

Interaction of hydrology and nutrient limitation in the Ridge and Slough landscape of the southern Everglades

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Abstract

Extensive portions of the southern Everglades are characterized by series of elongated, raised peat ridges and tree islands oriented parallel to the predominant flow direction, separated by intervening sloughs. Tall herbs or woody species are associated with higher elevations and shorter emergent or floating species are associated with lower elevations. The organic soils in this “Ridge-and-Slough” landscape have been stable over millennia in many locations, but degrade over decades under altered hydrologic conditions. We examined soil, pore water, and leaf phosphorus (P) and nitrogen (N) distributions in six Ridge and Slough communities in Shark Slough, Everglades National Park. We found P enrichment to increase and N to decrease monotonically along a gradient from the most persistently flooded sloughs to rarely flooded ridge environments, with the most dramatic change associated with the transition from marsh to forest. Leaf N:P ratios indicated that the marsh communities were strongly P-limited, while data from several forest types suggested either N-limitation or co-limitation by N and P. Ground water stage in forests exhibited a daytime decrease and partial nighttime recovery during periods of surface exposure. The recovery phase suggested re-supply from adjacent flooded marshes or the underlying aquifer, and a strong hydrologic connection between ridge and slough. We therefore developed a simple steady-state model to explore a mechanism by which a phosphorus conveyor belt driven by both evapotranspiration and the regional flow gradient can contribute to the characteristic Ridge and Slough pattern. The model demonstrated that evapotranspiration sinks at higher elevations can draw in low concentration marsh waters, raising local soil and water P concentrations. Focusing of flow and nutrients at the evapotranspiration zone is not strong enough to overcome the regional gradient entirely, allowing the nutrient to spread downstream and creating an elongated concentration plume in the direction of flow. Our analyses suggest that autogenic processes involving the effects of initially small differences in topography, via their interactions with hydrology and nutrient availability, can produce persistent physiographic patterns in the organic sediments of the Everglades.

Introduction

The peatlands of the southern Everglades are characterized by series of elongated ridges and

tree islands, oriented parallel to the predominant direction of water flow, with broader intervening sloughs that are tens of centimeters lower in elevation. This modest physiographic variation is

associated with a pronounced vegetation pattern, consisting of tall herbs or woody plants on the higher peat surfaces and shorter emergent or floating plants on the lower ones. As a fundamental landscape characteristic throughout much of the pre-drainage Everglades, this “Ridge and Slough” pattern, as it has come to be known, is an important but often misunderstood target for ecological restoration of the Everglades ecosystem (SCT, 2003). As a case in point, performance measures used in planning for Everglades restoration limit the depth and duration of flooding in the Ridge and Slough, while some portions of the landscape appear to require longer and deeper flooding. Moreover, though water quality is also recognized as an important issue in Everglades restoration, especially with regard to the concentration of phosphorus, the spatial linkages between hydrology, nutrient dynamics, and the communities and landforms within the Ridge and Slough are rarely considered. A thorough characterization of the critical drivers that sustain this landscape is needed to resolve these issues.

Though the dynamics of the Ridge and Slough landscape are not well understood, paleoecologic evidence from tree island tails suggests that at least some of the current vegetation pattern may have been relatively stable over long time periods. Both Orem et al. (2002) and Stone et al. (2005) report that long tree island tails forming downstream of prominent rock outcrops were vegetated by herbaceous species during early stages of the ca 6000-year history of the Everglades, but have been forested – therefore occupying a relatively elevated surface – for most of the last two millennia. Recently, several research groups have pointed out that autogenic processes involving the effects of initially small differences in topography could produce persistent physiographic patterns in the organic soils of the Everglades (Clark & Reddy, 2003; Givnish & Volin, 2003; Ross et al., 2003). An analogous situation occurs in northern peatlands, where habitat variability appears to be generated as a result of the influence of ponding on soil aggradation due to plant production and degradation due to decomposition (Foster et al., 1983, 1988; Swanson & Grigal, 1988). Despite their apparent stability under natural conditions, Ridge and Slough features in the Everglades can degrade

over decades, in conjunction with water management that creates unnaturally extended periods of high or low water (SCT, 2003). Therefore it is essential to understand the role that hydrology and its interactions with nutrients play in regulating this system.

Several studies of long hydroperiod marshes in remote portions of Everglades National Park (ENP) have identified hydrological variables involving water depth and/or duration as the principal determinants of vegetation pattern or dynamics (e.g., Gunderson, 1989; Olmsted & Armentano, 1997; Busch et al., 1998; Ross et al., 2003). These studies from relatively pristine marshes are in counterpoint to a second body of research in which phosphorus availability has been implicated as the primary driver of vegetation pattern along impact gradients created by regulatory deliveries of high P canal water (Doren et al., 1997; Miao & DeBusk, 1999; Childers et al., 2003). The interaction of Ridge and Slough hydrology, nutrients, soils and vegetation has not been extensively studied, despite strong indications that these components of the Everglades ecosystem are strongly interdependent.

King et al. (2004) demonstrated that the relative strength of association between vegetation composition and a broad suite of environmental parameters varied with spatial scale and with distance downstream from a delivery canal. These parameters included phosphorus and nitrogen concentrations in the soil as well as several hydrologic measures. In this paper, we address the complementary roles of nutrient availability and hydrology as determinants of landscape pattern within portions of ENP far from anthropogenic nutrient sources. We studied the variation in soil, pore water, and leaf nutrient (N and P) concentrations along a hydrologic gradient from the most persistently and deeply flooded marshes through forested wetlands that typically flood for 6 months or less. Using statistical analysis and hydrologic modeling we provide evidence in support of a mechanism by which vegetation, hydrology, and nutrient availability are linked as drivers in a self-organizing system that maintains the characteristic heterogeneity of the Ridge and Slough. The mechanism we propose is based on local evapotranspiration-driven fluctuations in the water table and the resultant flow gradients, and resembles

one recently proposed by Rietkerk et al. (2004) for bog patterning. We demonstrate that evapotranspirative forcing of convergent flow, coupled with strong directional groundwater and surface water flow, can produce a landscape in which nutrient-enriched ridges are propagated parallel to the regional flow path, as they are in the Everglades.

Study area

The vegetation of the Ridge and Slough includes a heterogeneous mixture of marsh and tree island assemblages (Olmsted & Armentano, 1997; Ross et al., 2003). The marsh component is by far the more extensive. In comparison to the species-rich, short-hydroperiod prairies that occupy marl or limestone substrates on the periphery of the Everglades, the long-hydroperiod Ridge and Slough marshes are low in local species diversity, especially when they are dominated by the large sedge *Cladium jamaicense* Crantz (sawgrass). Two forms of sawgrass community are recognized. Tall Sawgrass marsh is a dense, monospecific community that occupies many of the low relief “ridge” landforms, and Sparse Sawgrass marsh comprises the broad marsh matrix in most of the region. The “slough” element in the current Shark Slough landscape is Spikerush marsh, a more open, relatively rich mixture of emergent and floating macrophytes, dominated by spikerush (*Eleocharis cellulosa* Torr.) or maidencane (*Panicum hemitomon* Schult.), and often features a floating periphyton community (an integrated mat assemblage consisting of algae, bacteria, and microheterotrophs).

Three types of wooded community may be distinguished in the Ridge and Slough; Hardwood Hammock, Bayhead and Bayhead Swamp forests. Hardwood Hammock is characterized by a closed canopy that often exceeds 10 m in height and usually includes a rich mixture of woody species. The dominant species (e.g., *Bursera simaruba*, *Ficus aurea*, *Sideroxylon salicifolia*, *Sideroxylon foetidissimum*, *Eugenia axillaris*) are tropical in origin and are common on infrequently flooded rocklands of the Miami Rock Ridge or the Florida Keys. Bayheads are also closed-canopy forests, but rarely exceed 8 m in height. Characteristic trees include several of tropical origin

(e.g., *Chrysobalanus icaco*, *Annona glabra*), along with a temperate group common in wetlands throughout the southeastern US (e.g., *Salix caroliniana*, *Morella cerifera*, *Persea borbonia*). Finally, Bayhead Swamp forest is a shorter, more open community whose tree assemblage overlaps with that of the Bayhead type. It is distinguished by a well-developed understory flora that includes a large contingent of graminoids, vines, and shrubs.

Ridge and Slough soils are primarily organic, though some exhibit intermittent marl horizons suggesting that hydrologic conditions have not been uniform throughout their history. Today, peat production is the dominant soil forming process in the Ridge and Slough, while marl formation is more important in open, peripheral grasslands where flooding duration is low (Gleason & Stone, 1994). Phosphorus limits growth in south Florida wetland plant communities (Steward & Ornes, 1975; Daoust & Childers, 1999; Noe et al., 2001), as it does throughout the Atlantic and Gulf coastal plains (Parker et al., 1946; Black, 1968). However, South Florida soils are atypical for the southeastern US in their high pH, and hence in the potential importance of basic cations, especially calcium, in phosphorus dynamics (Newman et al., 1998). Most of the Southern Everglades is oligotrophic, with total P concentrations in the water column as low as 1 ppb. Higher amounts of P are introduced into the natural system as canal water seepage and flow, enriched with P from agricultural sources.

The climate of the south Florida mainland is sub-tropical with a rainy season that extends from the end of May to October followed by a pronounced dry season from November to most of May. Precipitation during the rainy season is bimodal, with peaks in June and September. Rainfall occurs mostly as either local, short duration, convection-driven storms, or regional, longer duration events associated with tropical weather systems. Seasonal evapotranspiration (ET) patterns are controlled by incoming solar radiation, air temperature and water depth, with lowest rates occurring from December to February and the highest rates from May to August (German, 2000).

Water levels in the southern Everglades are influenced by both local and regional climate and

by operation of the Central and South Florida water management system, a complex configuration of canals, levees, pumps, and gated structures that regulate water flow from Lake Okeechobee to the Everglades, Biscayne Bay and Florida Bay (Light & Dineen, 1994). Ground water and surface water are tightly linked via the highly conductive Biscayne Aquifer which is present at the surface. The Biscayne aquifer is composed of karstic limestone with solution cavities that range in diameter from a few centimeters to a meter or more. The sites examined in this study were remote from water management structures, and considered pristine in terms of ambient water quality.

The Everglades surface water/ground water system can be broken into three components: (i) surface water, (ii) a soil layer, and (iii) an underlying aquifer. The aquifer can be extremely

transmissive, with measurements of transmissivity ranging from roughly 250 to 22,000 m²/d (Fish & Stewart, 1991). Horizontal soil conductivity measurements are lacking, but vertical conductivity measurements for Everglades soils have median values of about 60 cm/d (Harvey et al., 2004).

Methods

Soil, pore water and plant leaf nutrient concentrations were sampled in January 2000 at the marsh and tree island locations indicated in Figure 1. These sites represent the six major Ridge and Slough vegetation types present in Shark Slough, ENP. Marsh characteristics were sampled at 29 locations within an extensive network in which vegetation and hydrology had

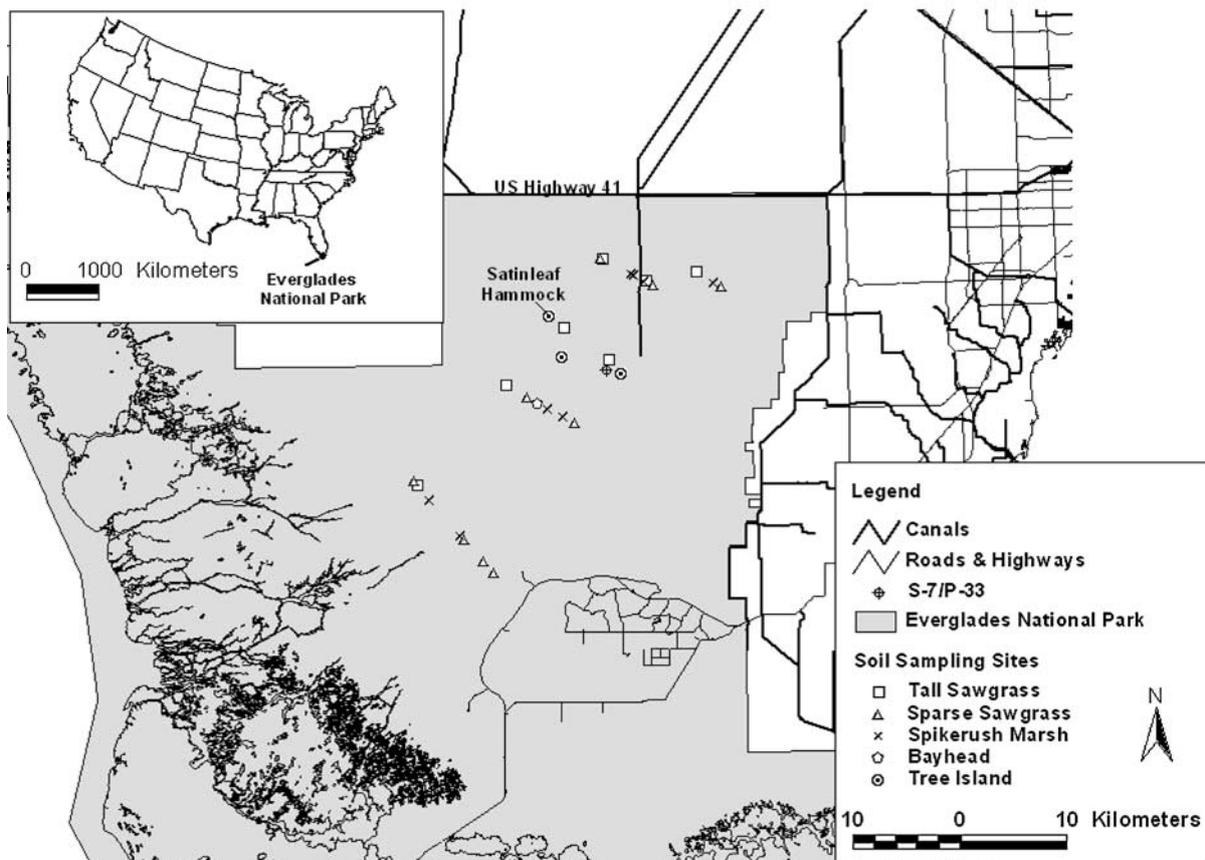


Figure 1. Distribution of sampling sites and environmental monitoring stations in Shark Slough, ENP. Inset shows position of the Everglades in the continental U.S.

been examined during 1998–1999 (Ross et al., 2003). Tree island sampling took place at 10 locations. One was in an isolated Bayhead forest, while the remaining nine locations were in Hardwood Hammock, Bayhead, and Bayhead Swamp zones within three complex Shark Slough tree islands.

Ross et al. (2003, 2004) derived broad quantitative links between hydrology and vegetation of the six cover types from estimated mean annual water depth, maximum annual 30-day water depth, and annual hydroperiod (days of surface flooding), based on concurrent measurements of water level and/or detailed topographic surveys in conjunction with nearby long term stage records. More detailed spatial and temporal trends in hydrology were explored in Satinleaf Hammock, a complex, teardrop-shaped tree island in Shark Slough (Fig. 1). Wells were installed in the Hardwood Hammock, Bayhead, and Bayhead Swamp portions of the island in January 2002. Each well consisted of a 2-in. diameter, screened PVC pipe, driven to the bedrock and capped at the base. Soil cores 7.6 cm in diameter were used as pilot holes for the wells, and sand was poured around the walls to prevent muck intrusion into the well. A water depth sensor (piezoresistor) was set 20 cm from the base of each well, and a cable was extended from the sensor to a circuit box installed about 1.5 m above the surface. Prior to installation, each sensor was calibrated to 0.5–1.0 cm accuracy in the lab. Sensor elevation was determined by topographic surveying from a benchmark of known elevation. Data were recorded in intervals of 30 min by a HOBO H8 datalogger (Onset Computer Corporation, Bourne MA, USA). Evapotranspiration and rainfall data from nearby USGS station S-7 and co-located ENP station P-33 (Fig. 1) were used to evaluate the monthly patterns of recharge during 1996–1999 (USGS, 2000; ENP, 2005).

Nutrient sampling protocols

Marsh sites

At each of the marsh nutrient sampling sites, a post-hole digger was used to extract a ~10 cm diameter soil core in sections down to bedrock,

usually from two or three nearby points. A single core was selected for profile description and subsampled in the field. One or more samples from each pedon were bagged separately, transported to the lab and refrigerated until analysis. At that time, a portion from each bag was transferred to a 100 cm³ plastic sample cup and analyzed for dry weight (80 °C), bulk density (Blake & Hartge, 1986), organic matter and carbonate content by loss on ignition (Dean, 1974), total C and N by Carla-Erba, and P by dry ashing followed by Solorzano & Sharp's (1980) method. Another subsample was diluted with distilled, deionized water to a nominal 1:1 dilution and homogenized in a blender for 90 s for determination of pH (McLean, 1982).

Interstitial (pore) water was collected via a "sipper" inserted into the soil to a depth of 10 cm at each sampling location. Sippers consisted of a filter (pore size 60 μm, Porex 6810, Interstate Specialty Products) fitted with Tygon tubing. 110 ml of soil solution was withdrawn by syringe, from which 30 ml filtered (Whatman GF/F, pore size 0.45 μm) and 80 ml unfiltered samples were collected. Samples were stored on ice until reaching the laboratory. Soil pore water samples were analyzed immediately (<24 h) or stored frozen until analysis (<30 d).

The unfiltered samples were analyzed for pH using an Ag/AgCl reference electrode (McLean, 1982), for electrical conductivity (EC) using a multi-range conductivity meter (Rhoades, 1996) and for total organic carbon (TOC: Shimadzu 500 TOC Analyzer; EPA 415.1), total nitrogen (TN: ANTEK Instruments model 7000), and total phosphorus (TP: ALPKEM Instruments model 305 & 501; Solorzano & Sharp, 1980; EPA 365.1). Filtered pore water samples were analyzed for dissolved organic carbon (DOC), NO₂-N (EPA 353.2), NO₃-N (EPA 353.2), NH₄-N (EPA 350.1), and soluble reactive phosphorus (SRP, EPA 365.1).

Within a ~30 m radius from each site, 10 culms of sawgrass and spikerush were randomly selected if present, and mature green leaves were collected. Samples were bulked by species and transported on ice to the laboratory, where they were dried at 80 °C for 72 h before grinding for analysis of total C, N, and P.

Tree islands

Soil sampling in the tree islands was done by soil auger, and was restricted to the upper 30 cm of the profiles, which frequently exceeded 1 m in depth. In the Bayhead Swamp and Bayhead sites, pore water samples were drawn with sippers, as in the marsh, but in the three Hardwood Hammock locations it was necessary to use a vacuum-equipped soil lysimeter (Soil Moisture Equipment Corp.) to extract samples. The lysimeters drew water from slightly deeper in the soil profile than the marsh sippers, i.e., ca. 20 cm depth, because hammock surface soils were relatively dry at the time of collection in late January 2001. As in the marsh, leaf collections in the tree islands involved two species. *E. cellulosa* was uncommon in our tree islands, but we were able to collect *C. jamaicensis* leaves from several of the tree island sites. We supplemented these samples with leaf collections from *C. icaco*, a species which was present in all sampled forest types. Soil, pore water, and leaf sample treatment and analytical protocols were identical to those used in the marsh, except that pore water TP and TN were not analyzed.

Hydrologic modeling

To illustrate how convergent flow and evapotranspiration can cause enrichment of a nutrient, simple steady-state single layer two-dimensional water balance and nutrient balance models were developed and implemented in MATLAB, using an integrated finite-difference scheme. The models broadly mimic processes occurring in the Everglades soil layer, but do not attempt to include surface-water and aquifer interactions. The steady state assumption was invoked as a computational simplification for this conceptual level modeling. A more detailed transient model is under development for the Ridge and Slough landscape (Stothoff & Mitchell-Bruker, 2003).

The governing equation for vertically averaged steady flow in a porous medium is

$$\nabla q = P - E \quad (1)$$

where vertically integrated flux q is, using Darcy's Law,

$$\nabla q = -bK\nabla h = -T\nabla h \quad (2)$$

The equation for steady transport of a nutrient with a source and concentration-dependent loss is

$$rq\nabla[rqc - (rbD\nabla c - (rD\nabla c))] = C_0 - \lambda c \quad (3)$$

In the above equations, h = hydraulic head (m), K = hydraulic conductivity (m/s), T = transmissivity (m^2/d), b = layer thickness (m), P = precipitation rate (m/d), E = evapotranspiration rate (m/d), c = porewater nutrient concentration (ug/cm^3), r = retardation factor accounting for biochemical nutrient cycling (unitless), D = dispersion coefficient (m^2/d), and C_0 = external nutrient source rate ($\text{mg}/\text{d}/\text{m}^2$).

To explore the interplay between the regional flow system, evapotranspiration, and nutrient concentrations in tree islands and ridges, a hexagonal array of 66 circular evapotranspiration zones are imposed on a square domain, with evapotranspiration decreasing radially from a peak value at the center of the zone to zero at and outside the boundary. Precipitation is assumed uniform everywhere, with a value selected such that net recharge over the domain is zero. The domain sides have lengths of 10 km, with a distance from each evapotranspiration zone to the center of its hexagon of 1 km. Each evapotranspiration zone has a radius of 100 m. The side boundaries of the domain are impermeable, the upstream and downstream boundaries have imposed heads and zero concentrations, and the nutrient is supplied at a uniform rate across the domain. The upstream and downstream head values impose a regional gradient of 0.03 m/km. Given the absence of relevant field data for many of the parameters in Table 1, the parameter set was chosen to illustrate the concept of evapotranspiration-induced nutrient concentration in a regional flow field, rather than to produce an exact simulation of the Everglades Ridge and Slough.

Statistical analysis

A nested three-way ANOVA (with the random variable Site nested within Type) was used to examine the fixed effects of Type and Species (*C. jamaicensis* and *E. cellulosa* only) on leaf N:P ratios. The analysis was based on the marsh data set, where the two species usually co-occurred.

Table 1. Parameters used for the example numerical simulation of flow and nutrient transport

Parameter	Value	Description
T	1000	Soil transmissivity (m^2/d)
E_0	0.003	Evapotranspiration rate at center of evapotranspiration zone (m/d)
R	0.033	Retardation factor accounting for biochemical nutrient cycling
C_0	10^{-4}	External deposition rate for nutrient ($\text{mg}/\text{d}/\text{m}^2$)
D	10^{-3}	Dispersion coefficient (m^2/d)
B	1	Layer thickness (m)

Statistical analyses were carried out using Statistica 6.1 (Statsoft, Inc., 2004). Appropriate data transformations were applied when necessary to homogenize the variance and meet assumptions of the statistical procedures. We used one-way analysis of variance (ANOVA) to examine differences among vegetation types in soil and pore water nutrient concentrations. If an effect of Type was demonstrated, a set of linear and quadratic contrasts was constructed to further examine trends in concentration, especially with regard to the hydrology associated with each type. To do so, we represented each treatment level (vegetation type) by its mean annual water depth (Table 2), and calculated coefficients for the linear and quadratic trends. Since mean water depths for the six types were spaced at unequal intervals, the coefficients were calculated using methods described in Keppel (1973). Soil data were consolidated by depth-weighted averaging among strata within the upper 10 cm of the profile. This range represented the soil zone most likely to influence the pore water

samples, which, except in the three hardwood hammock sites, were collected from 10 cm depth. Correlation coefficients were calculated to examine the associations between soil and pore water concentrations in N and P.

Results

Vegetation and hydrology relationships

Annual means for three hydrologic parameters are listed by vegetation type in Table 2. The six types comprise a long gradient from persistently flooded marsh communities to well-drained forests, but hydrologic variation among marsh types is relatively small in comparison to the variation distinguishing forest types. On average, Spikerush and Tall Sawgrass marshes differ by only 9 cm in maximum water depth and 22 days in hydroperiod, while the Hardwood Hammocks, which almost never flood, are immediately surrounded by Bayhead and Bayhead Swamp forests that flood for 5–9 months per year. Nevertheless, the subtle differences in hydrology among marsh types in Table 2 are locally consistent throughout the southern Everglades landscape (Ross et al., 2003).

Soils

Soil profiles at the marsh sampling locations are illustrated in Figure 2. The profile diagrams aggregate Shark Slough soil pedons into a few very broad compositional categories, i.e., peats, marls, and peaty marl mixtures. Soils varied broadly in depth (range, 10–180 cm) and horizonation, sometimes over very short distances. For the most

Table 2. Annual means of three hydrologic parameters in six vegetation types during the period May 1990 to April 2000, based on 314 marsh and 10 tree island sampling locations in northern and central Shark Slough

Vegetation type	N of sites	Mean water depth (cm)	30-day maximum water depth (cm)	Hydroperiod (days)
Spikerush marsh	78	41.2	64.0	344.1
Sparse sawgrass	182	36.9	57.8	339.3
Tall sawgrass	54	32.2	52.4	322.6
Bayhead swamp	3	13.0	33.8	262.7
Bayhead	4	−4.2	16.6	156.9
Hardwood hammock	3	−69.3	−48.4	0.2

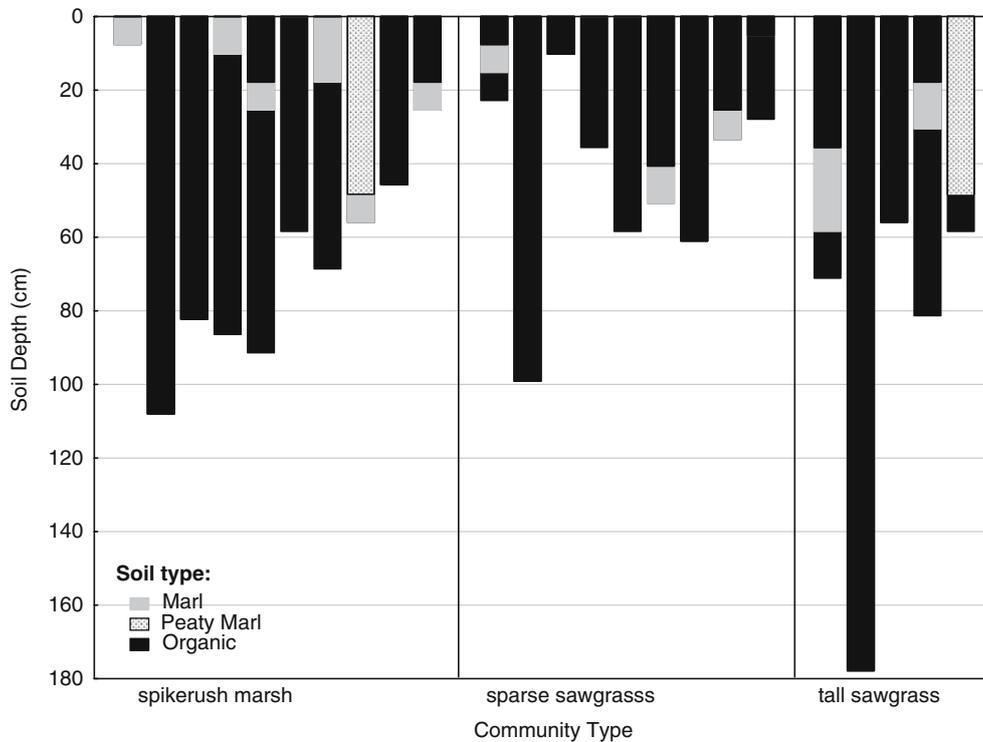


Figure 2. Soil profiles within three marsh vegetation types in Shark Slough.

part, they were peat-dominated, but interbedding of marls and other carbonate-rich layers was common. Large scale spatial patterning was not evident, in part because the sampling network did not extend into the shorter hydroperiod prairies on the flanks of the Slough, where marl-dominated soils would likely have become more prominent (Leighty & Henderson, 1958). The peat we observed throughout the study area was nearly black, non-fibrous, with a mixture of dead and live roots in the top 10–15 cm, and many fine dead roots in the sub-surface horizons. At all depths, most of the roots appeared to be sawgrass-derived. We found no evidence of the light-colored, fibrous, water lily-derived Loxahatchee peat described by several researchers (Davis, 1946; Jones et al., 1948; Leighty & Henderson, 1958). In general, we found that stratigraphy in the marsh soils was unrelated to the current vegetation, presumably because Everglades soils are the cumulative product of a long and variable environmental history, while current plant cover results from relatively recent conditions.

Characteristics of Shark Slough marsh and tree island surface soils are summarized in Table 3. Soils in both environments were highly organic, with correspondingly low bulk density, and did not differ in nitrogen or carbonate content. Some soil parameters differed between marsh and tree island, however. Marsh soils were circumneutral and low in total P, while tree islands were slightly acidic and extremely high in P. Among the 3 tree island forest types, Hardwood Hammock soils tend to be highest in pH, carbonate content, and P content, and lowest in organic matter (Ross et al., 2004).

Vegetation-associated variation in soil nutrients is presented in more detail in Figure 3 and Table 4. Total N was unaffected by vegetation type, though a nominal decrease from the most hydric type (Spikerush marsh) to the most mesic (Hardwood Hammock) was evident. Total P exhibited an opposite trend, increasing by several orders of magnitude across the same gradient (Fig. 3a). Both linear and quadratic contrasts were highly significant (Table 4), verifying the visual

Table 3. Means for several chemical and physical characteristics of surface soils (top 10 cm) in Shark Slough marshes and tree islands ($n=28$ and 10, respectively), with p -values for null hypothesis that the two groups were drawn from the same population

Soil characteristics	Marsh	Tree Island	p -Value
pH	7.16	6.64	0.010
Bulk density (g cc^{-1})	0.20	0.26	0.272
Organic matter (%)	66.00	66.4	0.965
Carbonate (%)	13.66	8.76	0.123
TN (%)	2.81	2.37	0.265
TP (%)	0.011	2.68	0.006

evidence of an accelerating increase in P at the mesic end of the hydrologic gradient. When phosphorus data from the Hardwood Hammock sites were excluded from the analysis, the linear contrast remained significant, but the quadratic contrast did not (Table 4). In fact, when all tree island data were excluded, differences among the

three marsh vegetation types were not observed for either nutrient.

In view of the opposing trends for N and P in Figure 3a, it is clear that soil N:P ratios (molar ratios: mean = 176, range = 0.4–398) decrease as vegetation progresses from hydric to mesic sites in Shark Slough. Since these ratios are based on total soil nutrient content, they may not provide as accurate a gauge of nutrient limitation as ratios that are based on available forms of nutrients in the soil solution. The latter relationships are described next.

Pore water nutrient concentrations

Total N in Everglades marsh pore water was dominated by inorganic forms (mean \pm s.d.: $70.1 \pm 21.7\%$), while inorganic P (SRP) comprised a small percentage of total P ($6.5 \pm 4.4\%$). Corresponding percentages for tree islands could not be calculated because total nutrient content was not analyzed in samples from those communities.

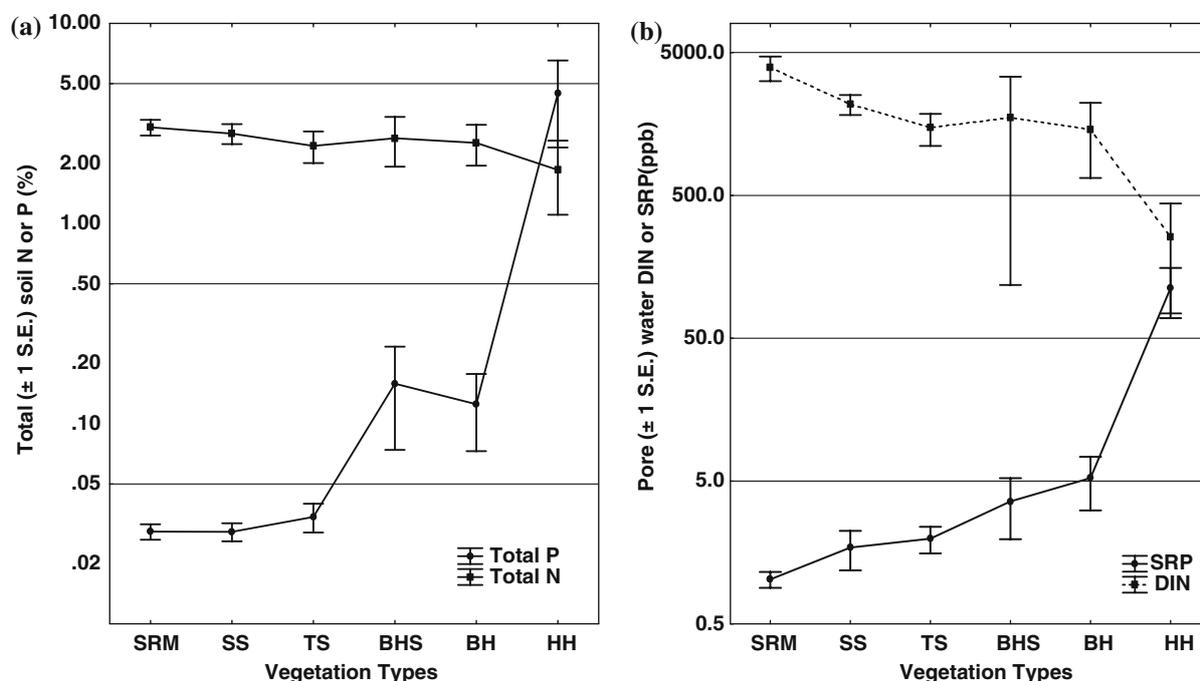


Figure 3. Soil and pore water nutrient concentrations in six Shark Slough vegetation types. (a) Total N and P content in soils; (b) DIN and soluble reactive phosphorus in pore water. Vegetation types are arranged from most persistently flooded at left to least flood-prone at right. SRM, Spikerush marsh; SS, Sparse Sawgrass marsh; TS, Tall Sawgrass marsh; BHS, Bayhead Swamp forest; B, Bayhead forest; HH, Hardwood Hammock.

Table 4. *p*-Values from statistical tests of effects of vegetation type on soil and pore water N and P fractions in four data sets. Data sets are: 1, all six vegetation types; 2, all types except Hardwood Hammock; 3, marsh types only; 4, forested types only

N & P fraction	Data set	Phosphorus			Nitrogen		
		1-way ANOVA	Linear contrast	Quadratic contrast	1-way ANOVA	Linear contrast	Quadratic contrast
Total N & P in soil	1	<0.001	<0.001	0.001	n.s.	–	–
	2	<0.001	<0.001	n.s.	n.s.	–	–
	3	n.s.	–	–	n.s.	–	–
	4	0.039	0.016	n.s.	n.s.	–	–
DIN & SRP in pore water	1	<0.001	<0.001	<0.001	0.023	0.034	n.s.
	2	0.008	<0.001	n.s.	0.052	n.s.	n.s.
	3	n.s.	–	–	0.020	0.012	n.s.
	4	0.018	0.007	n.s.	n.s.	–	–

Contrasts (described in text) were only run on effects determined to be significant in ANOVA. n.s., $p > 0.10$.

Ammonium-N accounted for most inorganic N in marsh communities (96.0 ± 8.0), but accounted for a lower, more variable proportion in forested wetlands (71.7 ± 23.1).

Figure 3b illustrates the variation in pore water concentrations of dissolved inorganic nitrogen (DIN) and SRP within and among the six Shark Slough vegetation types. Inorganic forms of both nutrients ranged over 2–3 orders of magnitude (DIN, $46\text{--}7406 \mu\text{g l}^{-1}$; SRP, $0.12\text{--}171 \mu\text{g l}^{-1}$), and strong differences among vegetation types were in evidence (Table 4). Linear contrasts were significant for both nutrients, but a significant quadratic trend was only observed for SRP. A monotonic decrease in DIN from the most frequently inundated vegetation type (Spikerush marsh) to the type least affected by flood (Hardwood Hammock) was evident in Figure 3b, and this decrease remained statistically significant when only the marsh portion was considered (Table 4). The trend for SRP mirrored that for DIN; the concentration increased steadily through the bayhead type, then rose abruptly in the hardwood hammock, rendering the quadratic term significant (Fig. 3b). In this case, differences among tree island types were significant, while marsh types were not statistically distinguishable (Table 4). We found statistically significant positive associations between log-transformed concentrations of N and P in pore water and their respective contents in surface soil. The soil:pore water association was considerably stronger for P ($r = +0.81$, $p < 0.001$) than for N ($r = +0.46$, $p = 0.005$).

Leaf nutrients

The N:P ratios of live leaves of *E. cellulosa*, *C. jamaicense*, and *C. icaco* are presented by vegetation type in Figure 4. In *C. jamaicense* and *C. icaco*, the range in N:P was broad, with the lowest N:P ratios found in the least hydric plant communities. *E. cellulosa*, which was only present in frequently flooded marsh vegetation, maintained a relatively constant N:P ratio both within and among types. All ratios except those of *C. icaco* in the hardwood hammock and bayhead types exceeded 36:1, and therefore are indicative of phosphorus limitation (Koerselman & Meuleman, 1996; Bedford et al., 1999). Table 5 clearly indicates that marsh N:P ratios of *E. cellulosa* and *C. jamaicense* are influenced by both vegetation type and species. The significant Species effect is a reflection of the lower N:P ratios maintained by *E. cellulosa* than *C. jamaicense* in all three marsh types (Fig. 4). Differences in N:P among vegetation types were primarily a function of variation in nitrogen, as phosphorus concentrations did not vary significantly among types (Table 5).

Ridge and Slough hydrology

Spatial and temporal patterns in climate and hydrology are strongly interrelated, with fairly consistent annual trends in precipitation, evapotranspiration, and water level from year to year. Figure 5 shows the average monthly evapotranspiration and precipitation in Shark Slough

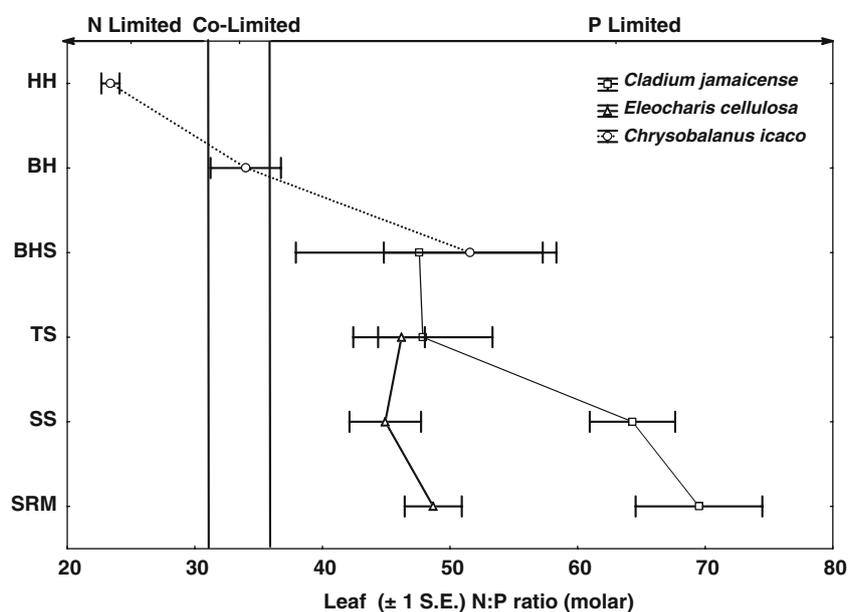


Figure 4. Molar N:P ratios of leaves of three common plant species in six Shark Slough vegetation types. Bottom to top, vegetation types are arranged from most persistently flooded to least often flooded. Vegetation acronyms are as in Figure 3.

(German, 2000). ET is minimum during the months of December and January and steadily rises to its highest level during the month of July, while precipitation is greatest in June with a minor peak in August–September. Thus, evapotranspiration dominates precipitation in the dry season from November to April, while precipitation dominates evapotranspiration in the rainy season from May to October.

Water levels at Satinleaf Hammock in 2002–2003 responded to the difference between evapotranspiration and precipitation, with seasonal lows in April, rising to a peak at the end of October, and gradually declining until the May rainy season started again (Fig. 6). The increase in water level from April to October was about 70–100 cm in each forest community. In all three forests, a diurnal drawdown cycle due to evapotranspiration was superimposed on the slower seasonal rise and fall of the water table. The diurnal cycle can be observed in detail in Figure 7, which shows water levels in two forests at Satinleaf Hammock during April 2003. A regular daily fluctuation is evident throughout April in the Hardwood Hammock, but becomes obscured in the Bayhead forest during the transition to the wet season in the last few days of the month, when repeated rainfall events begin to

saturate the soil column. ENP records show no diurnal fluctuation at a nearby long-term water level recorder in the flooded marsh. Figure 8 illustrates how the diurnal pattern develops and recedes seasonally in the Bayhead forest at Satinleaf. The hourly water level, averaged over the month, is shown for several dry season months. A diurnal signal is clearly demonstrated, featuring a rapid drop in water level starting several hours after sunup and culminating several hours after noon, followed by a recovery that slows as water levels near their starting point. The pattern appears relatively late in the dry season in the Bayhead forest and dissipates soon thereafter (Fig. 8), while a diurnal cycle is evident early in the dry season in the Hardwood Hammock and persists longer (data not shown).

The diurnal pattern described above suggests that tree island pore waters have a strong hydraulic connection with the surrounding marsh, but with a lag in recovery caused by resistance to flow in the soil. Typically transpiration starts at sunrise and peaks at solar noon, but the water level response in Figure 8 exhibits a phase lag of several hours, with lowest levels reached in mid-afternoon. Replenishment occurs due to lateral flow from inundated areas and vertical flow from the

Table 5. ANOVA table for effects of type and species on leaf nutrient concentrations in Shark Slough marsh communities

Source	Df	<i>p</i> Values		
		N	P	N:P
Plot (type)	30	0.364	0.068	0.121
Type	2	0.016	0.931	0.008
Species	1	0.017	< 0.001	< 0.001
Type*species	2	0.458	0.591	0.157
Error	20	–	–	–

underlying aquifer, but there is not sufficient data to quantify the relative contribution of each of these sources.

In areas where the soil is inundated, the surface water and aquifer are well connected and the horizontal gradients in the surface water, soil, and aquifer are essentially identical, with a regional gradient of about 0.03 m/km. Where soil is exposed, as in the tree islands and more briefly in the sawgrass ridges, larger water table gradients may be superimposed on the regional gradient in response to ET-induced drawdown of the water table. Other than in the hammocks, soil is only exposed during the dry season and early rainy season, when evapotranspiration dominates

recharge, so that the superimposed water table gradients are, on average, directed towards the centers of evapotranspiration. These local gradients may be several times steeper than the regional gradient; for example, diurnal variation in the Bayhead forest may produce a drawdown on the order of 1 cm relative to the marsh, which is approximately 100 m away. As a result of occasional soil exposure, then, the annual average soil water gradient may be significantly deflected from the regional gradient, even though gradients in the surface water and the underlying aquifer are not, with the soil water deflection becoming more pronounced as the period of exposure increases.

A simple analytic expression of a circular island describes ground water flow between marsh and tree island. Under steady state conditions, the difference between the ground water level in a circular island and the surface water level in the marsh, Δh , can be written as (Haitjema, 1995):

$$\Delta h = \frac{RL^2}{16T} \quad (4)$$

where, R = the recharge rate (m/d), L = distance from the center of the tree island to the nearest surface water in the marsh (m), and T = soil transmissivity (m^2/d).

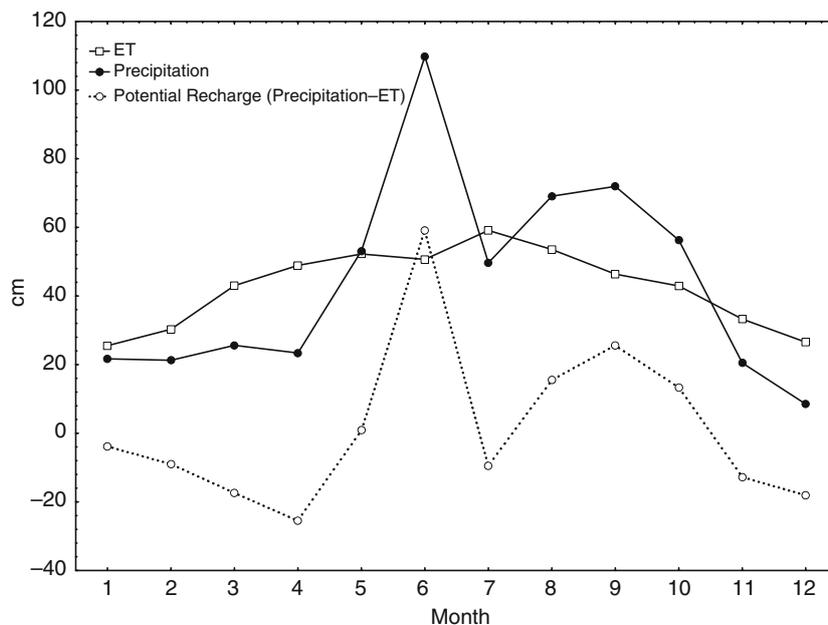


Figure 5. Mean monthly precipitation (P), evapotranspiration (ET), and potential recharge (R) in Shark Slough, ENP. ET data are from German (2000), and precipitation data are from USGS (2000).

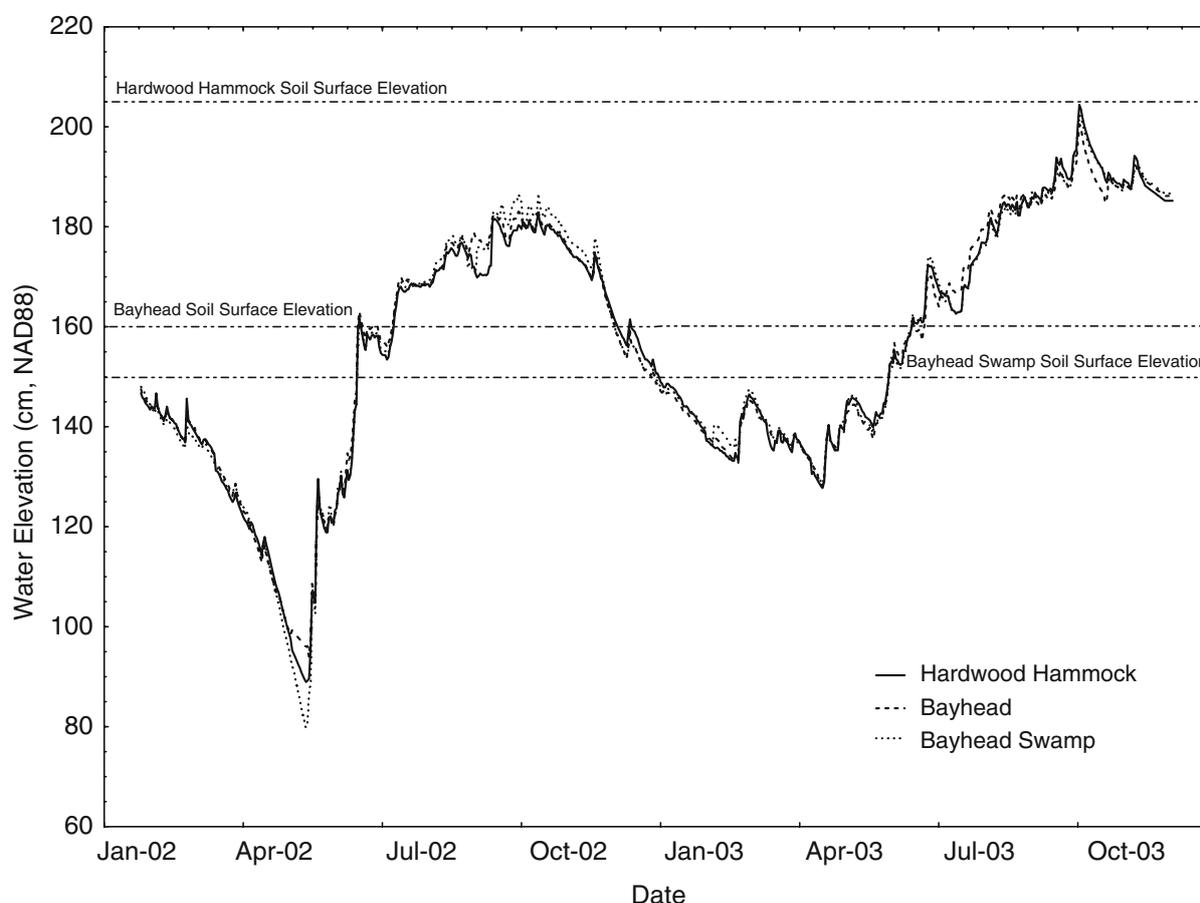


Figure 6. Hydrographs from three forest zones in Satinleaf Hammock, ENP, during 2002 and 2003.

Because the flow system cycles constantly between drawdown and recovery, steady state is never reached and Equation (4) can only be used to explore the general tendencies of the system. It is also important to note that Equation (4) is only valid when the water table is below the ground surface. From measured elevations and long-term water level records in and around Satinleaf Hammock, we know that in most years water is below the ground surface throughout the year in the Hardwood Hammock, during Dec-May in the Bayhead forest, and only during the month of April in the adjacent Tall Sawgrass marsh (Ross et al., 2004). The magnitude and direction of groundwater flow depends on the water level gradient, $\Delta h/L$, and the transmissivity of the tree island soils. When recharge rates are negative, as they are during the dry season months of

November to April, Equation (4) predicts water will flow from the marsh towards the tree island. As the wet season emerges in May and June, rainfall exceeds evapotranspiration and brings the water levels in the tree island above those in the marsh, causing water to flow from the tree island toward the marsh until water ponds on the Bayhead surface.

Equation (4) indicates that the magnitude of convergent flow decreases as the landform narrows. L , the distance between the center of the island and surface water on the adjacent marsh, influences the drawdown and thus the strength of convergent flow. In the classic tear-drop pattern of the tree islands, L is largest at the upstream end where the Hardwood Hammocks typically occur, decreases through the Bayhead and Bayhead Swamp forest zones, and is smallest in the

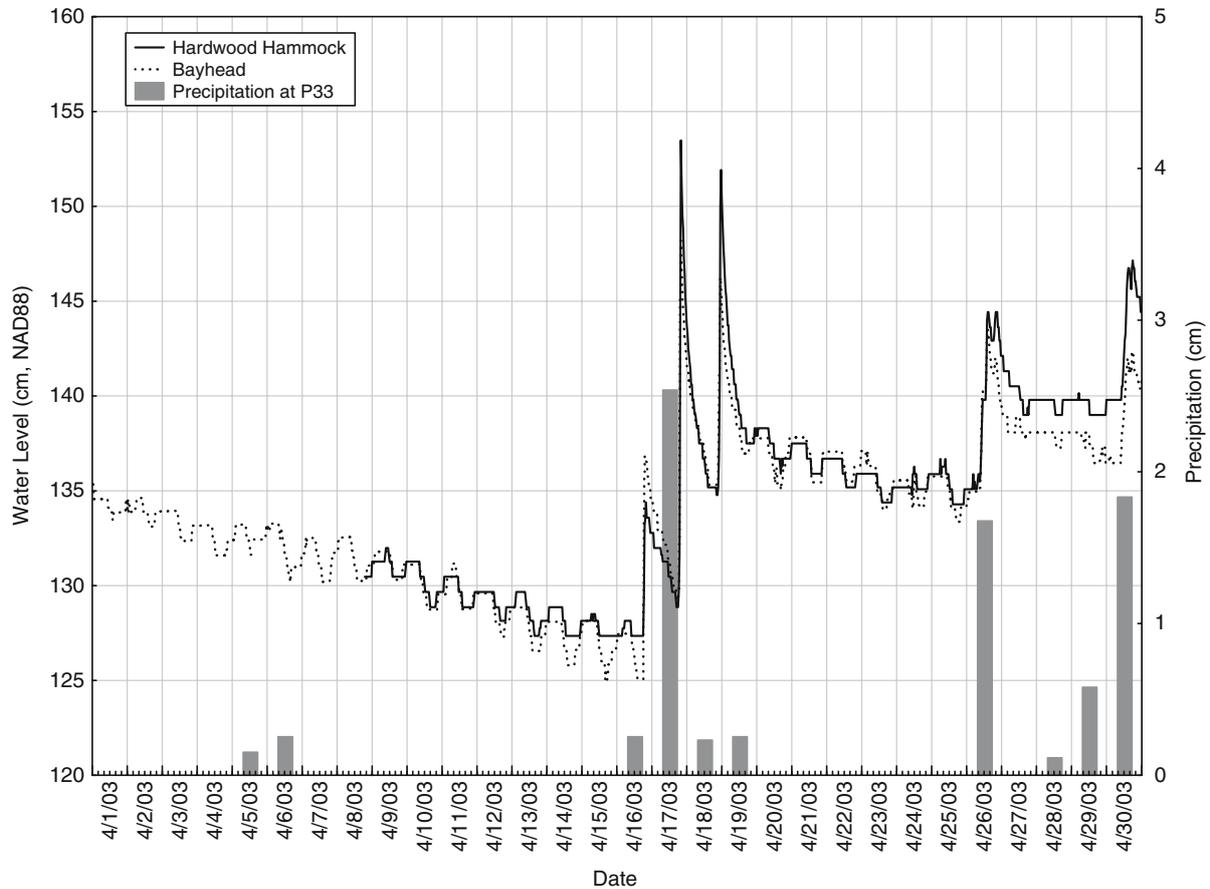


Figure 7. Hydrographs from Hardwood Hammock and Bayhead forests in Satinleaf Hammock, illustrating diurnal drop and recovery cycle during April 2003. Precipitation data at P-33 (see Fig. 1 for locations) is from USGS (2000).

elongated sawgrass tail. Isolated Tall Sawgrass ridges are usually narrower than any of the forest types, and therefore induce the least convergent flow. Moreover, assuming precipitation minus evapotranspiration as the recharge rate in Equation (4), convergent flow would also be enhanced if ET is higher in the tree islands than the surrounding marsh. Enhanced evapotranspiration in swamp forests is consistent with findings by Pauliukonis & Schneider (2001), whose lysimeter measurements showed that ET from three different wetland species were all larger than ET from open water (e.g., average evapotranspiration from a single small willow tree was seven times larger than from open water). Likewise, reduction of effective precipitation due to rainfall interception by forest canopies (e.g., Schellekens et al., 1999) would tend to increase convergent flow.

Nutrient transport

The deflection of water toward exposed wetland surfaces also results in a deflection in constituents of the water column, including nutrients. These effects are demonstrated using simple numerical models for steady-state flow and transport within the soil layer (Fig. 9). Enhanced evapotranspiration zone locations produce local peaks in the steady-state nutrient concentrations. Focusing of flow and nutrients occurs at the evapotranspiration zone, but the focused flow is not strong enough to completely overcome the regional gradient and allows the nutrient to spread downstream, creating an elongated concentration plume in the direction of flow. In the simulation, downstream evapotranspiration zones are relatively enriched because upstream zones enhance nutrient

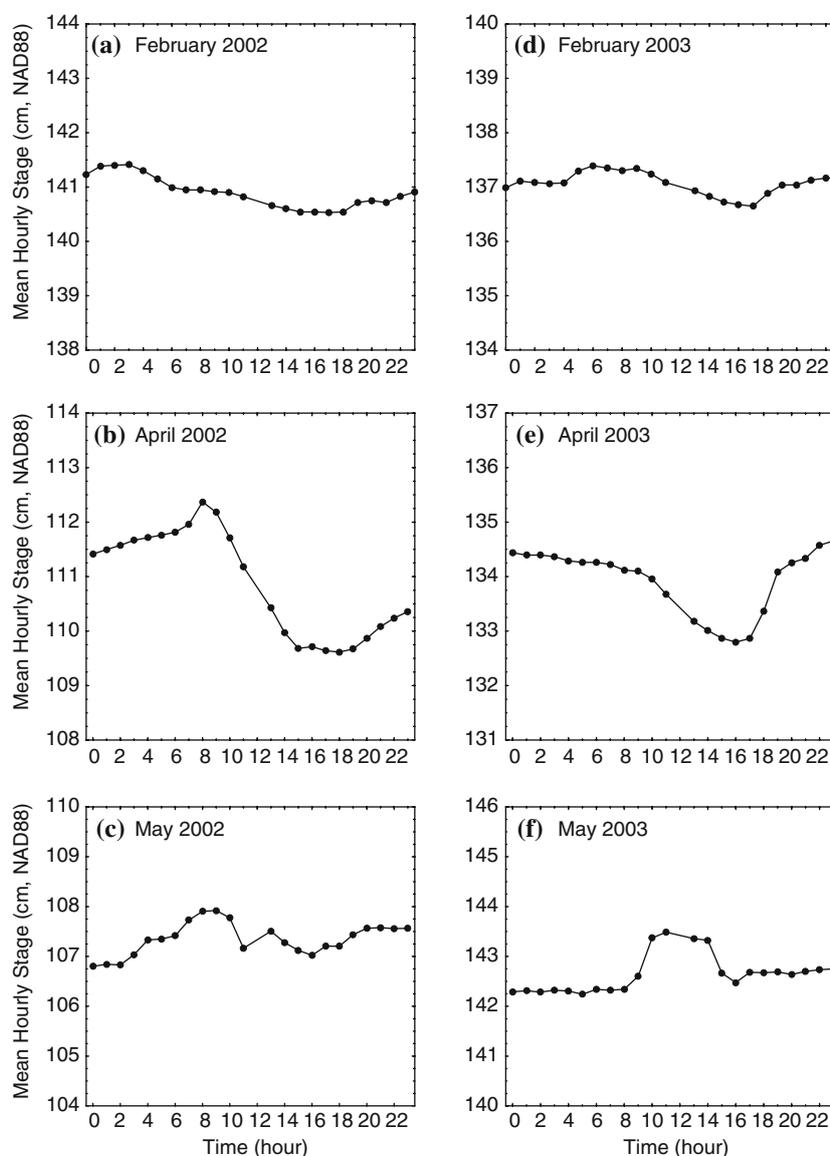


Figure 8. Development of the diurnal drop and recovery cycle in the Bayhead forest in Satinleaf Hammock in 2002 and 2003. Data are diurnal patterns consisting of hourly means averaged across all days of 3 months: early dry season (A and D), mid dry season (B and E), and late dry season (C and F).

concentration in the incoming water, which is subsequently transported downgradient. Other simulations, not shown, were performed to examine the behavior of the model with increasing regional flow. The effect of convergent local flow on nutrient concentration weakens, resulting in narrower tails and a more homogeneous concentration field.

Discussion

In the freshwater wetlands at the center of the Everglades, a subtle topographic mosaic forms the basis for a complex, highly organized vegetation pattern. In localized portions of this Ridge and Slough landscape, Spikerush and Sparse Sawgrass marshes usually occupy the lowest surfaces, Tall

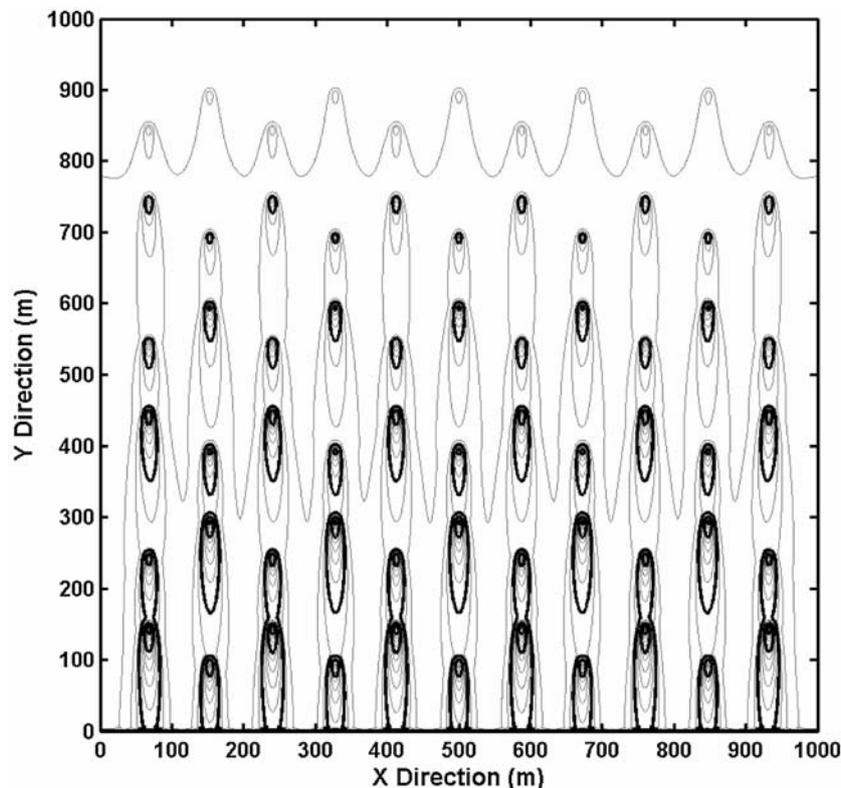


Figure 9. Steady-state concentration of pore-water phosphorus using the example parameters. Concentration range is 0–34 mg/m³, with light contours every 2 mg/m³ and dark contours every 10 mg/m³. Ratio of slough concentration to peak evapotranspiration-zone concentration is about 5.5 for downstream zones.

Sawgrass strands persist on slightly raised surfaces oriented in the direction of surface water flow, and elongated forests parallel the strands at the highest elevations. Against this topographic backdrop, seasonal fluctuations in water level create continuous spatial variation in hydrology and growth conditions, such that the marsh communities that are flooded longest and deepest are lowest in stature and support the most open canopies, while the strands and wooded communities that are less affected by flooding support denser and taller canopies (Table 2). Soil and pore water samples also reveal a nutrient gradient that coincides with these vegetation patterns. Our analyses demonstrate a mechanism by which wetland vegetation patterning in this environment is controlled by topography, hydrology and nutrient availability. The mechanism involves evapotranspiration-induced convergent flow towards dry or seasonally dry areas. This convergent flow concentrates the

limiting nutrient P, leading to increased production, a transition from P to N limitation, and a concurrent transition in species composition.

Distribution of nutrients in Ridge and Slough ecosystems

Soils

The response of soil nutrients along the vegetation/hydrology gradient we studied was scale-dependent. When we considered herbaceous wetlands separately, no significant differences in soil N or P among marsh assemblages were observed. These results are consistent with Childers et al. (2003), who also found no differences among major marsh vegetation units in the southern Everglades. However, when we extended our analysis to the entire marsh-forest gradient, we observed a very steep increase in total soil P from marsh to forest, and within forested communities, from the most flood-

prone to the least likely to be flooded. Concentrations of soil P in forest exceeded those in adjacent marsh communities by an order of magnitude or more, and P concentrations in well-drained Hardwood Hammock soils were far higher than in marshes that had received phosphate-rich water for decades (Koch & Reddy, 1992). Orem et al. (2002) also identified a gradient in soil phosphorus in two tree islands in nearby WCA-3B, with highest concentrations in the elevated head positions, intermediate concentrations in the tails, and lowest P in the adjacent marsh. Just as afforestation of grasslands frequently results in major changes in soil chemistry (e.g., Fisher & Eastburn, 1974; Jobbágy & Jackson, 2004), the centuries-long transition from marsh to swamp forest in the tails of the large Shark Slough tree islands over the course of Everglades development (Stone et al., 2005) may have left its imprint in the current patterning of soil nutrients in these environments.

Pore water

Patterns in N and P concentrations in Ridge and Slough pore waters paralleled those observed in soils, especially for P content. The strength of statistical association between total soil N and P content and the concentrations of immediately plant-available forms of these nutrients in the soil solution reflect the equilibrium between pore water and readily exchangeable forms on soil exchange sites, insoluble molecules held within the soil matrix, organically bound N and P, and ions in the overlying water column (Richardson & Vaithiyathan, 1995; McGlathery et al., 2001; Newman & Pietro, 2001). For phosphorus, the relatively strong correlation between soil and pore water ($r = +0.81$) is consistent with an active exchange between these two components. The weaker correlation between soil and pore water N ($r = +0.46$) reflects different distributional patterns: an indeterminate pattern for soil N, and a pronounced decrease in solution DIN from hydric to mesic sites. These patterns suggest that controls on the soil-porewater equilibria for the two nutrients differ, perhaps as a result of biotically mediated interactions, e.g., uptake, mineralization, N-fixation or denitrification.

With available forms of phosphorus present in limiting quantities in most Everglades environments, rapid biotic uptake prevents soluble

inorganic forms of P from comprising more than a small proportion of the total P present in the ecosystem at any one time (Gaiser et al., 2004). Productivity is therefore regulated by the rate of regeneration of the available P pool from the exchangeable, insoluble, and organic pools in the soils. Unlike acidic wetlands in which flooding increases P-availability (Patrick & Khalid, 1974), flooding appears to reduce the availability of phosphorus in the base-rich Everglades soils. Through its influence on biological demand, the availability of the limiting nutrient, P, may also regulate the accumulation of non-limiting nutrients in the soil solution. For instance, where available phosphorus is present in the lowest concentrations, i.e., in Spikerush marsh, the capacity of resident plants to utilize non-limiting nutrients may be reduced, causing mineralization of N to exceed uptake, and inducing accumulation of ammonium in the pore water. In contrast, where P is readily available, as in the tree islands, mineralized N may be taken up more rapidly by plants, causing its concentrations in the soil solution to decline. The interdependence of N and P availability in ecosystems has been established in numerous studies (e.g., Pastor et al., 1984; Troelstra et al., 1990; van Oorschott et al., 1997), and a few have demonstrated the accumulation of one nutrient under conditions of strong limitation of the second (Caffrey & Kemp, 1990; Short et al., 1993; McGlathery et al., 2001).

Vegetation

The general decrease in leaf N:P ratios from Spikerush marsh through Hardwood Hammock provides a strong indication of diminishing phosphorus limitation of growth with decreasing flooding frequency and depth in Everglades Ridge and Slough plant communities. Recent literature has shown leaf N:P to be a good indicator of nutrient limitation in wetland plants, with molar ratios >36 signifying P limitation, ratios <31 indicating N limitation, and ratios of 31–36 indicative of co-limitation by P and N (Koerselman & Meuleman, 1996; Bedford et al., 1999). It is important to note that the guidelines described above were developed exclusively for marsh vegetation, from total aboveground harvests of all macrophyte species in a wide range of European and North American wetlands. These community-

level relationships incorporate both intra- and inter-specific variation in N:P ratio, since co-occurring species often vary widely in leaf nutrient chemistry (e.g., Daoust & Childers, 1999). Conclusions from our study are based only on intra-specific variation, within three broadly distributed species that dominated at different locations along a long ecological gradient that included both herbaceous and forested communities. Two of the three species exhibited the positive correlation between flooding and leaf N:P described above, while *Eleocharis cellulosa*, the dominant species in the most P-deficient sites, was insensitive to the gradient. Though community-level relationships deserve further examination at our sites, our species-level data raises the possibility that in the heart of the Everglades, tree island microsites in which nitrogen limits or co-limits growth may coexist in close proximity to much more extensive marshes whose character is defined by phosphorus limitation.

A mechanism for Ridge and Slough nutrient patterns

Paleoecologic evidence from several Shark Slough locations indicates that the long tree island tails

were vegetated by herbaceous species during the early stages of Everglades development, but have been forested for much of the last two millennia (Orem et al., 2002; Stone et al., 2005). While such local changes from graminoid to tree dominance may have resulted from shifts in the external environment, especially those affecting the hydrology of the Everglades, it is also possible that they are self-generated and therefore represent an example of long term ecosystem succession. Ross et al. (2003) presented a conceptual model of Ridge and Slough landscape development that was primarily hydrologically driven, and emphasized the balance between aggradative and degradative processes. Figure 10 incorporates nutrient availability in the earlier model, an addition suggested by the strong co-variation of hydrology and nutrient concentrations documented in this study. A positive feedback between organic soil accumulation and productivity is proposed, with peat buildup limited by increasing susceptibility to fire during periodic droughts (Beckage et al., 2003) and by more rapid decomposition rates as surface elevations draw further above the water table. Within the aggradative cycle on the left side of Figure 10, it is reasonable to expect that enhanced nutrient availability on slightly raised sites would

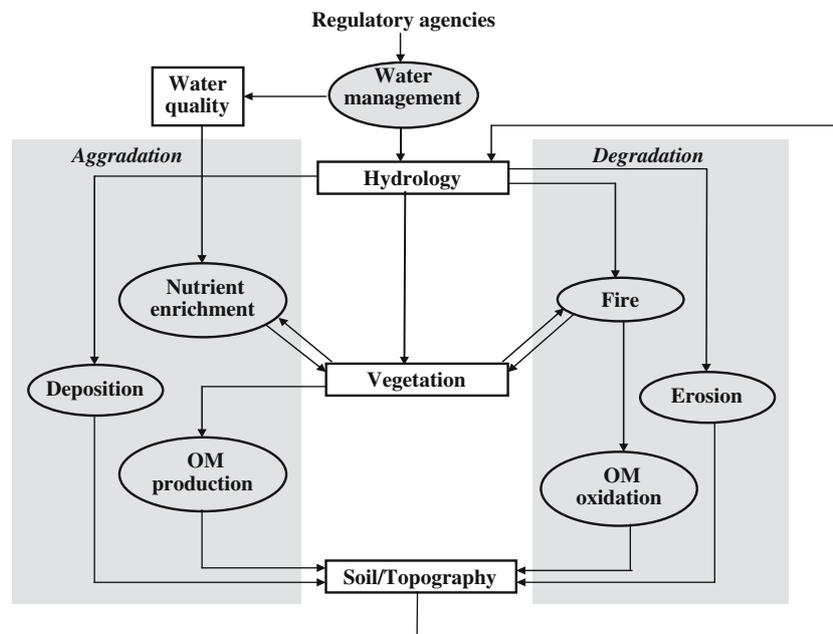


Figure 10. Conceptual model of landscape development in Ridge and Slough peatlands. State and process variables are represented by rectangles and ovals, respectively. Adapted from Ross et al. (2003).

accentuate the benefits of improved soil aeration on production and sediment accumulation. But what mechanism is responsible for the association of high levels of P with elevated locations in the Ridge and Slough?

The accumulation of high concentrations of P in the soil, pore water, and vegetation of Everglades tree islands and strands, while surrounded by a matrix of low-P substrates, requires selective deposition and/or selective retention of P. Orem et al. (2002) emphasized deposition processes, hypothesizing that the high P content of tree island soils was the result of centuries of guano deposition at the head of the island, followed by downstream transport by surface water flow to the tail. Our findings suggest another possible mechanism by which P may be raised at these sites, i.e., by subsurface transport of low-P water towards the tree islands and other raised Ridge and Slough landforms during the dry season, when recharge rates for Everglades marshes typically become negative. Toward the beginning of the dry season, water level in the Bayhead forest drops below the surface, eventually inducing flow from marsh to forest. In the absence of significant rainfall, seasonally increasing evapotranspiration in the Bayhead eventually exceeds the rate of resupply by groundwater flow, causing a lag in diurnal recovery that is evident in the late dry season. This mechanism does not require that ET is higher in the forest than the surrounding marsh, only that cumulative ET is larger than cumulative precipitation during the period the soil is exposed. However, if ET is greater in forest than marsh, as is often the case (Kelliher et al., 1993; Calder, 1998), the tendency of water to move toward the zone of low hydrologic potential beneath the forest would be accentuated. Such a transpiration-driven focusing of groundwater flow can result in significant lateral redistribution of ions in a wetland landscape. Jobbágy & Jackson (2004) demonstrated rapid accumulation of salts in soils of a eucalyptus plantation established in the Flooding Pampas of Argentina, where enhanced transpiration depressed the underlying water table by as much as 0.6 m relative to the surrounding marsh (Engel et al., in press). Our analysis also shows that the strength of converging flow and its nutrient concentrating effect increases with the width of the elevated surface, and therefore is less

for the rarely exposed, narrow sawgrass ridges than the higher and broader tree islands. These trends are paralleled by the measured P concentrations, which are much lower in the sawgrass ridge than in the tree island.

Whether drawn into the tree island in relatively dilute concentrations in groundwater, or deposited there directly by animals (e.g., Orem et al., 2002), the accumulation of soil P to concentrations more than 100 times greater than surrounding wetlands, as in our tree island sites, requires a strong retention mechanism. When hammock pore water concentrations are large relative to marsh concentrations, phosphorus is sequestered in the soil, and landforms associated with the high nutrient concentrations are stabilized for millennia. One aspect of nutrient retention, of course, is the efficiency of biological recycling processes; in forested ecosystems, this capacity is enhanced by the incorporation of nutrients into long-lived woody tissues, the relative resistance of such tissues to decomposition, and the capability of tree root systems to exploit deep soil layers. Edaphic factors also influence the retention of nutrients, especially in oligotrophic wetlands like the Everglades. Though phosphorus is a relatively immobile element (Black, 1968), the capacity of soils to retain it against leaching and export in surface waters can vary widely. In the northern Everglades, sorption studies indicate that phosphorus retention in organic soils is regulated primarily by calcium carbonate (Porter & Sanchez, 1992; Richardson & Vaithyanathan, 1995). Zhou & Li (2001) also found most soil P to be Ca-bound at high solution P concentrations in the southern Everglades, especially in marl soils. At low P concentrations phosphorus was bound by non-calcareous clay minerals, and organically bound P was never abundant. Thus, the carbonate-rich mineral soils of the hardwood hammocks would be especially retentive of P once it arrived, especially in comparison to nearby peats.

Effect of Regional Flow System

In well-preserved portions of the Ridge and Slough landscape, nearby ridge units parallel each other with great consistency, and are conspicuously elongated perpendicular to broad surface topographic contours (SCT, 2003; Ruiz & Ross,

2004). As such, the linkage between the genesis and maintenance of the landscape and flowing water is almost inescapable. The nutrient focusing mechanism discussed above is consistent with that linkage, but does not produce a Ridge and Slough-like landscape unless local convergent flow combines with a strong regional flow system. Rietkerk et al. (2004) demonstrated that spatial variation in transpiration can lead to nutrient and vegetation patterns that resemble those observed in northern bogs, where the linear features generally run perpendicular to flow direction and regional surface water flow is weak or absent. Our simulations indicate that for the Everglades, water flow is a potentially important factor in the development of nutrient and vegetation patterns. We illustrate that evaporative-induced convergent flow and concentration of nutrients can occur in Everglades tree islands and dry ridges with or without spatial variation in transpiration. Enhanced dry season soil drawdown effects can induce flow towards slightly elevated, non-ponded ridges, causing convergent flow and nutrient concentration, which in turn stimulates primary production and soil aggradation. This effect is increased if evapotranspiration in forested areas is larger than in marshes. This self-reinforcing loop is limited, in that increases in the volume of the unsaturated zone enhance conditions for soil loss due to oxidation and fire, and so the system is self-limiting.

Conclusions

The development of the Ridge and Slough landscape pattern took place over millennia but has degraded under water management practices of the last century. Our study suggests that a self-organizing process involving feedbacks between soils, hydrology, nutrients and vegetation may serve to sustain the ridges as ridges and the sloughs as sloughs. Subtle differences in soil elevation, evapotranspiration and water flow can induce the long-term redistribution and concentration of limiting nutrients, leading to nutrient-rich inclusions in a nutrient-starved wetland. We reached this conclusion based on the following observations: (1) Soil P concentrations were much higher in topographically elevated tree islands than in low elevation marsh communities; (2) Inorganic P

concentrations in pore water increased monotonically with surface elevation and the stature of the associated plant communities, while pore water N followed an opposite trend; (3) Leaf N:P ratios paralleled the trends in soil and pore water, i.e., decreasing from the lowest elevation marsh community (Spikerush marsh) to the highest elevation forest (Hardwood Hammock), and suggesting an upslope transition from P-limitation to N-limitation; (4) Diurnal patterns in tree island water levels reflected daytime water table drawdown due to evapotranspiration and nighttime recovery due to replenishment from the marsh or the underlying aquifer; and (5) Model simulations of evaporation-induced convergent flow superimposed on a regional flow system produced patterns of nutrient concentration similar to those observed at our study sites.

We have offered a mechanism driven by evapotranspiration and regional flow to explain nutrient patterning in the Ridge and Slough landscape. While it is possible that this mechanism alone could be responsible for the observed patterns, it is more likely that they evolved through the combined effects of water flow, dissolved nutrient transport, sediment transport and faunal deposition. It is important to recognize that the balance among these processes probably has changed during the long development of the Ridge and Slough. For instance, cores from the tails of several Everglades tree islands exhibit soil horizons that could only have been transported by flowing surface water, yet sediment transport under current water management is probably not adequate to support such transport (Mitchell-Bruker et al., 2005). Success in Everglades restoration requires the re-establishment of natural water flow patterns, while avoiding the introduction of excess nutrients to this heterogeneous landscape mosaic.

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