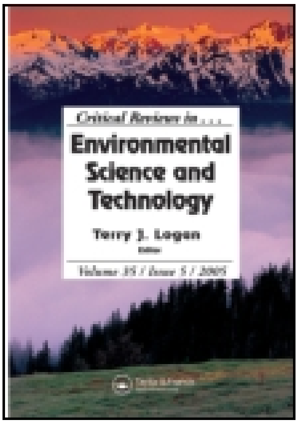

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Biogeochemical Processes on Tree Islands in the Greater Everglades: Initiating a New Paradigm

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Biogeochemical Processes on Tree Islands in the Greater Everglades: Initiating a New Paradigm

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Scientists' understanding of the role of tree islands in the Everglades has evolved from a plant community of minor biogeochemical importance to a plant community recognized as the driving force for localized phosphorus accumulation within the landscape. Results from this review suggest that tree transpiration, nutrient infiltration from the soil surface, and groundwater flow create a soil zone of confluence where nutrients and salts accumulate under the head of a tree island during dry periods. Results also suggest accumulated salts and nutrients are flushed downstream by regional water flows during wet periods. That trees modulate their environment to create biogeochemical hot spots and strong nutrient gradients is a significant ecological paradigm shift in the understanding of the biogeochemical processes in the Everglades. In terms of island sustainability, this new paradigm suggests the need for distinct dry-wet cycles as well as a hydrologic regime that supports tree survival. Restoration of historic tree islands needs further investigation but the creation of functional tree islands is promising.

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KEYWORDS: Everglades restoration, Focused Nutrient Redistribution model, Florida Everglades, groundwater flows, landscape modulation, nitrogen, phosphorus, sap flow, tree patches, tree transpiration, zone of confluence

INTRODUCTION

The vast, watery expanse of the Florida Everglades is punctuated with islands and strands of trees. The extant area covered by island forests varies widely, averaging ~14% in the northern Everglades (Brandt et al., 2000) and 3.8% of the area in the central Everglades (Patterson and Finck, 1999). At a landscape level, these forested wetlands are organized into nonrandom spatial patterns that vary across the Everglades and most likely result from a synergy of surface and groundwater flow patterns, seasonal water fluctuations and biogeochemical processes (Wetzel et al., 2009). Several forest spatial patterns are evident in the Everglades: round spots surrounded by water lily sloughs, teardrop-shaped islands oriented in the direction of surface water flow and surrounded by sloughs, long treed strands integrated with and parallel to sawgrass or marsh ridges interspersed with sloughs, and a labyrinth of trees with gaps occupied by herbaceous communities. The Everglades contains thousands of discrete tree islands that range in size from 0.01 to 70 ha. It is the discrete teardrop-shaped forested wetland communities that have been studied most extensively and will be the focus of this paper.

Results of a survey conducted by the authors in Water Conservation Area (WCA) 3A found that these forested islands have a ground elevation between 0.18 and 1.59 m ($n = 258$) above that of the surrounding herbaceous plant communities. Due to a decreasing elevation gradient from the upstream head to the downstream tail, vegetation is distributed into distinctive zones characterized by decreasing stature (Mason and van der Valk, 2002; Sah, 2004; van der Valk, 1998). The head, the point of highest elevation on an island, typically supports the largest trees in terms of both height and trunk diameter. Plant communities immediately downstream of the head, known as the near tail, are shorter in height and contain low stature trees, shrubs, and a dense herbaceous understory including shrubs, ferns, and forbs. Further downstream of the near tail are very dense herbaceous communities, dominated by sawgrass and sporadic shrubs, known as the tail. Eventually, in the far tail region, the tree island vegetation becomes similar to the surrounding marsh communities (Mason and van der Valk, 2002; Sah, 2004; Figures 1 and 7).

The structure and function of tree island vegetation communities are greatly influenced by hydrology (Loveless, 1959; Mason and van der Valk, 2002; McPherson, 1973; van der Valk and Sklar, 2002; Zaffke, 1983). The time that an island is inundated depends on the general elevation gradient within an island from head to tail and the overall elevation of the island relative to the surrounding marsh. The heads of the most highly elevated tree islands (e.g., tropical hardwood hammocks) are inundated only 3–7% of the year (Wetzel et al., 2008) or may never be inundated (Armentano et al., 2002; Ross et al., 2006). Lower elevation tree islands may be flooded 25% of the year or more, and even all year during particularly wet years (Armentano et al., 2002; Wetzel, 2002a; Wetzel et al., 2008). Because the near tail, tail, and far tail sections of the tree island are lower in elevation than the head they are correspondingly flooded with greater frequency than the head.

Hydrologic modifications, including compartmentalization and point source discharges, along with water management practices dramatically changed the natural hydrology pattern of the central Everglades, which affected tree island structure (Armentano et al., 2002; Wetzel 2002a; Wetzel et al., 2009). For instance, in the more elevated northern central Everglades increased drainage led to a greater number of fires, resulting in peat destruction that led to tree island loss (Loveless, 1959; Schortemeyer, 1980). In contrast, construction of the southern levees (e.g., L-67A levee and Tamiami Trail) led to the impoundment of water in WCA-3A, resulting in increased flooding of tree islands and an overall loss of tree island vegetation in the southern central Everglades beginning around 1950 (Alexander and Crook, 1975; McPherson, 1973; Patterson and Finck, 1999). The hydrologic alterations in the central Everglades between 1940 and 1995 resulted in a 54% decline of the total number of hardwood communities greater than 1 ha and a 67% decline in total treed area (Patterson and Finck, 1999). However, it is important to point out that the aerial extent of the treed regions in 1940 was probably unusually high due to lower water tables from early drainage practices (McVoy et al., in press).

Historically, tree islands in the Everglades were seen simply as a plant community of minor biogeochemical importance especially given their limited aerial extent. Early nutrient and biogeochemistry studies of the Everglades focused on the vast sawgrass plains and the establishment of the range of oligotrophy in the ecosystem. However, tree patches found in such diverse ecosystems as arid shrub lands, savannas, mountain tundra, and in patterned peat lands have long been recognized for their role in modulating local environmental conditions and for accumulating and cycling nutrients (Belsky and Canham, 1994; Breashears, 2006; Dean et al., 1999; Ellery et al., 1993; Glaser, 1987; Parker and Sanford, 1999; Rietkerk et al., 2002; Rietkerk et al., 2004; Shachak et al., 2008). The presence of tree patches results in the capture or convergence of limiting resources from the surrounding, unmodulated landscape creating spatially structured subsidies to the tree patch (sensu Polis et al., 1997). The influx of the limiting resource establishes a positive feedback loop by increasing the size of the tree patch and allowing an even greater capture of the limiting resource. Thus, positive and negative feedbacks between biomass and resources create a spatially organized landscape biocomplexity (Shachak et al., 2008). Furthermore, the presence of tree patches and their ability to create areas of altered resource availability also increases species richness (Belsky and Canham, 1994; Shachak et al., 2008).

The importance of tree patches for ecosystem cycles and the discovery that tree islands in the Everglades contain extraordinarily high levels of total phosphorus (TP) in their soil suggests that tree islands may play a major role in the biogeochemical cycles of nutrients in the Everglades (Sah, 2004; Troxler and Childers, 2010; Troxler et al., 2009; Wetzel, 2002a; Wetzel et al., 2009). Conceptual models of tree island biogeochemistry were first described by van der Valk et al. (1998) and have evolved over the last decade into the Focused Nutrient Redistribution (FNR) model (Givnish et al., 2007; Ross et al., 2006; Sklar and van der Valk, 2002; Wetzel et al., 2005). Many important ecological drivers of this tree island biogeochemistry model were suggested by studies from savanna and wetland patterned landscapes (Breashears, 2006; Ellery et al., 1993; Glaser, 1987, Rietkerk et al., 2002; Rietkerk et al., 2004) and have not been verified with data from the Everglades. The FNR model of tree island biogeochemistry, which is explored in this paper, has two major underlying hypotheses: (a) that patches of woody vegetation alter the local biogeochemical cycling in a spatially explicit manner and (b) that woody vegetation contributes to the oligotrophy of the Everglades (sensu Shachak et al., 2008).

According to the FNR model (Figure 1), tree aggregations in a marsh modulate their immediate environment by concentrating resources (especially phosphorus) on the landscape. FNR is predicted to occur by a combination of evapotranspirational pumping of surface and groundwater (McCarthy and Ellery, 1994; Ross et al., 2006; also see Rietkerk et al., 2004a), higher dry fallout deposition on trees (Krah et al., 2004; Weathers et al., 2001), and increased deposition of animal bones and feces under trees (Burton et al., 1979, Coultas et al., 2008, Frederick and Powell, 1994, Lund, 1957, Tomassen et al., 2005). Other possible sources of nutrient inputs to tree islands include groundwater transport of phosphorus to the tree island and the dissolution of phosphorus from limestone by the acidification of the rhizosphere by tree roots (Wetzel et al., 2005).

The FNR model also predicts that nutrients from the surrounding landscape contribute to the relatively high belowground primary production on an island, which in turn increases the rate of soil accretion on the island compared to the surrounding marsh, and thus increases the length, area, and elevation of a tree island. According to the FNR model, nutrients that were concentrated on the island may also move off the head of an island either by erosion during extreme flow events, by wind during a fire, or by leaching of nutrients into shallow groundwater or overlying surface water (Wetzel, 2002b; Wetzel et al., 2005). As islands enlarge more trees and shrubs become established, more nutrients accumulate, and island

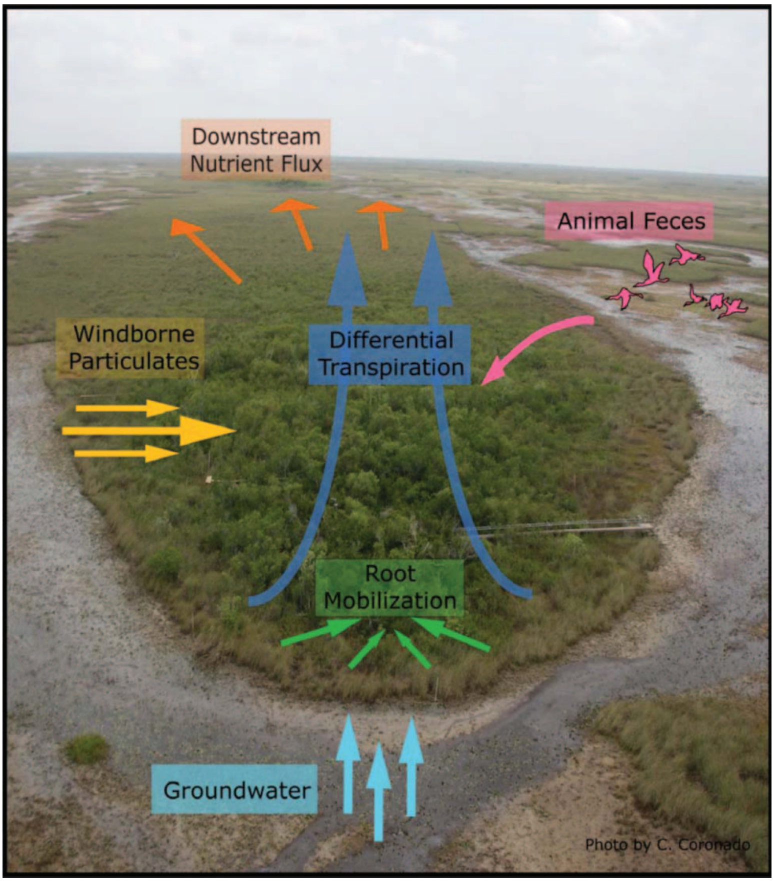

FIGURE 1. The Focused Nutrient Redistribution hypothesis proposes that forested islands capture and focus nutrients on the Everglades landscape through transpiration, attraction of animals, capture of aeolian deposits, groundwater upwelling, and alteration of the rhizosphere environment. Downstream nutrient fluxes enhance plant growth, increasing organic matter deposition and further tree growth, causing the island to expand. The photograph is of intensively studied Island 3AS3, located in the southwest WCA-3A. Note boardwalks on tree island head and near tail. (This figure is available in color online.)

elevation increases, allowing more trees to establish. This positive feedback loop means that islands can continue to grow in size until (a) an equilibrium (production equals decomposition) is reached, (b) a disturbance (e.g., hurricanes, fire, flooding) reduces tree abundance, or (c) there is a collapse of the focused nutrient redistribution cascade of interactions (Wetzel et al., 2005).

The biogeochemical pathways needed to establish new tree islands are not known nor likely explained by the FNR conceptual model. However, stratigraphic and paleoecological evidence from two tree islands indicates that tree islands were not present when the Everglades first developed and that they originated on sawgrass marsh sites between 3200 and 1700 years ago (Willard et al., 2002). Tree islands and forest strands are integrated into the patterned landscape, often forming sections of sawgrass ridges, both of which are separated by water lily (*Nymphaea* spp.) dominated sloughs and oriented parallel to the predominant historic surface water flow direction. This close proximity between tree islands and ridges, the physical integration of tree islands and sawgrass ridges, and the similar landscape orientation has lead to the development of a slough–ridge–tree island conceptual model (Givnish et al., 2007; National Research Council, 2003; Ross et al., 2006) where each landscape feature exists on an elevational continuum with the sloughs at the lowest elevation, followed by ridges at a midlevel elevation, and tree islands at the highest topographic elevation.

The purpose of this paper is to review and synthesize present biogeochemical information of tree islands including the plant, soil, and hydrologic processes that may explain why they are biogeochemical hot spots in the Everglades landscape. Although much of the information in this paper will focus on the biogeochemistry surrounding an individual island (3AS3) in WCA-3A, these data may have implications and inferences at multiple spatial scales throughout the ecosystem.

NUTRIENT DISTRIBUTION IN THE EVERGLADES LANDSCAPE

From a nutrient perspective two landscape patterns emerge in the Everglades. First, extremely high levels of nutrients—phosphorus in particular—are concentrated in discrete, localized areas on an otherwise oligotrophic landscape (Figure 2). Soil nutrient data from 31 tree islands located in WCA-3A and WCA-3B indicated that TP at a 0–10 cm depth on tree island heads was 2–240 times greater than in the surrounding marsh (Table 1). At the 0–10 cm depth TP values on the head of tree islands ranged from 736 to 96750 mg kg^{-1} and TP values within the marsh ranged from 227 to 571 mg kg^{-1} (Table 1, Figure 2A). A similar pattern was observed at the 10–20 cm depth with higher values on the head than on the surrounding marsh (Table 1, Figure 2B). Soil TP levels at both depths decreased an order of magnitude in the near tail portions of the island compared to the island heads but were still approximately 4 times higher than the surrounding TP levels in the marsh (Table 1).

Soil total nitrogen (TN) levels followed a pattern opposite of TP. TN levels were 30–40% lower on the tree island head compared to the marsh at both 0–10 and 10–20 cm depths (Table 1). Median total carbon levels were fairly constant on the islands and between islands and the marsh, although they varied widely (Table 1). Bulk soil densities averaged 0.34 g cm^{-3} on tree island heads compared to 0.07 g cm^{-3} in the marsh (Table 1). Drier conditions on the island heads may have resulted in higher organic matter

TABLE 1. Soil characteristics at two depths on tree island head, near tail and surrounding marsh environments located in WCA-3A and WCA-3B

Constituent and soil depth (cm)	Head ($n = 31$)	Near Tail ($n = 25$)	Marsh ($n = 31$)
Total P			
0–10			
Mean	11847 ± 3568	1814 ± 919	378 ± 13
Median	3335	804	363
Range	736–96750	498–23803	227–571
10–20			
Mean	16834 ± 4467	1164 ± 295	279 ± 15
Median	5756	661	261
Range	577–93450	395–6244	183–547
Total N			
0–10			
Mean	23753 ± 1557	27337 ± 1137	35330 ± 693
Median	26600	28000	36200
Range	6180–35800	6600–39200	26300–40000
10–20			
Mean	20070 ± 2099	26633 ± 1559	34409 ± 972
Median	22600	28500	36300
Range	2480–39700	4070–38000	26700–41200
Total C			
0–10			
Mean	383967 ± 4619	442633 ± 2815	456826 ± 1230
Median	450000	463000	462000
Range	108000–518000	103000–523000	371000–497000
10–20			
Mean	309140 ± 5504	409229 ± 3790	441636 ± 1601
Median	340000	451000	448000
Range	28000–503000	67600–492000	385000–515000
Soil bulk density			
0–10			
Mean	0.20 ± 0.03	0.13 ± 0.02	0.07 ± 0.01
Median	0.11	0.11	0.06
Range	0.03–0.68	0.07–0.99	0.02–0.13
10–20			
Mean	0.34 ± 0.04	0.21 ± 0.03	0.15 ± 0.01
Median	0.20	0.17	0.13
Range	0.07–1.02	0.09–0.88	0.10–0.20
TN:TP			
0–10			
Mean	15 ± 2	35 ± 3	69 ± 5
Median	13	36	65
Range	0.1–37	8.0–60	43–108
10–20			
Mean	19 ± 4	41 ± 4	104 ± 8
Median	10	48	95
Range	0.1–58	5–72	51–189

Note. Nutrient values = mg kg^{-1} ± *SE*; bulk density values = g cm^{-3}.

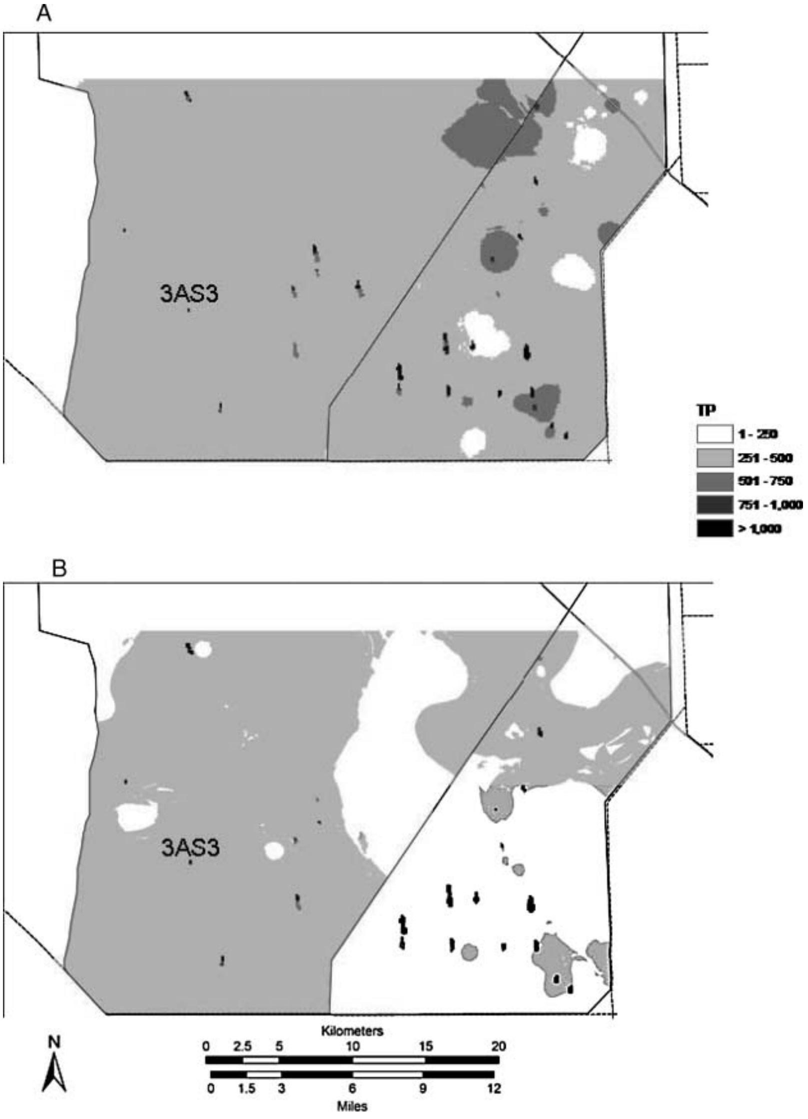

FIGURE 2. Spatial distribution of soil total phosphorus concentrations (mg kg^{-1}) in southern WCA-3A and WCA-3B. (A) Total soil phosphorus at 0–10 cm. (B) Total soil phosphorus at 10–20 cm deep. Only islands in which soil TP were measured are shown on these figures. There are many other tree islands in the areas depicted.

decomposition rates, resulting in higher soil bulk densities and the buildup of P on tree island heads over time. However, differences in bulk density (~50%) between heads and the marsh account for only a small amount of the nine fold median difference in their soil TP.

TN:TP ratios are lowest on the heads of tree islands and greatest in the surrounding marsh environment (Table 1). Ross et al. (2006) found the

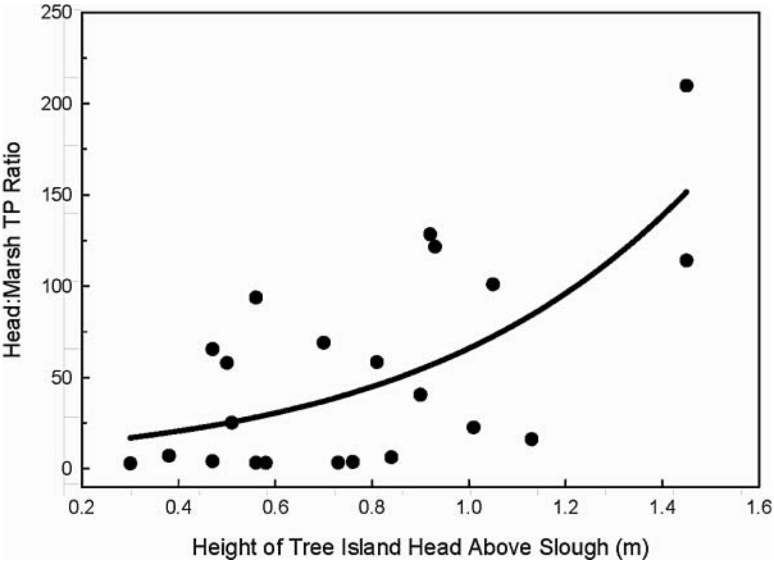

FIGURE 3. Relationship of height of tree island head above surrounding marsh and the ratio of island head to marsh total soil phosphorus levels (0–20 cm deep) for 31 islands located in WCA-3A and WCA-3B. For fitted line, $r^2 = .44$, $p = .004$.

same pattern in the molar N:P ratios in leaves of plants growing across a hydrologic gradient. Leaves of *Chrysobalanus icaco* growing on a tree island head and tail had N:P values of 23 and 52, respectively, suggesting N limitation on the tree island head and P limitation for the plants in the tail environment. The soil TN:TP ratio pattern along with the hydropattern found on tree islands may help to explain why tree basal areas, a factor that integrates primary production in forest ecosystems, are higher on the head of tree islands relative to the near tail (Sklar et al., 2006).

Results from the 31-island survey also indicate the tree island elevation is positively correlated with the head:marsh TP ratio, a simple measure of the strength of the nutrient gradient surrounding a tree island (Figure 3). Thus, tree islands with the highest elevations also maintain the strongest phosphorus gradients (see Shachak et al., 2008).

To date, studies of P in tree island soils measure TP only; the specific proportion of organic to inorganic phosphorus is unknown. Environmental factors such as the length of time that tree island soils are inundated affect the levels of organic and inorganic P retained in the soil. Given the organic nature of surficial soils, and that higher rates of organic matter oxidation are anticipated in regions of less inundation, then more P is expected to be stored as inorganic forms in surficial soils. In addition, guano inputs may increase the proportion of inorganic P. Limited results from two preliminary studies suggest that prediction is true. Sequential P fractionation from two tree island soils (0–10 cm) indicated that calcium bound P (HCl extractable

TABLE 2. Landscape mean values of TP in soil from tree island heads (0–30 cm) compared with marsh soils (0–10 cm)

Location	Tree Island TP ± *SE* (mg kg^{-1} dry wt.)[a]	Marsh TP ± *SE* (mg kg^{-1} dry wt.)
WCA-1	1478 ± 31 (*n* = 4)	405 ± 14 (*n* = 131)[b]
WCA-3A	2777 ± 1122 (*n* = 40)	402 ± 12 (*n* = 189)[c]
WCA-3B	10329 ± 3315 (*n* = 35)	371 ± 22 (*n* = 54)[c]
Everglades National Park	41073 ± 3097 (*n* = 70)	312 ± 10 (*n* = 310)[d]

[a] Ewe, 2008.
[b] Corstanje et al., 2006.
[c] Bruland et al., 2006.
[d] Osborne et al., 2011.

P) is higher on drier tree island heads and represents on average 70–90% of the TP pool compared to <20% of the TP pool found in the near tail and tail sites (Newman, unpublished data). Additionally, X-ray diffraction showed that the phosphorus mineralogy of tree island head soil samples was primarily amorphous apatite ($Ca_5(PO_4)_3(F, Cl, OH)$) (Bates et al., 2010).

The second landscape nutrient pattern to emerge is that soil phosphorus levels on tree island heads are lowest in the northern Everglades and generally increase southward (Table 2). Total phosphorus (TP) levels on islands in the Everglades National Park are 4 times greater than islands in WCA-3B and on average 28 times greater than soil TP levels on islands in WCA-1 (Table 2). Conversely, TP concentrations of marsh soils are lowest in the central and southern Everglades, compared to the northern portion. The reason for the pattern in TP observed in tree island soils is not known, but geology may play a role. Sand units underlie the western sections of the WCAs, while limestone is found at the surface in Everglades National Park (Harvey et al., 2006; Price et al., 2003). Underlying geology is important because phosphorus tends to leech from sandy soils and adhere to limestone. Human modification to the Everglades ecosystem may also play a role in this pattern of soil TP.

BIRDS AS NUTRIENT VECTORS

Birds have long been recognized as agents of nutrient transfers from water to land creating a confluence of localized nutrient concentration on the landscape (Anderson and Polis, 1999; Hobara et al., 2005; Hutchinson, 1950). The historically large flocks of wading birds in the Everglades (Ogden, 1994) suggest that they have been an important biotic vector of nutrient transfer. Nutrient inputs from birds are expected to vary with diet, the relative use of marsh and tree island habitats (Bancroft et al., 2002; Gawlik and Rocque, 1998), and nesting success (Bildstein et al., 1992; Frederick and Powell, 1994). The nutrient content of feces of both wading and passerine bird species varies widely by species but ranges between 5 and 13% TN and 1.6 and 1.9% TP (Fredrick and Powell, 1994; Gawlik, unpublished data). Passerine species that spend most of their time in tree island habitats may simply recycle nutrients within islands (D. Gawlik, Florida Atlantic University, personal communication, 2006). Other species of passerines, raptors, and wading birds feed mostly in marshes but roost and nest on islands and these species are likely to be the primary avian importer of nutrients to tree patches.

Actual avian nutrient fluxes onto tree islands have not been measured, but Frederick and Powell (1994) estimated avian nutrient transport and concentration for the overall Everglades. They calculated that wading birds historically deposited an average of ~13 metric tons of nitrogen and 5.1 metric tons of phosphorus onto colony sites each year. For phosphorus, the avian roosting deposits amounted to only 3% of the phosphorus deposited by precipitation over the entire Everglades annually. However, recent estimates of phosphorus in rainfall in the Everglades suggest that previous studies may have overestimated the actual rainfall contribution of P by 36% to 50% due to contamination during sampling and analysis (Pollman et al., 2002).

Frederick and Powell (1994) point out that birds are capable of focusing a tremendous nutrient load on a very small area. They estimated that in 1987 the 352 ha Rescue Strand colony with approximately 5450 nests received 20.3 g m^{-2} yr^{-1} nitrogen and 0.90 g m^{-2} yr^{-1} phosphorus, an input that is 20 times the average historical areal input of Davis (1994). In 1934 a very large 16 ha wading bird colony of 250,000 nests located in the Shark River was estimated to have deposited 331 g m^{-2} yr^{-1} nitrogen and 120 g m^{-2} yr^{-1} phosphorus, 3000 times more phosphorus than was deposited by precipitation. The effects of avian nutrient inputs in the form of changes to plant composition and biomass are known to persist for 6–50 years after the birds have left the site (Frederick and Powell, 1994; Herbert and Fourquean, 2008; Lund, 1957).

Despite the potential for avian nutrient inputs to be large for a local area, it is well known that the location of bird colonies shift through time (Bancroft et al., 1992; Frederick and Powell, 1994; Ogden, 1994) and presently there are many more tree islands than there are large rookeries or nesting sites. It has also been observed that a tree island that is intensely used as a rookery can result in a highly degraded forest structure and composition for an extended period of time (Coronado, personal observation). Knowing whether the high phosphorus in the soil of a tree island originated from bird feces would be useful to understanding island sustainability. Uric acid, the main end product of N metabolism in birds, is excreted as a dry solid and was hypothesized to be a possible biomarker in tree islands' soil cores that could be used to trace historic TP contributions from avian populations. Preliminary studies of uric acid in bird guano on Rescue Strand and 5 Mile Head tree island soil

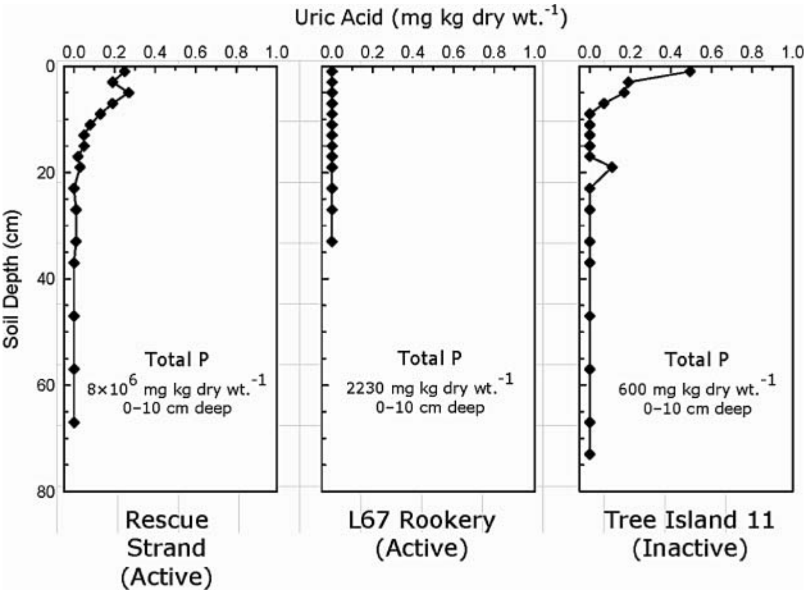

FIGURE 4. Distribution of uric acid with soil depth on two islands with active bird rookeries and an island with an inactive bird rookery.

samples were promising. High concentrations of uric acid were observed in bird guano, 316 mg kg^{-1}, and distinct down-core relationships between TP and uric acid were determined. In addition, uric acid concentrations were higher in soil from the heads of tree islands compared to the tail or marsh areas, providing further support for the potential causative relationship between TP and guano inputs. However, upon expanding the preliminary survey to include additional tree islands, the results are not as consistent (Bates et al., 2010). Uric acid in tree island head surface soil grab samples was found to be variable (from undetectable up to ~8 ppm) reflecting site variability, but the highest detectable amounts were greater than in any subsurface core sections by about a factor of 10. The upper core sections of this exploratory survey contained more uric acid than deeper sections, dropping off to undetectable levels below 25 cm depth (Figure 4). This result indicates that uric acid is greatly diluted in the soil and that uric acid is unstable and degrades over time. Degradation over time is suggested by the decrease in uric acid concentration with core depth, although TP also decreases with depth suggesting that TP may be correlated with guano inputs to the island.

One confounding finding was the result from L67 Rookery Island where virtually no uric acid was found even though an active wading bird rookery was present on the island (Figure 4). This finding could be the result of unusually low redox conditions at L67 (the core site was under water) due to its low relative elevation allowing bacterial degradation of uric acid (Karlsson et al., 1948). Unfortunately, these results suggest that uric acid may not be useful as an indicator of avian nutrient imports to tree islands. Further research is required to determine how soil conditions impact decomposition rates of uric acid in Everglades' soils.

TREE TRANSPIRATION AND ISLAND WATER CHEMISTRY

Phreatophytic or deep-rooted tree species are known to lower groundwater levels through transpiration and cause water levels to fluctuate in a diurnal pattern (Busch et al., 1992; Butler et al., 2007; Engel et al., 2005). Deep-rooted trees also uplift elements such as Ca, Mg, K, and P from soil minerals (Jobbágy and Jackson, 2004). The FNR model recognizes tree patches as important transpiration pumps on the landscape that facilitate hydro- and biochemical cycles. This phenomenon has been observed to play a major role in the nonrandom organization of other wetland ecosystems (Eppinga et al., 2008; Ramberg and Wolski, 2008; Rietkerk et al., 2004). The intensive study of a single tree island labeled 3AS3 (Figures 1 and 2) was used to discern if the Everglades exhibits similar characteristics. Results described in this section include the diurnal patterns of evapotranspiration by trees, the origin of the water that is transpired, and quantification of the lateral and vertical movement of nutrients within the shallow (<1 m) surficial soil layer and the deep groundwater layer (2.5–9 m) under and around this tree island.

To redistribute and focus nutrients on the Everglades landscape according to the FNR model, forest patches must be established and taller than the surrounding vegetation to (a) trap windborne nutrients and (b) transpire greater amounts of water than the surrounding vegetation. Trees on the heads of tree islands in the northern Everglades range from 2 to 7 m (Wetzel, 2002a; D. Mason, unpublished data), but range from 5 to 12 m tall on tropical hardwood hammocks in the southern Everglades (Armentano et al., 2002). In contrast, trees on the near tail are often shorter, with overall sparser foliage. On Island 3AS3, tree height averaged 4.9 m and 4.2 m on the head and near tail, respectively. Total basal area, an indicator of how much water can potentially be transpired into the atmosphere from an island (Vertessy et al., 1995), ranged from 15 to 90 m^2 ha^{-1} in the southern Everglades (Armentano et al., 2002). On Island 3AS3 total basal area on the head was 16.6 m^2 ha^{-1} and 11.3 m^2 ha^{-1} on the near tail.

Sources of water available to plants on tree islands vary spatially and temporally. They include pools of open standing water within the tree island, shallow soil water, deep soil water (~1 m below ground), and adjacent marsh surface water. Each source has different isotopic signatures of δD and $\delta^{18}O$ due to its percolation rate into the groundwater relative to its evaporation rate. Because surface waters have more enriched isotopic signatures

TABLE 3. Mean (± standard error) percent groundwater (1 m deep) used by dominant fern and tree species in the wet and dry season on the head and near tail of Island 3AS3

	Wet season		Dry season	
Plant species	Head	Near tail	Head	Near tail
Acrostichum aureum	−12 ± 10	—	87 ± 7	—
Blechnum serrulatum	19 ± 11	22 ± 2	82 ± 16	75 ± 9.1
Annona glabra	52 ± 15	56 ± 16	84 ± 14	92 ± 12
Chrysobalanus icaco	74 ± 14	22 ± 2	90 ± 16	78 ± 4
Ilex cassine	74 ± 10	23 ± 2	95 ± 20	74 ± 1.4
Magnolia virginiana	30 ± 6	33 ± 13	58 ± 9	85 ± 2
Persea palustris	—	37 ± 11	—	70 ± 11
Salix caroliana	19 ± 28	21 ± 14	66 ± 8	78 ± 4

compared to groundwater, then plant water uptake sources can be identified using isotopic analysis of plant stem water. Using these concepts, plant water oxygen (δ^{18}O) and hydrogen (δD) stable isotopes were measured on five individuals of each dominant tree species and two fern species on the head and near tail of 3AS3. Additionally, potential sources of plant water uptake (open puddles, marsh surface water, shallow soil (0–5 cm) and deep soil (~1 m) waters) were sampled for comparison. Results indicated that tree and fern water sources vary by season and tree island position (Table 3). Generally, if shallow soil water or marsh surface water are available, then the trees and ferns located on the head or near tail use that source water regardless of season. However, if the shallow soil and marsh surface water are not available, either because it is the dry season or the trees are significantly higher than the surrounding marshes, then plants obtain water from the deep soil water. These results indicate that there are significant differences in the sources of water used by plants, $F(6, 25) = 5.141$, $p < .01$, and among tree species. The use of deep soil water increased (up to 4 times) for all species during the dry season regardless of where on the island the species were growing (Table 3). Saha et al. (2008) also found that trees growing on the heads of islands in the southern Everglades made a similar seasonal shift in their source waters between the dry and wet seasons. However, *Annona glabra*, *Chrysobalanus icaco*, and *Ilex cassine* living on the island head did not follow this pattern. These species used deep soil water 52–74% of the time even in the wet season.

The fact that treed islands are using deep and shallow ground water sources was verified by analyzing the fluctuating water levels in sets of wells on and around Island 3AS3 (Adamski, 2008; Troxler et al., 2009). These data indicated that trees on the head of Island 3AS3 transpired enough water each day during the dry season to lower the water level in the root zone from 1.0 to 2.0 cm (Figure 5). Using this diurnal flux in water level, transpiration rates of groundwater from the tree island head were estimated following Loheide

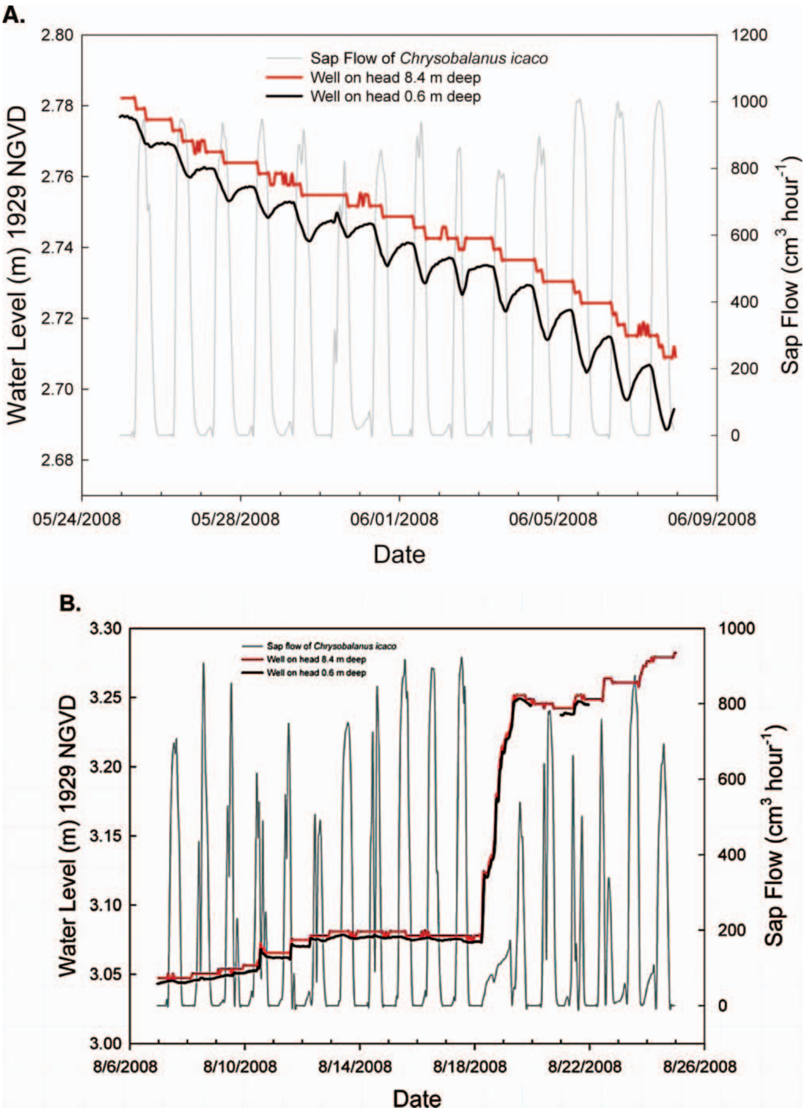

FIGURE 5. Diurnal well water levels and sap flow from the head of Island 3AS3 in dry and wet seasons. Daily sap flow velocities for *Chrysobalanus icaco* are also shown. (A) Dry season: Diurnal water level in root zone (0.6 m deep), shallow (2.8 m deep), and deep (8.4 m deep) wells. Data collected from 25 May to 8 June, 2008. (B) Wet season: Diurnal water level in root zone (0.6 m deep), shallow (2.8 m deep), and deep (8.4 m deep) wells. Data collected August 6–26, 2008. (This figure is available in color online.)

et al. (2005). Transpiration rates ranged from 3.4 mm d^{-1} (with a specific yield of 0.12; Tobias et al., 2001) to 9.9 mm d^{-1} (with a specific yield of 0.35; Shoemaker et al., 2008; Wilsnack, 2000). The low value is similar to values reported from a Kansas, USA, floodplain (Butler et al., 2007) and a

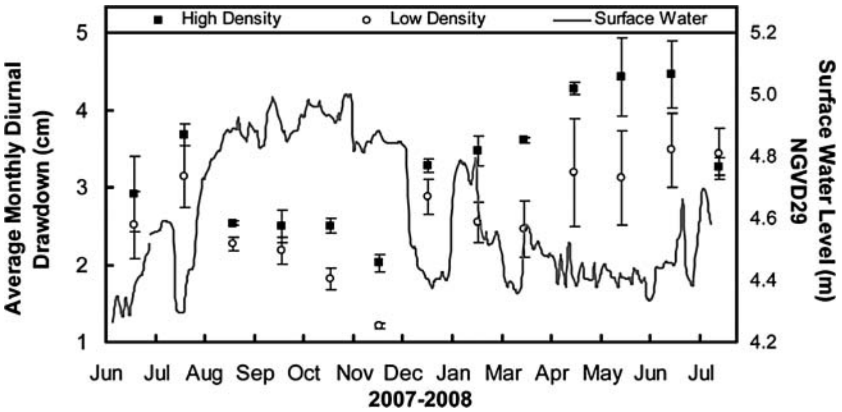

FIGURE 6. Average monthly diurnal drawdown from created tree islands at the Loxahatchee Impoundment Landscape Assessment facility. Two diurnal signatures are shown: one from a portion of the island with trees planted in high density (1 m spacing) and the second from a portion of the island planted with trees at low density (3 m spacing). Trees were between 4 and 5 years old. Surface water level during the data collection period is also shown.

Eucalyptus plantation in central Argentina (Engel et al., 2005). However, the high evapotranspiration value is higher than literature reports and reflects the soil porosity and the subtropical climate of the Everglades.

Diurnal water table fluctuations have also been observed in the Everglades National Park (Ross et al., 2006) and on created islands in the Loxahatchee Impoundment Landscape Assessment (LILA) facility. Ross et al. (2006) found that the diurnal drop in water level of a Bayhead forest averaged 0.8 cm at the beginning of the dry season, reached a maximum of 3.0 cm in the middle of the dry season, and declined to ~1.1 cm by the end of the dry season. At the LILA facility the experimental planting of trees at different densities (high 1 m spacing or low 3 m spacing) on created tree islands produced two patterns (Figure 6). The first pattern was that the high tree density plots produced a greater average monthly diurnal drawdown than low density plots. Secondly, average monthly diurnal draw-downs were greatest when surface water levels were lowest (Figure 6), similar to the pattern reported by Ross et al. (2006).

What is fascinating and new at island 3AS3 was the occurrence of a diurnal transpiration signature in the deep 2.8 m and 8.4 m wells. Although this daily water head drop was much less than in the root zone at ~0.5 cm, it was highly synchronized with day time photosynthetic activity as reflected in the peak sap flow rates (cm^3 hour^{-1}) of *Chrysobalanus icaco* (Coco Plum), the dominant woody species (Figure 5). In addition, during the wet season the diurnal transpiration signature was muted or not apparent even though the trees produced sap flow fluxes that were the same magnitude as those produced during the dry season (Figure 5). This pattern indicates that trees transpire similar quantities of water in the wet season compared to the dry season.

In general, groundwater flows under and around 3AS3 varied seasonally. During 2007 and 2008 (measured four times annually), the groundwater beneath the tree island was continuously recharged by water infiltrating through the root zone (Figure 7). At lower depths, groundwater flow direction alternated between recharge (flowing downward) and discharge (flowing upward) conditions from 2003 to 2008 (measured continuously; Figure 7). The dry season was nearly evenly divided between periods of vertical recharge and discharge under the island head between 2.8 and 8.4 m deep. However, groundwater recharge during the wet season increased to 66% of the time (Figure 7). The magnitude of the majority of the deep groundwater head differences was small ranging from 0 to 2 cm (Figure 7). Despite differences in measurement frequency, there were times under 3AS3 when shallow recharging waters and deeper discharging groundwater met in a zone of confluence between the depths of 0.3 and 2.8 m.

Seasonal shifts in water ion concentrations and composition also occurred in the confluence zone. The concentration of ions at the waters surface and at depths of 2.8 and 8.4 m in both the tree island head and adjacent marsh were nearly equal during both the dry and wet seasons (Figure 8). However, during the dry season, ion concentrations of water under the head more than doubled in the rooting zone (depths of 0.3 and 0.5 m) compared with concentrations in the marsh (Figure 8). There was also an increase in sodium and chloride ions vertically beneath the island head, particularly during the dry season. The increase of Na and Cl reached a maximum in the waters of the 0.6 m well where they were nearly 10 times greater than in the waters of the 8.4 m well. Mg concentrations also increased ~5 times in the rooting zone, while $CaCO_3$ concentrations increased 33–60% compared with the deep well composition (Figure 8). During the wet season, Na and Cl ion concentrations on the head dropped ~50% under the tree island head. These patterns in ionic concentration and composition suggest that as trees transpire they are removing water and the dissolved solutes required for their growth and excluding others. Thus, the salinity of the groundwater in the zone of confluence is increased slightly under the tree island head during the dry season. This concentration of salts is diluted or washed away by the seasonal rise of the regional water table during the wet season when Na and Cl concentrations are closer to the concentrations found in marsh waters (Figure 8). Accumulation of salts (at much higher levels) because of transpiration of trees under tree islands was also observed in the Okavango Delta, Botswana (McCarthy et al., 1993).

Similarly, tree transpiration may lead to progressive precipitation of calcium carbonate. Groundwater around the wetland surrounding tree island 3AS3 is supersaturated with gypsum ($CaSO_4\ 2H_2O$) and calcite ($CaCO_3$; S. Krupa, South Florida Water Management District, unpublished data), which

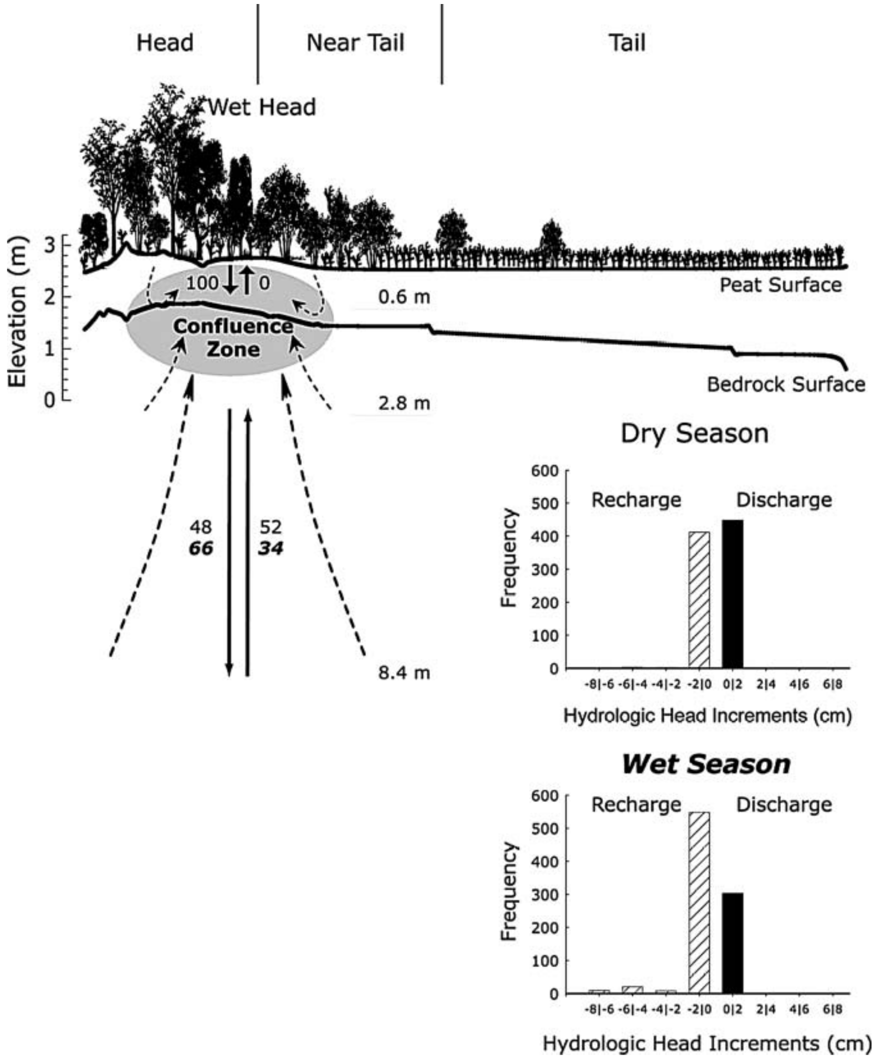

FIGURE 7. Hydrologic movements under Island 3AS3 for dry (November–April) and wet (May–October) seasons (data collected August 2003 to June 2008 unless otherwise noted). Arrows indicate the percentage of time that water was discharging or recharging at designated depths (data at 0.6 m collected from 2007 and 2008). Bold, italicized numbers indicate wet season. Dotted arrows represent water movement from tree transpiration. Tree transpiration and the confluence of recharge and discharge create a chemical mixing zone of higher ionic concentrations and salinity that is most strongly present during the dry season. Histograms depict magnitude of hydraulic head in groundwater movement between 2.8 and 8.4 m deep. The *x*-axis values are 2 cm increments of head difference; the *y*-axis is the daily frequency of each increment. Surface and bedrock lines are from D. Mason (Indiana Dunes National Park, unpublished data).

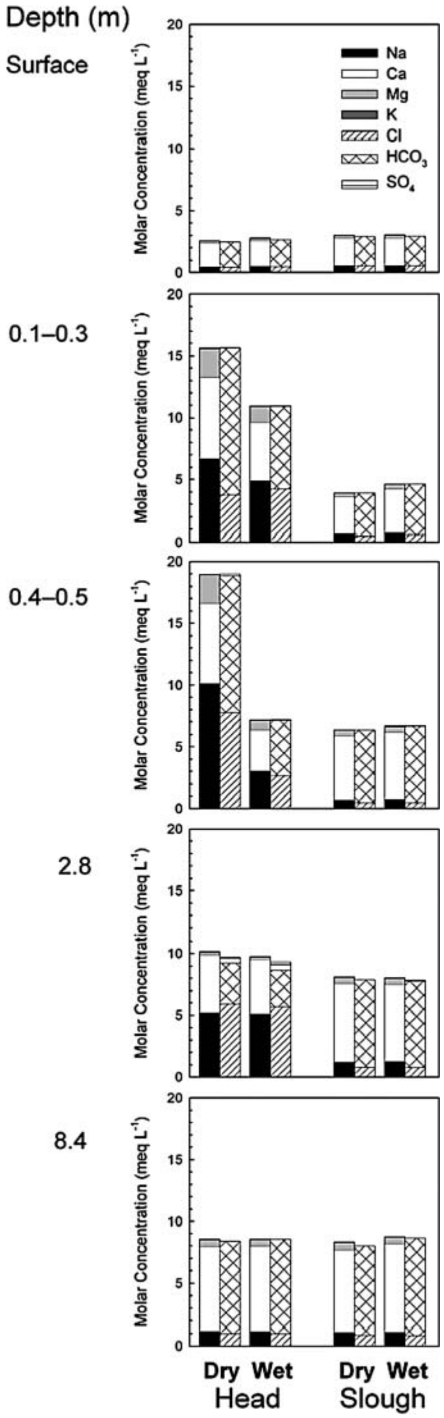

FIGURE 8. Mean ionic composition of water from wells located on the head of Island 3AS3 and surrounding marsh at various depths during dry (November–April) and wet (May–October) seasons. Data collected between 1999 and 2005.

could help to explain the newly discovered calcrete (hardened deposits of calcium carbonate) layer under tree islands in the Shark River Slough (Graf et al., 2008). Tree transpiration derived from progressive accumulation and eventual calcite precipitation was also found under tree islands of the Okavango Delta (Ramberg and Wolski, 2008), where it is great enough to increase the volume of the soil, causing those islands to steadily grow in size (McCarthy, 2006).

TREE-MEDIATED NUTRIENT CONCENTRATION

The broader and highly significant question concerning tree transpiration is whether the resultant movement of water transports P toward an island. Data from LILA indicate that trees may concentrate nutrients in the groundwater under an island. Concentrations of TP were significantly higher ($p < .1$) in the shallow groundwater under island locations with high tree densities compared to low tree density locations. In WCA-3A, measurements of TP in the pore water and groundwater on Island 3AS3 indicated that TP levels at the island head were significantly greater on average in the zone of confluence (0.3–2.8 m deep) than at the other locations on the island or in the marsh (Figure 9). Median TP levels in the wells on the island head ranged from about 2 μM in the 2.8 m and 8.4 m deep wells to a high of 7 μM in the root zone porewater wells, a pattern that was consistent in both dry and wet seasons. The relatively low TP in the deep (8.4 m) well suggests that the higher TP in the 2.8 m well is not originating from deep groundwater sources. However, high TP levels in the root zone are also not coming from surface water. Total phosphorus was lowest in surface waters ($\sim$0.4 μM) whether measured at the island or marsh locations. Such a low phosphorus value is not surprising because any free phosphorus in the water column would be readily immobilized by microorganisms and periphyton or chemically precipitated (Noe et al., 2001; Reddy et al., 2005). The highest concentrations of P under a tree island occur in the confluence zone although the source of that TP is not clear. In theory, tree transpiration could concentrate TP in the groundwater from specific geologic formations or from local hydrologic conduits similar to mechanisms found in coastal groundwater discharge into mangrove forests (Price et al., 2006). Phosphorus cycling on a tree island, regulated by the organic content of the soil (i.e., phosphorus sorption) and by carbonate-rich soils (i.e., phosphorus precipitation; Reddy et al., 2005) is mediated by microorganisms—both fungi and bacteria when soils are aerated and exclusively by bacteria in anaerobic conditions. At the same time, downward and lateral flux of phosphorus in the soil occurs through diffusion and water forced infiltration, while plant transpiration causes phosphorus to flux upward in the soil environment (Reddy et al., 2005). All of these fluxes work together in the FNR model.

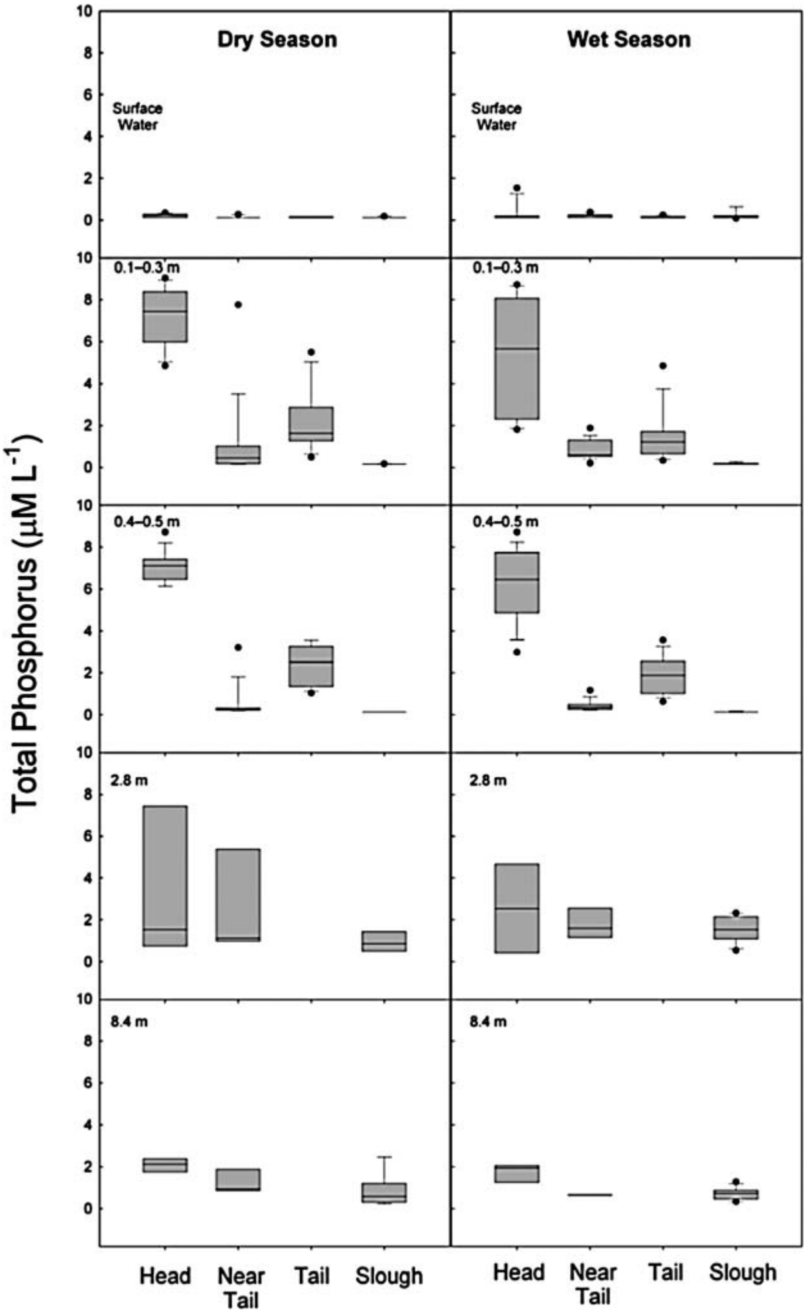

FIGURE 9. Total phosphorus in wells located on Island 3AS3 head, near tail, tail, and surrounding slough at various depths during dry (November–April) and wet (May–October) seasons. Data collected between 1999 and 2005.

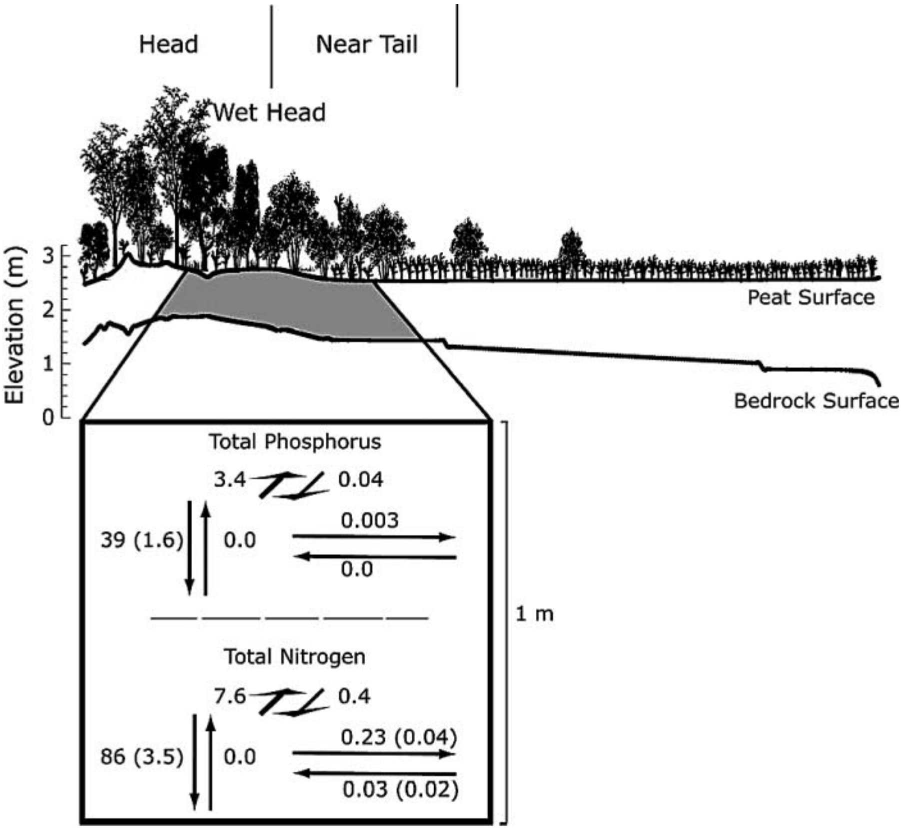

FIGURE 10. Dry season infiltration and lateral nutrient fluxes in the root zone on wet head and near tail of Island 3AS3. Total phosphorus and nitrogen fluxes (mg m^2 d^{-1}) between 0.3 and 0.6 m deep. Lateral fluxes are the sums of averaged values across a transect. Dry season data collected from March 2 to 21, 2007.

The FNR model predicts that the high TP levels in the root zone (0.1 to ~0.6 m deep, Figure 9) concentrated on the head of an island can move downstream to the near tail and tail sections in shallow groundwater flow (Figure 1). To evaluate this, a series of five shallow piezometer clusters along four transects (see Troxler et al., 2009) on the wet head and near tail of Island 3AS3 were used to summarize the net movement of nutrients across the island. Each well cluster included a 0.3 m and 0.6 m deep piezometer and was sampled in January, March, May, June, and August of 2007 and 2008 (Troxler et al., 2009). The dominant phosphorus and nitrogen flux in the dry season was infiltration (Figure 10). Downward phosphorus and nitrogen fluxes were greater during the dry season than during the wet season (39.1 ± 1.6 compared with 17.2 ± 0.6 mg m^2 d^{-1} for TP and 86.0 ± 3.5 compared with 38.0 ± 0.6 mg m^2 d^{-1} for TN). Phosphorus and nitrogen fluxes other than infiltration during the wet season were either negligible or zero and therefore are not shown on Figure 10. What happens to the nutrients that infiltrate vertically is not known at this time. These nutrients may flux upward by plant transpiration or infiltrate to deep soil layers particularly as regional water levels drop during the dry season. If nutrients infiltrate the deep soil layers, they may eventually reach the water table and may be transported with groundwater flow. Harvey et al. (2006) reported that the groundwater and surface water actively exchange (mix) in the upper 8 m of the surficial aquifer beneath WCA-2. Eppinga et al. (2008) found higher concentrations of potassium, magnesium, phosphorus, and nitrogen in groundwater under elevated ridges compared to the hollow/slough of the Great Vasyugan Bog. They attributed these elevated concentrations to (a) higher evapotranspiration rates on the ridge compared to the hollow, which caused a net flow of dissolved nutrients and ions toward the ridges, and (b) a local recycling effect of nutrients caused by higher order vascular plants on ridges.

Surficial downstream fluxes from the wet head to the near tail during the dry season were small for TP (0.003 ± 0.000 mg m^2 d^{-1}) and modest for TN (0.23 ± 0.6 mg m^2 d^{-1}; Figure 10). Contrary to the FNR model, these values do not suggest a large nutrient movement downstream, even though the downstream vegetation appears enriched compared to the surrounding marsh (Coronado, personal observation). However, preliminary results of the budget studies by Troxler (in review) using these well clusters suggest that island heads are annual net exporters of TP and that near tails are net importers. The minimal TP and TN flux downstream of the wet head may reflect the efficiency with which P is sequestered downstream of the wet head plant community. The mechanism of how nutrients on the head move downstream on an island as predicted by the FNR model is still unclear but may be related to groundwater flow directions. For example, the observation that ion concentrations under the island described earlier nearly disappear in the wet season (Figure 7) may indicate a seasonal nutrient pulse at the beginning of the wet season, after which there is not much movement. Reflooding after a drawdown event was found to stimulate microbial activity in other Everglades' soils resulting in nutrient fluxes to the pore- and surface waters and potentially redistributing P and N over a wider area (Corstanje and Reddy, 2004; Fisher and Reddy, 2001). Alternatively, the particular sampling times of this piezometer study on Island 3AS3 may not have coincided with the wet season flush of nutrients.

Although smaller in magnitude than the infiltration fluxes, 3.4 mg m^2 d^{-1} of TP and 7.6 mg m^2 d^{-1} of TN moved laterally away from the center of the island during the dry season (Figure 10). Unfortunately, transects of piezometers did not extend to the marsh surrounding Island 3AS3, so there was no clear evidence that lateral export of phosphorus and nitrogen extends off the island and into the surrounding marsh. However, the measured lateral export of nutrients lends some support to the finding that nutrients may be transported off of tree islands, influencing the composition of local plant communities surrounding tree islands (Givnish et al., 2007). Givnish et al. (2007) reported that the vegetation association of *Peltandra virginica* and *Sagittaria latifolia*, a plant association that grows only in nutrient rich soils, was more likely to be found in the proximity of tall tree islands.

CONCLUSIONS AND IMPLICATIONS FOR RESTORATION

The data presented indicate that tree islands are clearly biogeochemical hot spots on the Everglades' landscape. Through mechanisms that are still not clear, tree islands are nutrient sinks and average surface soil concentrations of TP on island heads can range between 1,478 and 41,000 mg kg^{-1} in the extant ridge and slough landscape (Table 2). This phosphorus is highly conserved on the island by the carbonate-rich soils (Reddy et al., 2005) and nutrient efficient vegetation communities (Ross et al., 2006; Troxler-Gann et al., 2005). Elevation of an island relative to local hydrology and soil nutrient content was found to be consistent with the Wetzel et al. (2009) finding that highly elevated islands (>1.0 m above the marsh) can have 3–130 times the soil TP concentrations of the surrounding marsh.

Water transpiration by the trees on a tree island can reduce water levels in shallow and deep groundwater wells, thereby extending the unsaturated zone and allowing for vertical flow to dominate. This vertical movement of water (Figure 5) during the dry season was in synchrony with the diurnal sap-flow dynamics of the dominant tree species. Significant upward movement of water, combined with a concentration of ions and an increase in salinity and nutrients between 0.6 and 2.8 m deep suggested a concentration or confluence zone under island heads. It is important to note that the shallow wells on the study island indicated a significant downward movement of water and material (Figure 10) and a paucity of lateral flow across the surficial interface of marsh and island. Ion concentrations decreased during the wet season suggesting that the regional groundwater flows are important for moving nutrients downstream on the tree island.

Tree islands may focus landscape nutrients in multiple ways, most notably by serving as perches and nesting sites for wading birds. Although there was some evidence for historic avian inputs of phosphorus gleamed from uric acid signatures in island soil, this information was confounded by biodegradation in the deeper core segments (Figure 4). Tree islands are also expected to capture greater amounts of aeolian deposits than marsh vegetation, although this potential focusing mechanism has not been measured. Knowledge of the rate and magnitude of windborne nutrient deposits on tree islands represents a major gap in scientists' understanding of tree island biogeochemistry and needs to be studied.

What then does all this mean for the restoration of tree islands? It means that tree patches have a pivotal role in localized nutrient cycling. Tree patches may also have a widespread biogeochemical effect on the Everglades as a whole. The hydrologic seasonality and extent of drawdown of water levels relative to island elevation is an important driver of the accumulation of TP on the head and tail of tree islands. The hydrologic alteration between dry and wet seasons appears to play a critical role in nutrient cycling on tree islands and a possible role in the flushing of nutrients downstream to the tail on an island. Dry–wet cycles are also critical for the survival and nesting success of wading birds (Frederick and Ogden, 2001), which in turn may be a major nutrient concentrating vector for tree island survival. Nonetheless, further studies are needed to determine the biogeochemical role of tree islands at the landscape level.

This review and the work of others (Givnish et al., 2007; Ross et al., 2006) have determined that tree islands by their very nature are the result of material fluxes operating at multiple spatial and temporal scales. The material fluxes that possibly create and help maintain an individual tree island extend far beyond its visible boundaries. A clearer understanding of this concept is needed for the restoration of the tree islands, and by extension, the Everglades itself. For example, water transpired by trees moves groundwater beyond the boundaries of a tree island as seen in wells in the marsh around Island 3AS3; wading birds transport nutrients many kilometers to an island; and guano deposited decades prior by nesting wading birds can continue to enrich tree island vegetation for many years. Tree islands are the result of material fluxes of a limiting resource (i.e., TP) at multiple scales and the creation of strong biogeophysical gradients, which in turn has increased the biocomplexity on the Everglades landscape (Margalef, 1968). It may be that the difference in the hydrologic and nutrient levels between tree islands and the surrounding marshes are positively correlated with the level of landscape biocomplexity.

The practical and logistical aspects of tree island restoration and creation is daunting in the face of all the uncertainties presented in this paper. However, significant gains in understanding have been made in recent years. Results from the LILA facility indicate that tree islands with some apparent hydro- and biogeochemical function similar to natural tree islands can be created, demonstrating that functional tree islands can be produced on a human time scale. Manipulative environmental strategies to restore islands that are degraded or lost and adaptive management (Holling, 1978) to sustain islands that are healthy and vital should now be at the forefront of Everglades ecosystem restoration.

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