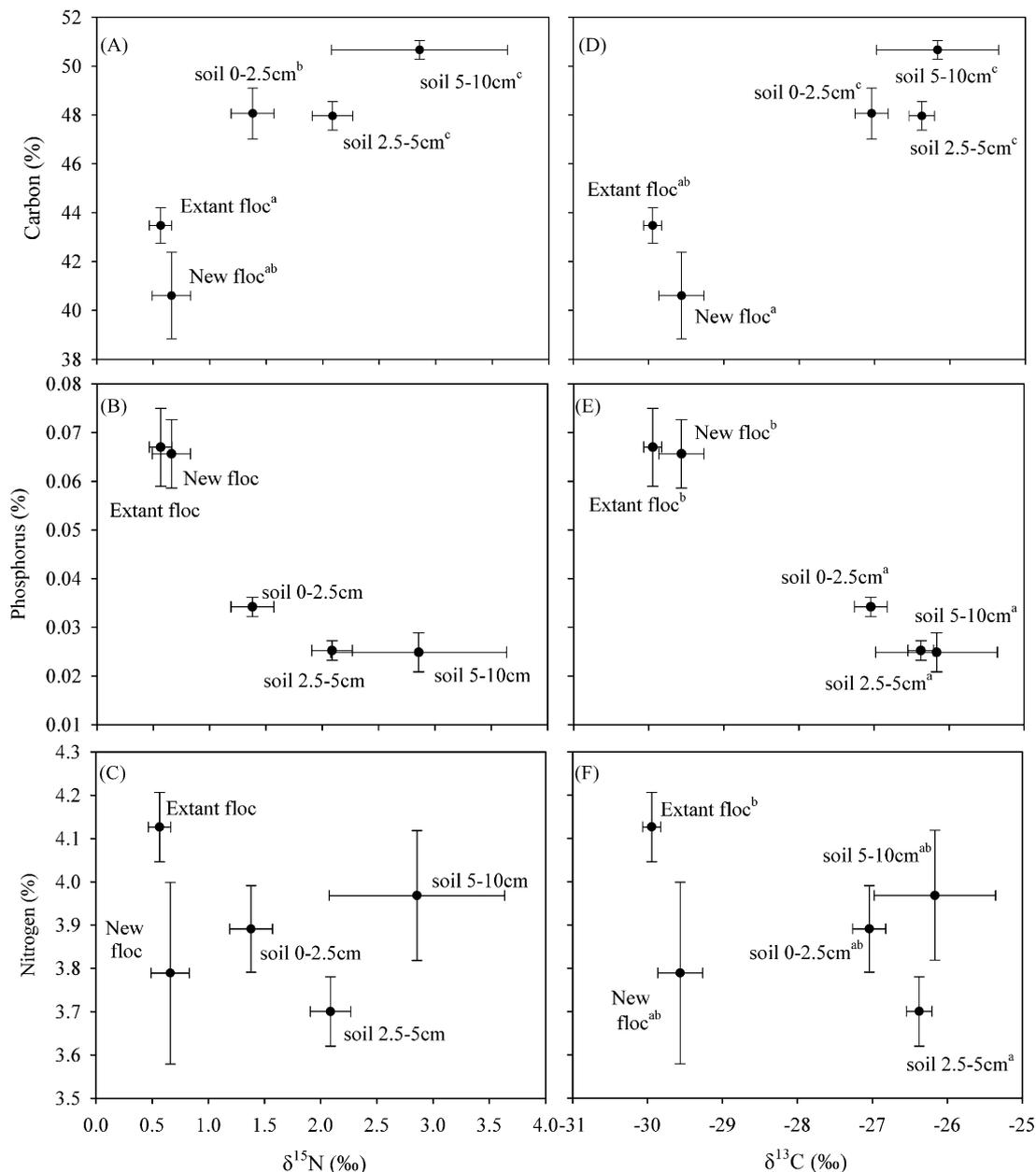
<sup>b</sup>  $1/x$ ,  $1/y$ .

When nutrient concentrations and molar ratios were regressed against isotopic composition for floc and soil, we found a positive, linear relationship between  $^{13}\text{C}$  and C concentration, and a strong negative, linear relationship between  $^{13}\text{C}$  and P concentration (Fig. 1A and B; Table 4). We found no relationship between  $^{13}\text{C}$  and N concentration (Fig. 1C), but C isotopic composition explained 98%, 94%, and 94% of the variability in C:N, C:P and N:P ratios, respectively, and these were positive relationships (Fig. 1D–F). Nitrogen isotopic composition explained 81% of the variability in soil and floc C concentrations among soil and floc (Fig. 2A; Table 4). Log-transformed x and y variables revealed a strong negative relationship between %P and  $^{15}\text{N}$ , where flocculent materials had higher %P but lower  $^{15}\text{N}$  than soils (Fig. 2B). We found no relationship between  $^{15}\text{N}$  and nitrogen concentration (Fig. 2C). A reciprocal transformation of x and y variables revealed the best fit model for the relationship between  $^{15}\text{N}$  and C:N (Fig. 2D), whereas linear models best described the positive relationships between  $^{15}\text{N}$  and C:P and N:P (Fig. 2E and F).

## 4. Discussion

### 4.1. Relating isotopic composition, nutrient status and ecophysiological constraints on dominant slough species

In the Everglades deep slough, C and N isotopes were useful tools for differentiating photosynthetic pathways and nutrient use among plant species. Values of  $\delta^{13}\text{C}$  for *N. odorata* were on average 5.4‰ higher than those for *Utricularia* species. These two species likely have similar photosynthetic pathways (inferred from published values of  $\delta^{13}\text{C}$ ; Osmond et al., 1981; Keeley and Sandquist, 1992; Jähren et al., 2006) and were intermixed in open water, suggesting that neither photosynthetic pathway nor conditions of the aquatic environment influenced this difference in  $\delta^{13}\text{C}$  values. The rooted, floating-leaved *N. odorata* and rootless, submerged, and highly dissected *Utricularia* species, however, have very different plant life forms. The  $\delta^{13}\text{C}$ -DIC of Everglades water and atmospheric  $\text{CO}_2$  is similar ( $-8.7\text{‰}$ ; Kendall et al., 2005). Assuming 100% utilization of atmospheric and dissolved sources by *N. odorata* and *Utricularia* sp., respectively, and a similar isotopic signature of carbon utilized, *Utricularia* sp. would be expected to have relatively enriched values of  $\delta^{13}\text{C}$ , because in submerged plants, boundary layer diffusion resistance increases reliance on internally recycled sources of  $^{13}\text{C}$  ( $-18\text{‰}$  to  $-22\text{‰}$ ; Keough et al., 1998). However, *Utricularia* species are a unique type of submerged



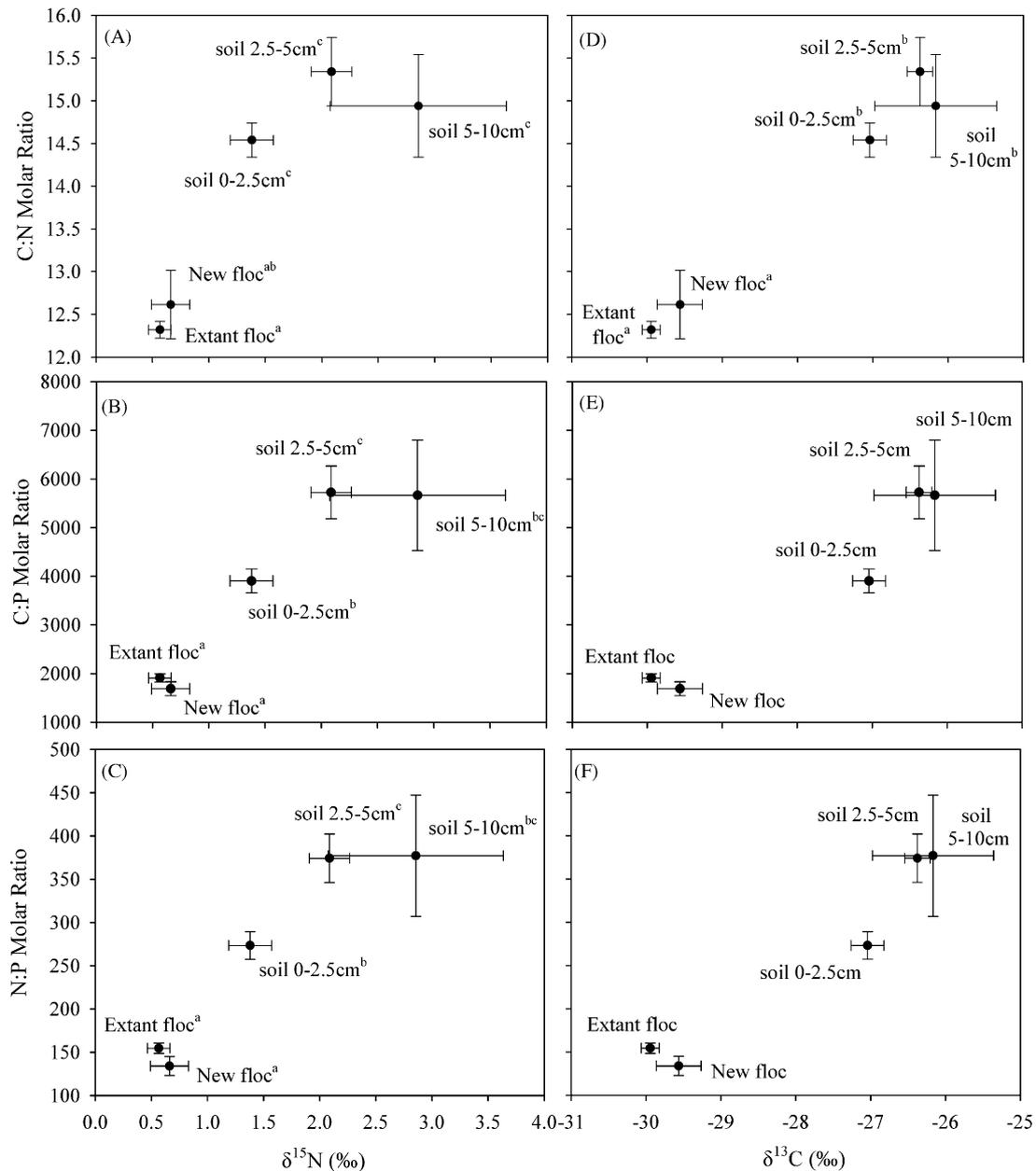
**Fig. 1.** Scatterplots of N and C isotopic composition and C, N and P concentrations along a hypothesized decay continuum from “new” floc to soil at 5.0–10.0 cm depth. (A–C) Nitrogen isotopic composition vs. %C, %P and %N, respectively. In panel (A), letters indicate means that are significantly different with “a” the lowest homogeneous group for Tukey multiple comparisons of  $x$ -axis values ( $\delta^{15}\text{N}$ ). (D–F) Carbon isotopic composition vs. %C, %P and %N, respectively. Letters indicate means that are significantly different with “a” the lowest homogeneous group for Tukey multiple comparisons of  $y$ -axis values.

aquatic plant, as they are considered to be carnivorous, and have been shown to have assemblages of microorganisms persisting in their bladders (Richards, 2001). Furthermore, Adamec (2006) showed that several *Utricularia* species exhibit higher rates of respiration in occupied bladders, as compared with leaf tissue, suggesting a respiratory contribution by bladder-associated microorganisms. Thus, additional DIC from respiration of heterotrophic components within the bladders may contribute to the depleted values reported here for *U. foliosa* and *U. purpurea*. These values are typical of those reported for other *Utricularia* species ( $-33.7\%$  to  $-31.3\%$ , Osmond et al., 1981;  $-36.2\%$  to  $-33.1\%$ , Keough et al., 1998).

*N. odorata*, *N. aquatica*, and *E. elongata* had more enriched  $\delta^{13}\text{C}$  than the bladderworts. *E. elongata* exhibited  $\delta^{13}\text{C}$  values similar to emergent macrophytes, while *N. odorata* and *N. aquatica* had more

positive values. *N. aquatica* is a rooted, floating-leaved aquatic similar to *N. odorata* but with smaller leaf blades. At our sites we found *E. elongata* at shallower water depths, often growing around clumps of less water-tolerant vegetation in the slough habitat. The differences in  $\delta^{13}\text{C}$  values among these floating-leaved and emergent species may reflect differences in use of atmospheric vs. internally recycled C. The positive relationship we found between  $\delta^{13}\text{C}$  values of *N. odorata* and water level suggests that limits to boundary layer diffusion and reliance on internally recycled C of this species are influenced by seasonal hydrologic variability.

Interspecific variation in nitrogen isotopic composition suggested greater N demand by submerged species, followed by emergent, and floating-leaved species. However, N content was similar between *N. odorata* and *U. foliosa*. *N. odorata*, as well as *U.*



**Fig. 2.** Scatterplots of N and C isotopic composition and C:N, C:P and N:P molar ratios along a hypothesized decay continuum from “new” flocc to soil at 5.0–10.0 cm depth. (A–C) Nitrogen isotopic composition vs. C:N, C:P and N:P molar ratios, respectively. Letters indicate means that are significantly different with “a” the lowest homogeneous group for Tukey multiple comparisons of y-axis values. (D–F) Carbon isotopic composition vs. C:N, C:P and N:P molar ratios, respectively. In panel (D), letters indicate means that are significantly different with “a” the lowest homogeneous group for Tukey multiple comparisons of x-axis values ( $\delta^{13}\text{C}$ ).

*foliosa*'s congener *Utricularia inflata*, have been shown to assimilate cesium, and thus presumably nutrients, directly from the water column (Kelly and Pinder, 1996; Pinder et al., 2006), whereas the  $\delta^{15}\text{N}$  value of *U. foliosa* may also reflect N content of algae, zooplankton, and particulate detritus found in its bladders (Richards, 2001). A synoptic survey of N and C isotopic composition of Everglades algae, zooplankton, and particulate detritus indicates that these components approximate the N isotopic composition that we found for both *Utricularia* species (Kendall et al., 2005). Thus, N content and N isotopic signature of *N. odorata* may reflect N use, while *U. foliosa* N content and N isotopic signature may reflect both its N use and its mutualistic association, ultimately yielding different  $\delta^{15}\text{N}$  values between the two species. Finally, *U. foliosa*'s increase in  $^{15}\text{N}$  and C concentration with increased water level may reflect an increased growth rate and consequent higher N demand

that occurs with greater  $\text{CO}_2$  assimilation. *U. foliosa* in the southern Everglades grew more than twice as fast in May and June, which are both warmer and wetter, as compared to February, which is both cooler and drier (Childers et al., 2006).

*N. odorata* and *U. foliosa* also had the highest phosphorus content, which was on average double that of the other species. As these species appear to concentrate P relative to other species of the slough community, *N. odorata* and *U. foliosa* likely have an important role in phosphorus uptake and cycling in the oligotrophic Everglades wetlands. In contrast to *U. foliosa*, *U. purpurea* has a low P content, although the two species are more similar in N content and  $\delta^{15}\text{N}$ , resulting in a much higher N:P and thus potentially greater P limitation in *U. purpurea*. Richardson et al. (2007) have proposed *U. purpurea* stem density as an indicator of P levels in the oligotrophic Everglades.

#### 4.2. Carbon pathways including mechanisms for peat development in deep slough

Carbon and nitrogen isotopes can also help elucidate pathways for organic matter degradation (Keough et al., 1998; Hornibrook et al., 2000; Gonçalves et al., 2004; Dai et al., 2005). Because carbon and nitrogen isotopic values were not available for senesced leaf tissue, our degradation continuum began with freshly deposited flocculent materials (new floc). Thus, we predicted that new floc represented the least degraded product along the continuum, and soil at 5–10 cm depth was the most degraded material.

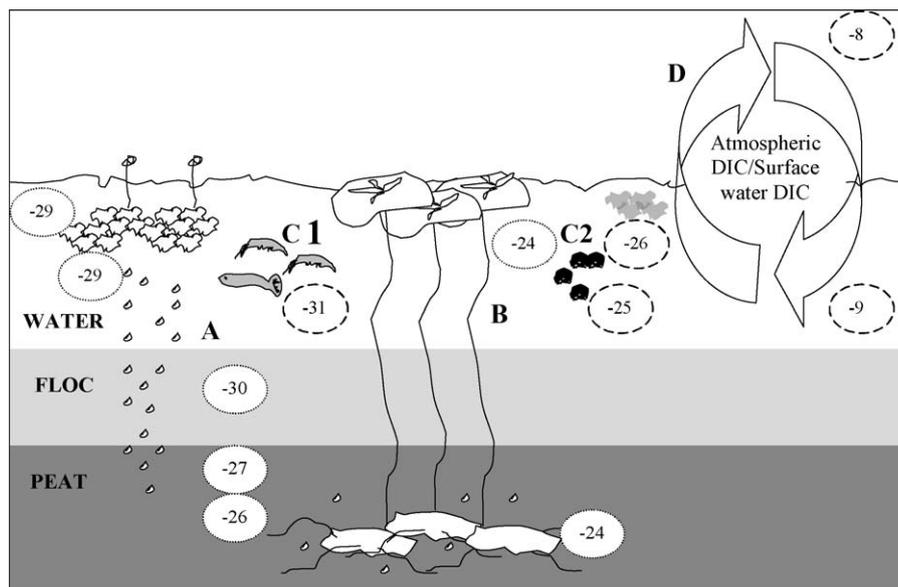
When using carbon isotope composition to elucidate a degradation pathway, previous work suggests that a carbon mixture should match the source of carbon that is degraded. This has been shown to occur because  $^{13}\text{C}$  enrichment by accumulation of bacterial biomass counter-balances the loss of labile, enriched proteins and corresponding relatively increased lignin content, causing little net fractionation along a degradation continuum (Benner et al., 1987; Macko et al., 1987; Wieder and Yavitt, 1994; Hornibrook et al., 2000; Ekblad et al., 2002; Dai et al., 2005). We found more enriched  $\delta^{13}\text{C}$  values going from least to most degraded material, i.e., new floc to deepest soil; these values corresponded to increased C content, C:N, C:P and N:P ratios, and decreased P concentration along the same gradient. In addition, as we found a more pronounced enrichment of  $^{13}\text{C}$  than has been reported based on microbial respiration alone (3–4‰ in our data vs. ~1‰; Wieder and Yavitt, 1994; Ekblad et al., 2002), our results suggest that the source material changed with soil depth.

To gain a better understanding of the possible source material, we estimated the balance between inputs of *N. odorata* and *Utricularia* species to our carbon end-points, floc and peat. A simple, two end-member mixing model provides a relative estimate of the contributions made by carbon sources to carbon end-points in ecosystems if the  $\delta^{13}\text{C}$  value of source material matches its contribution to a mixture (Shearer and Kohl, 1993; Keough et al., 1998). The model follows the form:  $(\text{Source B} - \text{Mixture}) / (\text{Source B} - \text{Source A}) \times 100 = \% \text{ contribution from}$

Source A. We estimated source contributions from *U. purpurea* and *N. odorata* to floc and soil components, so that the source values were the isotope values of the potential plant sources, while the mixture was the isotope value for soil or floc, respectively. Our model results showed that if live plants of *Utricularia* and *Nymphaea* do not undergo significant  $^{13}\text{C}$  fractionation upon decay, *Utricularia* comprises 100% of flocculent materials, and contributes approximately 59%, 47% and 43% of the carbon to peat at depths of 0–2.5, 2.5–5.0 and 5.0–10.0 cm, respectively. Thus, degradation processes and carbon flow in the deep slough ecosystem appear to be somewhat compartmentalized, where *Utricularia* degrades to become flocculent material, with some contribution to surface peat accumulation, whereas *Nymphaea* degrades to become the primary component of accumulating peat that increases with peat depth (Fig. 3A and B).

Hornibrook et al. (2000) demonstrated a similar phenomenon where contributions from aquatic species (i.e. algae) contributed to depleted surficial  $\delta^{13}\text{C}$  values, just as we found that the submersed, rootless *Utricularia* contributed to flocculent materials. Hornibrook et al. (2000) also reported a progressive enrichment of  $\delta^{13}\text{C}$  values with soil depth, and attributed this to possible variation in contributions of plant carbon sources. Although we did not measure what carbon isotopic composition variation occurs upon *Nymphaea* leaf decay, Benner et al. (1987) predicted a fractionation of less than 1‰ associated with the corresponding increase in lignin concentration after 1.5 years of leaf decomposition. Thus, this study suggests that an important carbon input to peat soils in the Everglades deep slough is generated from *N. odorata*, likely via root decomposition (Fig. 3B).

Evidence suggests that N isotopic composition is progressively enriched through the loss of more labile components and subsequent breakdown of proteins via degradation (Dai et al., 2005). We found a clear progression of more enriched  $\delta^{15}\text{N}$  values along a continuum from floc to soils at 5–10 cm depth; this  $\delta^{15}\text{N}$  enrichment was strongly correlated with decreasing phosphorus and carbon concentrations, and increasing C:N, C:P and N:P ratios, following our hypothesized decay continuum. Considering the



**Fig. 3.** Model for slough decomposition processes and compartmentalized carbon flow with representative  $\delta^{13}\text{C}$  values shown for major biotic and abiotic components (dotted and dashed bubbles; values for dotted bubbles are from this paper, while those for dashed bubbles were obtained from Kendall et al., 2005). (A) *Utricularia*–floc complex: Flocculent materials are derived almost exclusively from *Utricularia* spp., which also contribute organic matter to soil at surface depths of up to 10 cm. (B) *Nymphaea*–peat complex: *Nymphaea* obtains carbon from internal recycling of atmospheric carbon, producing leaves with enriched  $^{13}\text{C}$  values. *Nymphaea* roots decompose within the peat soil, causing progressively enriched  $^{13}\text{C}$  values with depth. (C) Consumer complex: (1) Secondary consumers (e.g., river grass shrimp and mosquito fish) consume bladders of *Utricularia*, while (2) detritivores (e.g., amphipods) consume leaf detritus of *N. odorata* and periphyton as part of their diets, transferring degraded materials through the food web. (D) Atmospheric–water complex: Atmospheric  $\text{CO}_2$  and surface water DIC are exchanged.

average  $\delta^{15}\text{N}$  value for *Nymphaea* leaf tissue, we found that *Nymphaea* fits our decay model of  $\delta^{15}\text{N}$  vs. P concentration. The  $\delta^{15}\text{N}$  values for *Utricularia* species do not fit this decay model, perhaps because of these species' higher N demand and mutualistic associations through their traps. Because floc  $\delta^{15}\text{N}$  values were significantly less enriched than *Utricularia* species'  $\delta^{15}\text{N}$ , upon senescence the bladderworts must undergo significant isotopic depletion before deposition as floc or are disarticulated from senescing plants and thus likely transferred to another part of the system, possibly directly through food webs (Williams and Trexler, 2006). Interestingly, values of  $^{13}\text{C}$  for both fish and shrimp consumers most closely match the depleted  $^{13}\text{C}$  values we found for *Utricularia* spp. (Kendall et al., 2005; Williams and Trexler, 2006, Fig. 3C1). Some proportion of *N. odorata* leaf detritus must also cycle through food webs. Its  $^{13}\text{C}$  value closely matches values found for a common Everglades detritivore, *Hyalella azteca* (Kendall et al., 2005; Williams and Trexler, 2006). Periphyton, a complex green algae/diatom assemblage also shown to be important in food web dynamics in Everglades sloughs (Browder et al., 1994), was not always present at our sites and thus was not considered in our study.

While it is known that the loss of deep slough habitat in the Florida Everglades produced a detrimental shift in Everglades landscape structure and ecosystem function, we have not known how dominant biotic components of sloughs contribute to slough development or maintenance. This study suggests three important insights about Everglades slough ecosystem dynamics: (1) *Utricularia* species comprise the primary components of floc materials; (2) *Nymphaea* organic matter has an increasing contribution with peat depth and may influence peat accumulation through root production and decomposition; and (3) *N. odorata* and *U. foliosa* maintain high concentrations of P as compared to other slough ecosystem components, serving as important end-members in P and organic matter cycling. *Nymphaea* and the *Utricularia* species emerge as important contributors to Everglades slough dynamics, especially in peat accumulation and food web dynamics.

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