

A DELICATE BALANCE: ECOHYDROLOGICAL FEEDBACKS GOVERNING LANDSCAPE MORPHOLOGY IN A LOTIC PEATLAND

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Abstract. The Everglades ridge and slough landscape is characterized by elevated sawgrass ridges regularly interspersed among lower and more open sloughs that are aligned parallel to the historic flow direction. Landscape degradation, characterized by topographic flattening, has coincided with a century of drainage, levee construction, nutrient enrichment, and flow reductions. Here we develop a conceptual model of Everglades landscape dynamics based on a literature synthesis and supported by the numerical model PeatAccrete. We propose that two feedback mechanisms govern landscape characteristics. The first, simulated with PeatAccrete, involves differential peat accretion governed by water level and phosphorus concentration, leading to the attainment of an equilibrium ridge elevation relative to slough. Differential peat accretion, however, cannot produce a characteristic ridge width or landscape wavelength. Instead, we propose that feedback between channel morphology and sediment mass transfer controls lateral and longitudinal topographic features, consistent with processes in anabranching rivers. This sediment transport feedback was critical in pattern initiation and evolution, and sediment redistribution from slough to ridge provides a plausible mechanism for preventing gradual ridge expansion. However, PeatAccrete model results show that, in the absence of sediment transport, ridges expand only on the order of meters per century. This result suggests that a combination of factors has driven the widespread disappearance of sloughs over the past century, including altered vertical peat accretion rates that lead to slough infilling. Sensitivity tests indicated that changes in duration and depth of surface water inundation, phosphorus supply, and redox potential have altered differential peat accretion rates in a way that favors topographic flattening. These factors are relatively well defined compared with the role of sediment transport, which requires further quantification. Because both positive and negative feedback processes interact in the Everglades, the trajectory of landscape evolution in time will depend upon current conditions, with areas of remnant ridge and slough topography being more likely than areas of degraded topography to respond to changes in water management in ways that enhance landscape heterogeneity over human timescales. Dual feedbacks between peat accretion and sediment transport are likely important controls on landscape evolution in low-gradient peatlands worldwide with pulsed, unidirectional flow.

Key words: *anabranching; Everglades; Florida; geomorphology; landscape ecology; peatland; ridge-slough; wetland; wetland hydrology.*

INTRODUCTION

Landscape heterogeneity and patterning increase environmental complexity and biodiversity (Kolasa and Rollo 1991). In lotic ecosystems and floodplains, physical and biological heterogeneity affect and/or are influenced by flow patterns and processes, species distribution and persistence, flux of materials and energy among ecosystem compartments, and predator-prey interactions (Palmer and Poff 1997). Fluvial dynamics often play a major role in regulating ecosystem heterogeneity, and changes in flow management can disrupt the interactions that create heterogeneity, resulting in decreased biodiversity (Ward et al. 1999).

Many low-gradient, lotic wetlands exhibit spatial heterogeneity and even patterning in vegetation distri-

bution, which may develop parallel (longitudinal) or perpendicular to the flow. Examples of wetlands with longitudinal patterning include the ridge and slough landscape (RSL) of the Florida Everglades (Science Coordination Team 2003, Ogden 2005), water tracks in boreal fens (Glaser et al. 1981), the Okavango Delta (Ellery et al. 2003, Gumbricht et al. 2004), morichal wetlands in Colombia and Venezuela (San Jose et al. 2001), buritizal wetlands in the Brazilian Pantanal (Silva et al. 1999), and some floodplain riparian wetlands (Hupp 2000, Steiger and Gurnell 2003). In these wetlands, islands or ridges with trees or herbaceous vegetation are interspersed among open-water conduits and aligned parallel to the flow direction. Here, mechanisms for creating and maintaining environmental heterogeneity are complex, involving feedback between physical and biological processes including peat and organic matter production and redistribution of material

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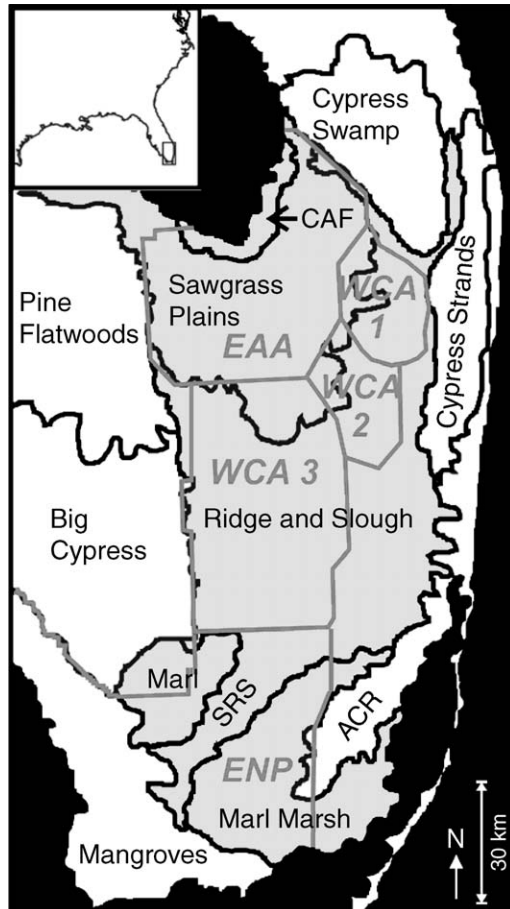


FIG. 1. Map of Greater Everglades, Florida, USA. This map labels the major historic vegetation communities of south Florida (outlined in black [Science Coordination Team 2003]) and shows the historical extent of the Greater Everglades (shaded in gray) and current managed compartments (outlined and labeled in dark gray). Key to abbreviations: EAA, Everglades Agricultural Area; WCA, Water Conservation Area; ENP, Everglades National Park; CAF, cistern apple forest; ACR, Atlantic Coastal Ridge; SRS, Shark River Slough. The inset shows the study site location in the southeastern United States.

and nutrients through transport processes. To better understand the dominant ecological feedbacks controlling the landscape dynamics in these patterned wetlands, new theories and testable ecohydrological models are needed.

The importance of hydrology in shaping wetland landscape dynamics has been widely recognized for boreal peatlands (Siegel 1988, Glaser et al. 1997, 2004) and riparian wetlands (Naiman and Decamps 1997). Ecohydrological models have provided tools to test hypotheses about feedback mechanisms and compare against observed landscape characteristics (e.g., Ingram 1982, Baird 1999). For example, models have been used to explain hydrologic linkages and geographical distributions of mires (Siegel 1983, Siegel and Glaser 1987, Reeve et al. 2000) or to explore feedback mechanisms

responsible for vegetation self-organization (Thiery et al. 1995, Hardenberg et al. 2001, Rietkerk et al. 2002, 2004). Models have also upheld the hypothesis that development of cross-slope patterning in striped fens occurs in a stability space defined by hummock-to-hollow hydraulic conductivity ratios and regional slope, in which lower hydraulic conductivity ratios and steeper slopes favor pattern development (Swanson and Grigal 1988, Couwenberg 2005, Couwenberg and Joosten 2005). However, application of ecohydrological models to elucidate landscape patterns and processes in longitudinally patterned peatlands has been much less common.

This paper begins to close this knowledge gap by synthesizing a new conceptual model of controls on landscape morphology and vegetation patterning in the Everglades based on feedback between flow, sediment entrainment, and deposition, and between nutrient delivery, vegetation distribution, and the differential accumulation of peat. Secondly, the paper presents a numerical model, PeatAccrete 1.0, of differential peat accretion feedback processes to test whether observed landscape features and long-term stability can arise from this class of feedback processes alone. This numerical model serves as a first step toward validating the conceptual model as a whole. Results and insight gained from the conceptual and numerical models provide an improved mechanistic understanding of how the landscape may have formed, persisted throughout millennia, and degraded concurrent with changes in water flow, water storage and water quality that resulted from increasing human influences over the past century. This synthesis establishes a framework for future research and modeling efforts intended to inform and predict the effects of restoration decisions.

SITE DESCRIPTION

Historically, the RSL occupied approximately half of the extent of the Everglades (Fig. 1; C. McVoy, *personal communication*). An ombrotrophic peatland, its estimated total phosphorus (TP) concentrations ranged from 5 to 8 $\mu\text{g/L}$ (Davis 1994, Miao and Sklar 1998, Newman et al. 2001). During rare storm events, overflow from Lake Okeechobee would deliver nutrients and mineral sediment to the northern Everglades, but otherwise, the Fibric Histosol substrate was autochthonously produced (Gleason and Stone 1994). A regional topographic gradient of 3 cm/km toward the south-southwest (Kushlan 1990) drove shallow, diffuse, laminar to transitional (Harvey et al. 2005) flow with an estimated average velocity of 4 cm/s (Fennema et al. 1994). Ridges, which rose ~ 1 m higher than the bottoms of sloughs, were spaced on the order of 100 m and aligned parallel to the flow (Science Coordination Team 2003). Coupled to wet (May–October) and dry (November–April) seasonality (Duever et al. 1994) that is thought to have caused water levels to fluctuate from just above ridge surfaces to slough bottoms (Science Coordination Team 2003), this elevation difference produced a difference in

TABLE 1. Current status of hypotheses of the mechanisms governing RSL formation and maintenance.

No.	Hypothesis	Source†	Status	Status source
1	Sediment transport during mean flows or episodic events prevented net sedimentation in sloughs. Loss of flow promotes sedimentation.	SCT (2003)	A likely mechanism for preventing lateral ridge spreading. Presently under consideration.	this study
2	Altered hydroperiods permit the colonization of sloughs by emergent vegetation or allow for changes in decomposition rates that induce topographic flattening.	SCT (2003)	Cannot explain degradation that has occurred in some areas with unaltered hydroperiods. Under consideration as a factor that may contribute to flattening.	SCT (2003), this study
3	Ridges accrete peat at higher rates than sloughs. Decreased flow may reduce the availability of nutrients and oxygen in surface water and decrease slough decomposition rates, causing infilling and topographic flattening.	SCT (2003)	First part of hypothesis under consideration in this study. A likely mechanism for promoting equilibrium elevation differences between ridge and slough.	this study
4	Sloughs may have been formed by erosion, arising from a "consequent drainage" pattern on a "recently uplifted surface."	SCT (2003)	Unlikely. The RSL was aggrading at the time of its formation, and the landscape formed in a deep-water environment.	Bernhardt et al. (2004), Willard et al. (2001)
5	Fire, burning overdrained tongues of peat, may have created the RSL patterning.	SCT (2003)	Unlikely, due to the wet origin of the landscape, its stability over millennia, and the pervasive occurrence of RSL patterning throughout the Everglades.	Bernhardt et al. (2004), Willard et al. (2001)
6	RSL patterning reproduces underlying bedrock topography.	SCT (2003)	Unlikely. Recent bedrock surveys show little correlation between bedrock and peat surface topography.	C. McVoy (<i>personal communication</i>)
7	Slight water chemistry differences between ridge and slough create differences in microhabitat that maintain separation between ridge and slough. Changes in flow alter the surface/subsurface geochemical exchange that results in this separation.	SCT (2003), this study	Under future analysis by authors.	
8	Secondary circulation flow patterns may alternately scour and deposit sediment in the form of longitudinal proto-ridges and reinforce existing ridge morphology. Decreased flow would diminish secondary circulation.	this study	Unlikely, due to scaling arguments and lack of a plausible mechanism for pattern wavelength evolution.	this study

† SCT = Science Coordination Team.

the duration and depth of inundation. Sawgrass (*Cladium jamaicense*) colonized the higher ridges, while water lily (*Nymphaea* spp.), bleeding heart (*Nymphoides aquatica*), bladderwort (*Utricularia* spp.), spike rush (*Eleocharis* spp.), and beakrush (*Rhynchospora* spp.) dominated sloughs (Gunderson and Loftus 1993, Gunderson 1994, Lodge 1994). The resulting heterogeneity was associated with high species richness and abundance (Ogden 2005).

The RSL originated 2700 years BP under much wetter conditions, and centers of modern ridges and sloughs have remained invariant over the past millennium (Bernhardt et al. 2004). Ridge width increased and decreased during drier and wetter climatic periods, respectively (Willard et al. 2001). Only in the past 100 years has sawgrass overtaken sloughs, producing or exploiting topographic flattening and forming monocultures (Bernhardt et al. 2004) in over 25% of the

landscape (Ogden 2005). This landscape degradation coincides with nearly a century of wetland drainage, isolation of wetlands by levees and canals, land subsidence, and discharge of P and sulfate from agricultural areas. The shallow, diffuse flow that once characterized the landscape is now limited in scale, with a mean velocity of only 1.15 cm/s in Shark River Slough (Riscassi and Schaffranek 2003).

As a result of this degradation, the Science Coordination Team (SCT; a research group within the South Florida Ecosystem Restoration Task Force), has outlined candidate hypotheses and research priorities for mechanisms responsible for RSL formation and maintenance (Science Coordination Team 2003). Additionally, the National Research Council (2003) has identified flow processes and resulting transport of suspended sediment as key uncertainties in the Comprehensive Everglades Restoration Plan (U.S. Army Corps of

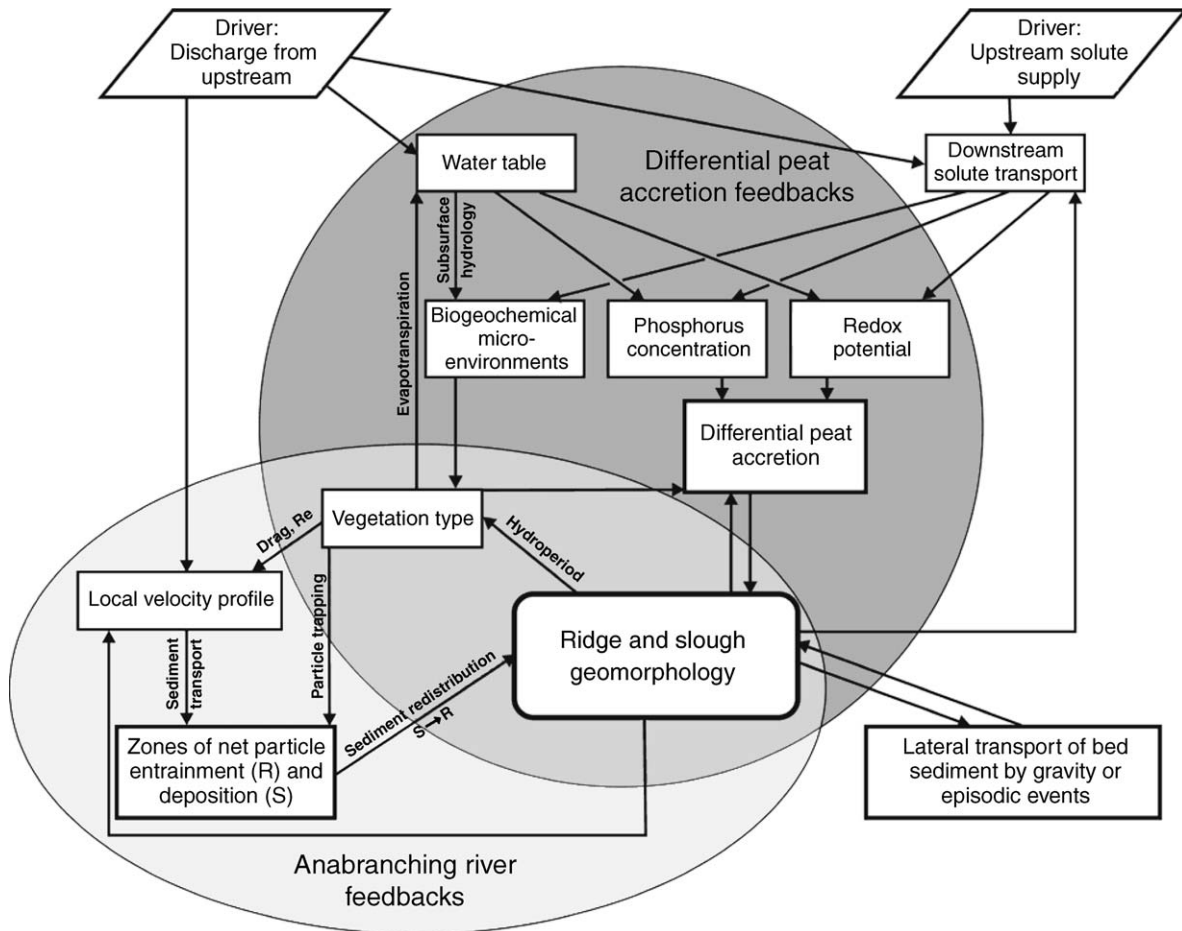


FIG. 2. Proposed conceptual model of the feedback mechanisms and processes governing Everglades ridge and slough landscape (RSL) morphology. The two major classes of feedback mechanisms (differential peat accretion and anabranching river feedbacks) are delineated with shaded ellipses. Reynolds number is abbreviated “Re.”

Engineers 1999). Table 1 presents a summary of the specific mechanisms for RSL degradation and maintenance postulated by the SCT and others and synthesizes the current status of the hypotheses.

DEVELOPMENT OF A CONCEPTUAL MODEL FOR THE ORIGIN AND STABILITY OF THE EVERGLADES RSL

Anabranching rivers as an RSL analogue

Our conceptual model of the RSL (Fig. 2) arises from a consideration of anabranching rivers as a functional landscape analogue. The RSL network shares many geomorphic similarities with the anabranching rivers described in the literature, which consist of parallel channels separated by islands or ridges that are aligned with the flow and bed slope and remain stable on the timescale of decades or longer (Nanson and Knighton 1996).

Both the Okavango Delta in Botswana (McCarthy et al. 1988, 1992, McCarthy and Stanistreet 1991) and Narew River in Poland (Gradzinski et al. 2003) have an aggrading peat substrate, abundant emergent vegeta-

tion, and low flow energies similar to the Everglades. Like Everglades sloughs, open water areas in the Narew River feature steep sides, flat bottoms, and very low slopes and sinuosity (Gradzinski et al. 2003). In addition, the Everglades shares geometric features with the Bagmati River in India, which exhibits an anabranching pattern across a 30 km wide floodplain (Jain and Sinha 2004), and the Marshall River in Australia, which contains ridges up to 1 km long that have length-to-width ratios (up to 100) similar to those found in the Everglades (Fig. 3; Tooth and Nanson 2000, 2004).

Like the Everglades, anabranching rivers occur in locations with a highly variable/seasonal flow regime (Nanson and Knighton 1996, Tooth and McCarthy 2004), banks that are cohesive or can be stabilized by vegetation, and high inputs of sediment relative to stream power (Tooth and Nanson 1999). Parallel channels can provide a means to achieve equilibrium by enhancing sediment discharge relative to single-thread reaches through reduction of overall boundary

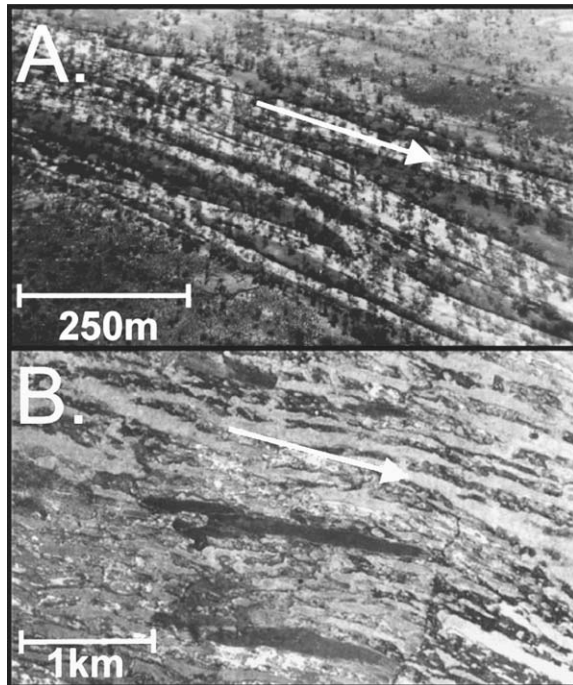


FIG. 3. Comparison between the geomorphology of the anabranching Marshall River, Australia, and the Everglades RSL, south Florida. Arrows indicate direction of flow. (A) An oblique aerial view of the anabranching Marshall River (image from Tooth and Nanson [2000]). (B) Satellite image of the RSL from Science Coordination Team (2003). Light features are ridges, and dark features are sloughs. The very dark feature at the center of the image is a tree island. Panel (A) is reproduced with permission from John Wiley and Sons.

roughness (Nanson and Huang 1999) or through sediment capture by vegetation stems during overbank flow, which reduces sediment loading to the main channels (Jansen and Nanson 2004).

Proposed origin and evolution of the RSL

Application of the emerging theory associated with anabranching rivers provides unique insight into potential geomorphic processes associated with RSL development and the maintenance of long-term landscape stability. Based on observations of the evolution of a ridge-form anabranching stream similar in morphology to the RSL (Fig. 3) from a single-thread channel (Tooth and Nanson 2000), we develop a conceptual model of ridge initiation in the Everglades, summarized in Fig. 4. Starting from the wetter conditions in which the RSL originated (Bernhardt et al. 2004), flood pulses (Dong 2006) deposited sediment in random locations on the stream bed or around preexisting patches of emergent vegetation. During the low-flow season or periods of drought, sawgrass, which requires an exposed peat surface for germination (Lorenzen et al. 2000), colonized the deposits. The sawgrass or other emergent vegetation would have provided stability during subsequent high-water periods, trapped suspended particles (Saiers et al.

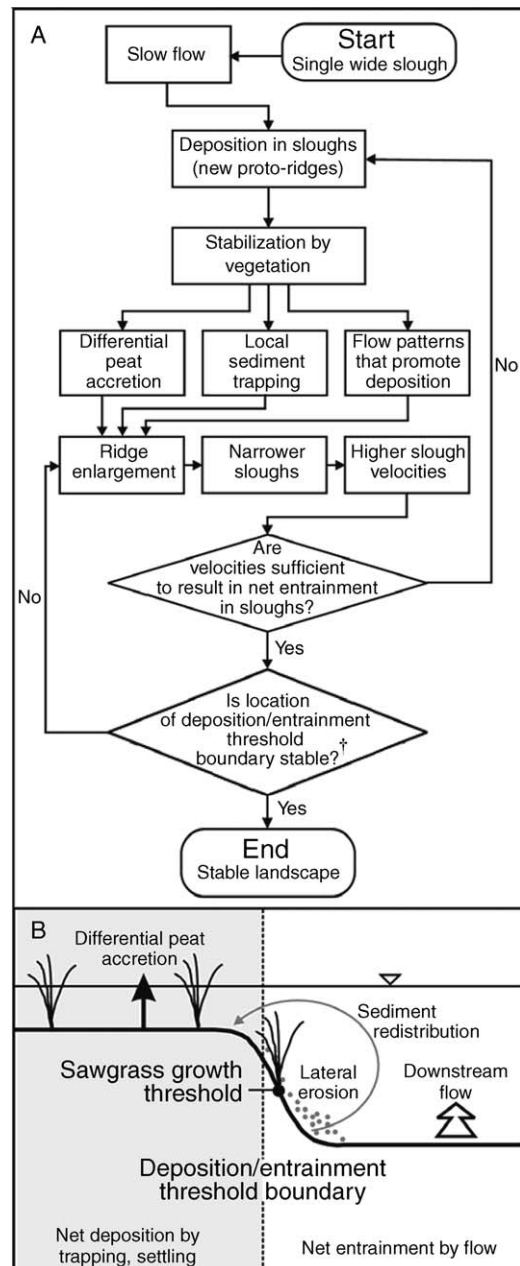


FIG. 4. (A) Flow chart and schematic diagram of proposed RSL evolution, beginning with regional slough conditions (Bernhardt et al. 2004) and ending with a stable, regularly patterned landscape. In the equilibrium landscape, the characteristic ridge width and spacing reflect the morphology in which the capacity for sloughs to transport sediment and organic matter downstream and to ridges balances in situ organic matter production and gravitational erosion so that the NPA within sloughs is equivalent to that on ridges. The question followed by a dagger (\dagger) symbol asks whether the boundary between net entrainment of bed sediment and net deposition of bed sediment moves slough-ward over time. (B) Diagram clarifying concepts outlined in (A), providing more detailed insight into the processes governing ridge width and spacing at a transition region between ridge and slough.

2003, Palmer et al. 2004), and slowed local flow velocity (Harvey et al. 2005), promoting additional sedimentation (e.g., Stumpf 1983, Hosokawa and Horie 1992, Leonard et al. 1995, Palmer et al. 2004). Under the differential peat accretion hypothesis (Table 1 and Fig. 2), these sawgrass patches may have also accreted peat more rapidly than sloughs, causing further topographic differentiation to an equilibrium elevation difference between ridge and slough, similar to that attained between hummocks and hollows in boreal bogs (Nun-gesser 2003). This overall hypothesis for the origin of RSL also shares key features with the development of strand tree islands in the Everglades: initialization/colonization during a dry period (the Little Ice Age, in the case of tree islands), followed by continued topographic differentiation through differential rates of peat accretion during the subsequent return to wetter conditions (Willard et al. 2006).

Once incipient proto-ridges were initiated, current shadows behind the deposits, ridge coalescence, and/or the development of roughness-induced secondary circulation cells (McLelland et al. 1999, Nepf and Koch 1999) would have promoted elongation and eventual channelization of the flow (Tooth and Nanson 2000). Ridges divided the system into multiple channels, each with a greater depth and hence transport capacity (Leopold et al. 1995) than the former single-thread flow environment. As proto-ridges continued to form on slough bottom, the wavelength of the ridge-slough pattern decreased until shear stress within sloughs was sufficient to entrain sediment and counteract the tendency towards infilling promoted by in situ peat production and diffusion-like gravitational spreading of unconsolidated sediment. Filled-in sloughs or proto-ridges spaced more closely than the equilibrium wavelength may have been re-incised through avulsion during high-flow events (e.g., McCarthy et al. 1992, Wende and Nanson 1998, Jain and Sinha 2004).

The final equilibrium wavelength of the landscape reflects the morphology in which the capacity for sloughs to transport sediment and organic matter downstream and to ridges balances in situ organic matter production and gravitational erosion so that the net peat accretion (NPA) within sloughs is equivalent to that on ridges. Thus, in the RSL spatial constancy in the rate of aggradation replaces the classical "graded" stream (Mackin 1948) as the state of landscape equilibrium. Equilibrium channel widths are determined by a balance between shear stress at channel margins (which responds to the cross-sectional form of the channel) and shear strength at ridge edges (Fig. 4B), with vegetation exerting a dominant control over both factors (e.g., Ellery et al. 2003, Allmendinger et al. 2005). Disruption of the maximum-efficiency, equilibrium morphology may then result from either a change in sediment transport/entrainment capacity via altered flow, altered rates of net sediment production, and/or a change in the zone of tolerance for emergent

macrophytes, all of which will be discussed later in this paper.

Differences between the RSL and classical anabranching streams

In some respects, the behavior of the RSL superficially differs from that of classical anabranching streams, but these differences can be reconciled with the essential physics underlying the dynamics of pattern maintenance. For instance, the shapes of vertical flow profiles differ between the RSL, subject to a laminar-to-transitional flow regime (Harvey et al. 2005) and vegetal drag, and classical anabranching streams, often with turbulent flow regimes and relatively little obstruction by vegetation. However, a particular flow profile shape is less important to the process of pattern development than the existence of feedback between landscape morphology, flow velocity, and sediment mass transfer dynamics. These processes presumably were coupled in the pre-drainage Everglades, with changes in landscape morphology resulting in an altered depth distribution. Changes in the depth distribution would correlate with altered flow velocity (Leonard et al. 2006) and ultimately shear stress, which governs sediment deposition and often entrainment.

In contrast to classical anabranching streams, sediment entrainment in the Everglades can also result from processes other than mean shearing flow, such as bioturbation (Science Coordination Team 2003), shallow mixing due to wind (Science Coordination Team 2003), vertical mixing due to outgassing from the peat (Kadlec and Knight 1996), or thermal overturn, which occurs as a result of diurnal heating and is associated with the production of turbulence (Schaffranek and Jenter 2001). Higher water velocities associated with infrequent high-energy events, such as tropical storms or cold fronts (Kang and Trefry 2003), might also induce scour and deposition at the heads and edges of ridges. For instance, Hurricane Andrew redistributed the *Utricularia*, periphyton mat, and dead macrophyte stems from sloughs to ridge edges (Science Coordination Team 2003), and we observed the same phenomenon following the passage of Hurricane Wilma in October 2005 (see Plate 1). These alternative means of sediment entrainment in the Everglades, together with the porous, flocculent, organic nature of the sediment (floc), may in fact explain how a morphology dependent on dynamic sediment transport can develop in the Everglades, which possesses the shallowest slope and slowest flow velocity of any anabranching river described in the literature to date. Still, regardless of whether these alternative processes dominate overall sediment entrainment in the RSL, coupling between flow and transport/deposition processes (and hence mass transfer dynamics) remains, thereby preserving the utility of the anabranching river analogy.

The long-term presence of vegetation in the flow of the Everglades causes differences not only in the shape



PLATE 1. Aerial view of the ridge and slough landscape looking south, July 2006, Florida Everglades, USA. Flow is toward the south, parallel to the elongated axis of the ridges (darker features). At this point, nine months after Hurricane Wilma passed over the landscape, wrack lines of debris are still visible as light narrow bands within ridges near the ridge/slough transition zone. The blackened ridge in the lower left corner of the image burned during the dry season. Photo credit: L. Larsen.

of flow profiles for the RSL and classical anabranching streams but also in the spatial variation of mass transfer dynamics. Vegetation can enhance deposition by increasing drag (Nepf 1999, Lee et al. 2004, Lightbody and Nepf 2006) and directly intercepting particles on stems and leaves (Palmer et al. 2004). In emergent vegetation (e.g., ridges), these effects are exerted throughout the water column, promoting preferential deposition relative to areas without emergent vegetation. Evidence for preferential deposition on ridges is supplied by observations of greater particle transport by mass in sloughs relative to ridges (Leonard et al. 2006) and of heightened particle capture efficiency on inundated ridges in an anabranching stream in Australia relative to channels (Jansen and Nanson 2004). In the latter study, preferential deposition on vegetated islands enhanced the hydraulic efficiency of the network of streams by increasing the flux of sediment and water through the channels, promoting maintenance of channel equilibrium. However, while classical anabranching streams, in which vegetated islands only rarely experience flooding,

attain equilibrium largely through an efficient channel morphology (Nanson and Huang 1999), particle capture by the seasonally inundated sawgrass ridges likely plays a more dominant role in the attainment of hydraulic efficiency and equilibrium in the Everglades.

The putative dominance of the role of particle capture in Everglades suspended sediment dynamics leads to the prediction that the morphology of the RSL, in contrast to classic anabranching streams, should not result in large total suspended solids (TSS) concentrations discharged to the Gulf of Mexico. Observation of relatively small TSS in the freshwater Everglades (<3 mg/L [Noe et al. 2007]) and in Everglades water discharging to the Gulf ($5\text{--}105$ mg/L [Sutula et al. 2003]) verifies this prediction. Using a dry bulk density of 0.06 g/cm³ for Everglades peat (Harvey et al. 2004), an average freshwater discharge of 3 m³/s (Hittle et al. 2001), and assuming that particles only originate from half (sloughs only) of the 365 000-ha aerial extent of the RSL (Ogden 2005), this sediment discharge equates to the removal of 3×10^{-3} to 9×10^{-2} mm of sediment per

year from slough bottoms. Assuming north–south flow through the Everglades ceased, the resulting sediment gain (assuming no redistribution of sediment to ridges) would not be sufficient to explain topographic flattening over the 100-year time scale of human management. In contrast, redistribution of sediment from slough to ridge would both explain low TSS discharges to the Gulf of Mexico, as observed, and provide a flow-related mechanism of RS maintenance that could explain landscape degradation following diminished flow.

In summary, both classical anabranching rivers and the Everglades RSL likely attain equilibrium through the interaction between channel form and mass transfer of sediment. In classical anabranching streams, ridges or islands completely separate anabranches and increase sediment transport for long distances downstream, but in the RSL, where sloughs are separated by regularly inundated ridges, sediment redistribution from sloughs to ridges is a key mechanism that maintains landscape pattern. This process may be similar to the redistribution of sediment that occurs in mangrove swamps fringing tidal channels, where suspended sediment from the channels is deposited within the swamps at measured rates of 10 mm/yr (Furukawa et al. 1997) and in floodplain wetlands (Heimann and Roell 2000, Steiger and Gurnell 2003).

Validation of ridge and slough conceptual model

Validation of the conceptual model presented in Fig. 2 could take the form of numerical analysis and/or field observation and experimentation. A numerical evaluation would involve simulating key feedback processes using inputs that reflect the conditions under which the landscape developed and persisted and then comparing simulated to actual landscape characteristics. Model parameters could then be adjusted to explore the impact of anthropogenic perturbations on landscape development.

A complete numerical validation of the conceptual model would require simulating differential peat accretion feedback processes, gravitational erosion of sediment, and feedback between landscape morphology, flow, and sediment mass transfer. Simulation of the latter, anabranching river-type feedback would involve formulating flow through heterogeneous vegetation communities and flocculent suspended sediment dynamics. At this time, the experimental data required to parameterize such a simulation are unavailable, so rigorous validation of the anabranching river feedback processes remains beyond the scope of this paper. However, equipped with observations reported in the literature, we formulate a numerical model of differential peat accretion and gravitational erosion processes in the Everglades as a first step toward validating the conceptual model as a whole. Explicitly, such a simulation tests the hypothesis that these feedback processes *alone* can explain the existence and stability of a patterned RSL. This type of simulation could

likewise apply to other locations where differences in the rate of autochthonous peat accretion, governed by vegetation distribution and availability of a limiting factor, may result in regular differentiation of landscape elements.

NUMERICAL MODEL DEVELOPMENT

In the Everglades, dominant controls on the distribution and productivity of macrophytes, rates of decomposition of organic matter, and ultimately rates of NPA consist of the availability of P, the chief limiting nutrient in the Everglades (Davis 1994, Noe et al. 2001, McCormick et al. 2002, Sklar et al. 2002), depth and duration of inundation (Harris et al. 1995, Busch et al. 1998), and species-specific differences in net annual primary productivity rates and tissue lignin/cellulose content (DeBusk and Reddy 1998). Appendix A provides a review of the specific processes through which P concentration and redox potential affect productivity and decomposition in Everglades ridges and sloughs. Based on these processes, we have synthesized the numerical model PeatAccrete 1.0, a mechanistic, quasi-two-dimensional simulation of the feedback between P concentration, water table, and peat topography for a ridge/slough cross-section. Transport of sediment by flow and feedback between landscape morphology and local flow are not simulated. Using PeatAccrete, we compare the differential height attainment of the modeled landscape with actual characteristics of the Everglades, with the finding that the model can reproduce some of the essential topographic characteristics of Everglades ridges and sloughs. Overall, PeatAccrete can verify the existence, relative importance, and sensitivity to perturbation of differential peat accretion feedback mechanisms governing the morphology of the RSL and can prioritize research questions (principally, sediment transport via the anabranching mechanism) that should be addressed numerically and experimentally to fully assess controls on heterogeneity in the RSL.

The PeatAccrete model domain extends in one dimension from the center of a slough, across a ridge head, to the slough center on the opposite side, perpendicular to flow direction. For each point in the domain at each instant in time, coupled governing equations produce solutions to four state variables: peat topography, water table topography, vadose zone water content, and TP concentration in water. Values of constants employed in the model are defined in Appendix B, which also provides the expected range of values for the Everglades supplied in the literature.

Peat topography

Governing equation.—Changes in peat elevation (z) at each node on the cross-section over time are formulated as a function of gravitational erosion and net vertical peat accretion at that point:

$$\frac{\partial z}{\partial t} = D_{\text{sed}} \frac{\partial^2 z}{\partial x^2} + \text{NPA} \quad (1)$$

where x is the spatial (cross-sectional) coordinate, t is the time coordinate, and D_{sed} is the soil diffusivity. The first term is the gravitational peat erosion function, formulated as a diffusion expression that spreads peat laterally across the domain. In the literature, the diffusion equation has been applied numerous times to successfully simulate erosion on hillslopes (e.g., Rosenbloom and Anderson 1994) and aquatic depositional settings (e.g., Pasternack et al. 2001). This approach assumes that erosion proceeds such that the rate of change in elevation is linearly proportional to topographic curvature, which has been verified for terrestrial hillslope erosion (Heimsath et al. 1997). Pasternack et al. (2001) reviews the conceptual basis for applying the diffusion equation to evaluate erosion in aquatic depositional settings and concludes that this approximation is appropriate for slopes of less than 45°. The diffusion coefficient, D_{sed} , is a poorly constrained parameter (Pasternack et al. 2001) and is a function of cohesiveness of the substrate, flow, mixing by wind, and bioturbation.

Autochthonous peat accretion in Cladium jamaicense.—Two alternative approaches may be employed in simulating NPA (term II, Eq. 1): (1) a reductionist, mass-balance approach, which would need to include gross above- and belowground biomass production rates, biomass turnover and selective decomposition, and compaction of refractory components to form peat (Morris and Bowden 1986), or (2) a phenomenological approach that uses a data set of observed rates of NPA or biomass production along a P enrichment gradient (Craft and Richardson 1993b, Reddy et al. 1993) in Water Conservation Area (WCA)-2A (see Fig. 1) and under different E_h (redox potential) treatments (Kludze and DeLaune 1996, Pezeshki et al. 1996; Appendix C). We deemed the phenomenological approach favorable over a mass-balance approach because of lack of data and considerable uncertainties surrounding a more process-based description. Still, it is important to recognize the simplifications associated with this approach. Notably, a variable mixture of cattail (*Typha domingensis*) and sawgrass dominates the enrichment gradient, with the relative abundance of cattail increasing with proximity to the source of enrichment at the upstream end of WCA-2A. NPA rates likely differ between cattail and sawgrass, but at the present time, the aforementioned data set is the only one that provides long-term peat accretion data for a plant community inclusive of sawgrass along a P enrichment gradient. (We exclude data points from sampling stations within *Typha* monocultures.) Moreover, all of the numerical experiments reported here use only the oligotrophic portion of the parameter space, with water TP concentrations <10 µg/L. In the corresponding oligotrophic regions of WCA-2A, sawgrass is the dominant

vegetation, so NPA rates simulated in the oligotrophic portion of the parameter space are quantitatively robust. We believe the use of this empirical dataset is the best way to begin a landscape dynamics modeling exercise and that in the future the processes simulated in the model can be expanded as necessary.

To derive an algorithm for NPA in sawgrass, we assume that P concentration (C) and water depth are the dominant independent variables, so that $\text{NPA} = f(C, h - z)$, where h is hydraulic head. In oligotrophic conditions, P concentration and water depth can be assumed independent, so that $\text{NPA} = f(C)f(h - z)$. In non-oligotrophic conditions, the assumption of independence would be violated because P enrichment increases oxygen demand (Amador and Jones 1993, 1995, 1997, Drake et al. 1996), thereby reducing the optimum water depth for biomass production (Lissner et al. 2003).

The P concentration effect, $f(C)$, was based on observations of NPA and TP as a function of distance along the WCA-2A transect (Craft and Richardson 1993b, Reddy et al. 1993). As shown in Appendix D, we fitted exponential and logarithmic functions to the distance vs. NPA data set and distance vs. water column TP data set using a least-squares procedure, excluding data points from *Typha* monocultures. By combining these two regressions, we formulated a relationship between TP in water and NPA for the hydrologic regime present along the WCA-2A transect:

$$\text{NPA} = \left\{ -2.0 \ln \left[\frac{-0.42}{\ln(4.6 \times 10^2 C)} \right] + 6.5 \right\} \times f(h - z) \quad (2)$$

where units of C are in µg/L, and NPA is given in mm/yr. Eq. 2 is formulated so that $f(h - z)$ must be unity when $h - z$ equals the mean water depth along the eutrophication gradient.

The water depth effect for NPA in sawgrass, $f(h - z)$, is based on an observed relationship between sawgrass biomass and E_h for unenriched portions of the Everglades (Appendix C; Kludze and DeLaune 1996) and assumptions about the relationship between biomass and NPA and between E_h and water depth. First, we assume that TP concentrations in the unenriched Everglades were sufficiently limiting for the magnitude of change in decomposition rates to vary little with changes in water level (Amador and Jones 1997). Thus, the expression for NPA as a function of E_h is proportional to the expression for sawgrass biomass, B , as a function of E_h . Secondly, noting that except for at highly anaerobic and highly aerobic values of E_h , the relationship between E_h and water depth in many wetlands is approximately linear (deMars and Wassen 1999), we assume a linear variation in E_h with water depth. Combining constants of proportionality into the single constant α , we thus arrive at the following expression:

$$f(h - z) = \alpha B(h - z). \quad (3)$$

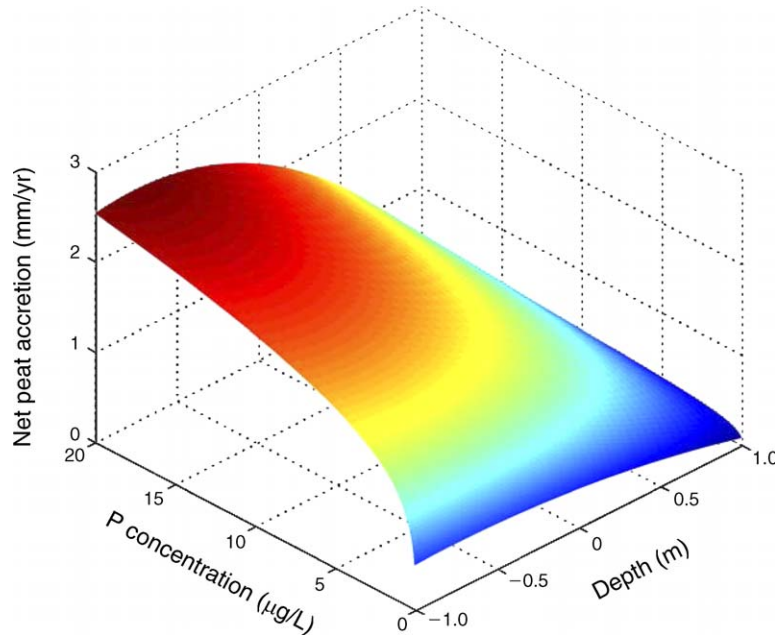


FIG. 5. Response surface of simulated net peat accretion (NPA) to total phosphorus (TP) concentration and depth. Negative depths refer to cases in which a free-water surface is present. Since depth controls redox potential in the oligotrophic Everglades (Appendix A; Kludze and DeLaune 1996), the depicted function may also be considered proportional to the relationship between NPA, TP, and redox potential (E_h), with E_h decreasing along the depth axis. The color of the response surface emphasizes net peat accretion rate values, with warmer colors corresponding to high net peat accretion rates and cooler colors corresponding to low net peat accretion rates.

In the literature, measured E_h values average between -100 and -200 mV during the wet season in WCA-2A and attain values greater than 300 mV during the dry season (Koch-Rose et al. 1994). The more oligotrophic soils of Everglades National Park, however, average between 75 and 250 mV during flooded periods (Bachoon and Jones 1992) and remain highly oxidized throughout much of the year (Amador and Jones 1995, Noe et al. 2001). For the model, we tested a variety of cases with different linear relationships between depth and redox potential to evaluate the range of possible results. A quadratic equation was then fitted to each depth vs. biomass relation using least-squares regression:

$$B(h-z) = a(h-z)^2 + b(h-z) + c \quad (4)$$

where a , b , and c are regression coefficients provided in Appendix E. In all cases, R^2 values were above 0.99 .

Finally, we solve for α by employing the constraint that $f(h-z)$ must equal unity when water depth equals the average depth along the central WCA-2A study area. Using a mean water level of -0.75 m (the negative sign indicates an aboveground water surface), we obtain the values of α reported in Appendix E.

Cladium response surface.—Fig. 5 provides the graphical solution to Eq. 2 for case B1 (see Appendix E) and a range of water levels and TP concentrations. The shape of this response surface is consistent with the mechanisms underlying NPA in the Everglades. Sawgrass is highly limited by P (Davis 1994, Noe et al. 2001,

McCormick et al. 2002, Sklar et al. 2002), so an increase in TP produces a substantial increase in NPA (Davis 1989, 1991, Miao et al. 1997, Miao and Sklar 1998) after an initial delay (Koch and Reddy 1992, Chiang et al. 2000). As TP concentrations increase, the rate of increase in NPA slows because of enhanced decomposition (Reddy et al. 1998, Qualls and Richardson 2000, Newman et al. 2001). However, effects of increased primary productivity continue to outweigh the effects of enhanced decomposition, due to the high lignin content of sawgrass (DeBusk and Reddy 1998, Vaithyanathan and Richardson 1998). NPA is more responsive to changes in water level under higher nutrient enrichment, because in these conditions, the limiting factor shifts towards redox potential (Urban et al. 1993, Craft et al. 1995). Nevertheless, in highly oligotrophic conditions, when TP does not vary significantly, changes in NPA are primarily linked to variations in water depth, with moderate water depths producing the highest rates of sawgrass total biomass production and NPA (Toth 1987, Kludze and DeLaune 1996, Pezeshki et al. 1996).

Consistent with these mechanisms, the response surface curve suggests several hypotheses about how ridge growth will proceed in the PeatAccrete model. Namely, as ridges grow relative to slough bottoms, sawgrass roots will be displaced from the mean average water level, and eventually, ridge NPA will slow and come into equilibrium with slough NPA. In oligotrophic areas, an increase in TP due to dry-season evaporative

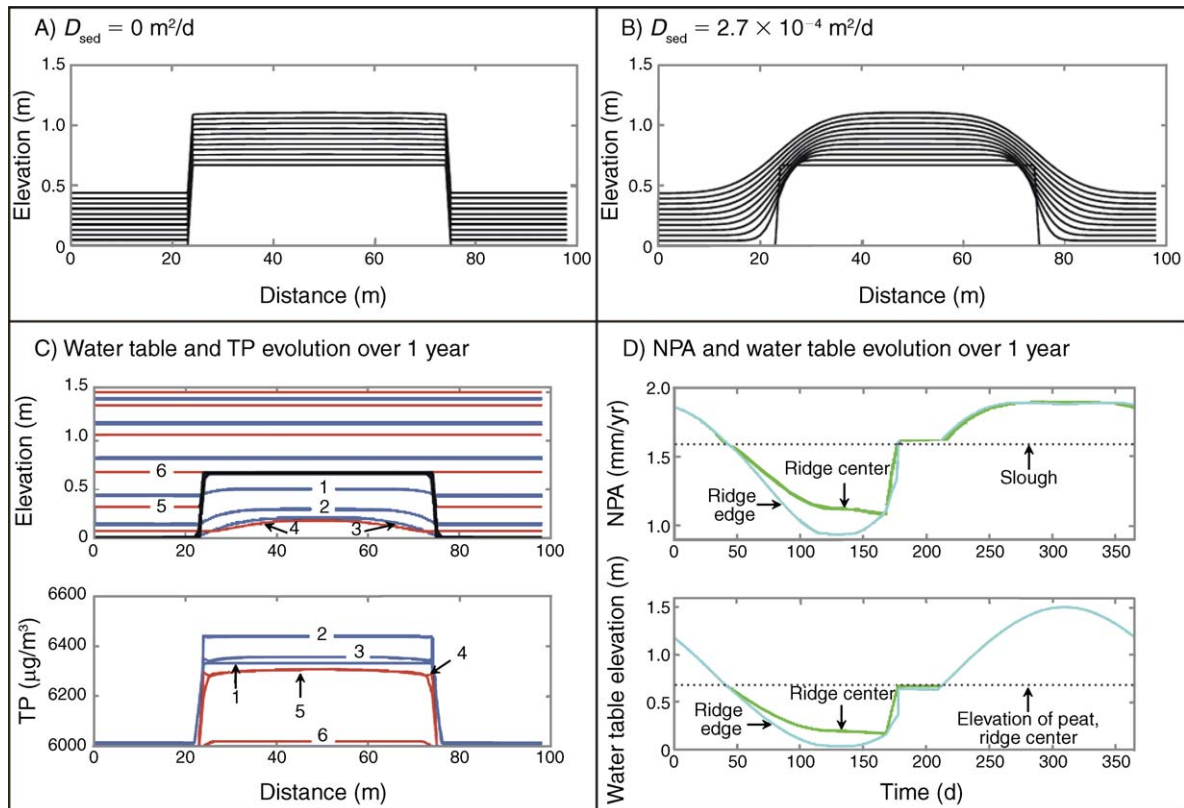


FIG. 6. PeatAccrete 1.0 simulation results for depth/redox case B1 (Appendix E). In (A) and (B), peat surface topography is depicted for 100 000 days (~ 274 years) of simulation. Peat surface elevation is plotted against cross-sectional distance for the initial time step and 10 intermediate time steps, evenly spaced in time (every 10 000 days throughout the simulation). Plot (A) shows the evolution of state variables when lateral erosion of soil has been turned off. In plot (B), erosion is turned on, with the soil diffusivity coefficient (D_{sed}) set equal to the default value in Appendix B. Plots (C) and (D) show the evolution of total phosphorus (TP), water table, and net peat accretion (NPA) over the course of one year for the nonzero D_{sed} case, with (C) depicting TP and water table values along a cross-sectional transect for 12 evenly spaced times throughout the year (red and blue lines distinguish between periods of rising water level and periods of falling water level, respectively, while the black line shows the ridge topography) and (D) depicting the continuous evolution of NPA and water table at two points on the ridge in response to seasonal changes in evapotranspiration and precipitation. In (C), not all TP profiles are apparent, as profiles are flat, featureless, and equivalent to the background concentration of TP when water covers ridge surfaces. During the dry season, when ridges are exposed, an evaporative concentration signature is apparent in the elevated TP concentrations. Apparent TP concentration profiles and their corresponding water table are numbered accordingly.

concentration, if significant, could also exert control over ridge NPA. Enhanced dry-season growth of ridges relative to sloughs would be expected in response to the local increase in TP. The result would be an enhancement of vegetative and topographic distinctness, as in Rietkerk et al. (2004), whose numerical simulations showed that differential evapotranspiration in boreal bogs caused P to accumulate under hummock vegetation at the expense of hollow vegetation. Under Rietkerk's "nutrient accumulation mechanism," outward expansion of hummocks was restricted by the depleted concentrations of P in the areas immediately adjacent.

Autochthonous peat accretion in sloughs.—The model is divided into slough cells and ridge cells based on cell elevations relative to the low point of the slough. Cells above a threshold elevation for sawgrass growth (z_{thr} ,

ranging from 0.1 m to 0.6 m above the slough in different implementations of the simulation, are designated ridge cells. As explained earlier, PeatAccrete employs an empirical approach to solve for net rates of peat accretion under sawgrass. Data for the response of slough vegetation biomass, decomposition, or peat accretion to a range of environmental conditions are limited, species-specific, and often conflicting (e.g., Busch et al. 2004, Chen et al. 2005). Net rates of peat accretion under sloughs are instead formulated as a constant, time-averaged rate of 1.59 mm/yr, based on dating of peat produced prior to anthropogenic impacts (Davis 1946, McDowell et al. 1969, Craft and Richardson 1993a). We believe this simplification is robust for several reasons. First, due to extreme oligotrophic conditions in the natural system, slough NPA and decomposition may not have exhibited large variations

TABLE 2. Effects of P enrichment and altered redox potentials on slough net peat accretion (NPA), with and without slough species replacement.

Condition	Without species replacement	With species replacement
P enrichment	productivity ↑ (probably†) decomposition ↑ NPA?	productivity ↑ decomposition ↓ NPA ↑
Sustained low redox potentials	productivity ↑ (probably†) decomposition ↓ NPA ↑	productivity ↓ decomposition ↑ NPA ↓
Sustained high redox potentials	productivity ↓ (probably†) decomposition ↑ NPA ↓	productivity ↑ decomposition ↓ NPA ↑

Note: The table is based on the review presented in Appendix A.

† Conflicting report of Chen et al. (2005) found no significant effect of P or redox potential (E_h) on *Eleocharis cellulosa*.

with normal water depth fluctuations (Urban et al. 1993, Amador and Jones 1997, Chen et al. 2005). Second, while biomass production within sloughs may be sensitive to increased P in oligotrophic conditions (Busch et al. 2004, Daoust and Childers 2004), model results (see *Model results and discussion*) showed minimal evaporative concentration of TP in sloughs during the dry season (Fig. 6C; see also Vaithyanathan and Richardson 1998, Newman et al. 2004).

The assumptions behind the simplification of the slough NPA formulation would be violated in non-oligotrophic conditions, when rates of slough decomposition (e.g., DeBusk and Reddy 1998, Qualls and Richardson 2000, Newman et al. 2001) and biomass production (Busch et al. 2004, Daoust and Childers 2004) would increase, or in sustained low redox conditions, when rates of decomposition would decrease (Craft and Richardson 1993a, Reddy et al. 1993, DeBusk and Reddy 1998) and biomass production would increase (Busch et al. 2004, Newman et al. 2004) or remain constant (Chen et al. 2005). The effects of sustained P enrichment or redox potential changes on slough NPA are more complex when they lead to a shift in vegetation species assemblages, and both P enrichment and higher redox potentials would tend to increase NPA through replacement of floating vegetation with less decomposable, more productive emergent species (Vaithyanathan and Richardson 1999, McVoy 2006). Experimental data required to simulate species replacement is currently lacking, but for all simulations reported here (with the possible exception of one run in which mean surface water elevation was perturbed downward), replacement is not expected to occur. Table 2 summarizes the probable direction of change of slough NPA in response to P enrichment and altered redox potentials.

Hydrological transport processes affecting water level

The PeatAccrete model domain is subdivided into pore water cells, defined as cells in which the water table is below the surface of the peat, and surface water cells, in which a free water surface is present. Due to fluctuating water levels and the presence of micro-

topography, boundaries between these domains are dynamic; at a given time of year, the model domain may be occupied exclusively by pore water cells or surface water cells, or both pore water and surface water cells may coexist. Pore water cells are transformed into surface water cells when precipitation or drainage from adjacent cells fills all available pore space within the peat and the free water surface rises above the peat surface. Throughout model development, terms specific to the pore water domain are subscripted “pw,” while those specific to surface water are subscripted “sw.”

PeatAccrete simulates a free water surface that fluctuates sinusoidally in response to seasonal changes in the water balance. In a manner consistent with historical descriptions given in Science Coordination Team (2003), the free water surface head with respect to a vertical datum (z_{dat}) ranges between slough bottom and 1.5 m over the slough bottom over the year as follows:

$$h_{\text{sw}}(t) = -0.75 \cos\left(2\pi \frac{t - 127}{365}\right) + 0.75 - z_{\text{dat}} \quad (5)$$

where the spatial unit is meters and the time unit is days.

Physically, hydraulic head changes in response to processes of lateral pore water flow, evapotranspiration, and inputs of new water through precipitation and runoff in the PeatAccrete simulation. We assume that exchange fluxes between pore water and groundwater within the underlying sand and limestone aquifer are negligible compared to exchanges between surface water and pore water. In interior portions of the Everglades, head gradients and exchange between surface water and peat pore water alternate in direction on a monthly to seasonal timescale and tend to cancel out in the long term (Harvey et al. 2004). The general mass conservation governing equation for hydraulic head is written as follows:

$$\frac{\partial h}{\partial t} = \frac{K}{S_1} \frac{\partial}{\partial x} \left(h \frac{\partial h}{\partial x} \right) - \frac{\varepsilon}{S_2} + \frac{(\bar{P} + \bar{R})}{S_3} \quad (6)$$

where h is hydraulic head with respect to a vertical datum, x is the spatial coordinate parallel to the model

domain, K is hydraulic conductivity (length per unit time), ε is an evapotranspiration function, and \bar{P} and \bar{R} are the rates (length per unit time) of water addition through precipitation and runoff, respectively. S_1 , S_2 , and S_3 are the dimensionless storage coefficients associated with each process. Within the surface water domain, storage coefficients are set to unity. In the pore water domain, storage coefficients associated with each term differ because the processes that remove pore water can apply suction to extract water to different extents, and the storage coefficients associated with processes that add pore water reflect the integrated history of prior extraction. The values of storage coefficients for the pore water domain will be discussed later.

The solution for Eq. 6 is computed using a specified head at the boundary between pore water and surface water cells given by Eq. 5. As described previously, the position of the left and right boundaries that divide the surface water cells located on the outer edges of the domain from the pore water cells in the central part of the domain shift with time. In the absence of a free water surface, periodic boundary conditions are applied.

The first term on the right-hand side of Eq. 6 represents lateral flow. Within the pore water domain, K is assumed to be spatially invariant because measurements currently available for the central Everglades cannot reliably distinguish between ridge and slough (Harvey et al. 2004). In pore water, S_1 is defined based on whether head gradients cause the water table to rise or fall:

$$S_1 = \begin{cases} S_y & \left| \frac{\partial}{\partial x} \left(h \frac{\partial h}{\partial x} \right) < 0 \right. \\ S_{\text{rise}} \equiv n - \frac{H_{vz}}{z - z_{\text{dat}} - h} & \left| \frac{\partial}{\partial x} \left(h \frac{\partial h}{\partial x} \right) > 0 \right. \end{cases} \quad (7)$$

For a falling water table, S_1 simply equals specific yield, S_y , defined as the volume of water drained by gravity per unit volume of saturated, unconfined aquifer, and the first term of Eq. 6 is equivalent to the solution of the Boussinesq equation (Freeze and Cherry 1979). For a rising water table, S_1 equals S_{rise} , defined as the volume percent of pore space available to be filled, where n is porosity, z is the peat surface elevation with respect to a vertical datum, and H_{vz} is the equivalent height of an open column of water containing all water within the vadose zone with a horizontal projected area equivalent to that of the domain cell (see *Vadose zone water content*). S_{rise} is always greater than or equal to S_y , due to the effect of the greater suction applied by plant roots to remove water via evapotranspiration than that associated with gravity drainage processes.

In surface water, the only contribution to the lateral flow term is the volume of water lost or gained through

the boundaries between the surface water and pore water domain (obtained from the negative of the solution of the lateral flow term at the pore water boundaries). To maintain a reasonable level of simplicity in the simulation, the volume of water crossing boundaries between surface water and pore water cells is distributed equally among all surface water cells within a time step. This approach has the effect of setting K for surface water cells arbitrarily high and is a reasonable assumption for situations where gradients in the free water surface are negligible (i.e. where flow in surface water is very fast relative to flow in the subsurface).

The second term in Eq. 6 represents head changes due to evapotranspiration. Both a Priestley-Taylor algorithm (German 2000) and a pan evaporation formulation modified by crop coefficients and water table depth (Fennema et al. 1994) are widely used to estimate local evapotranspiration in the Everglades. PeatAccrete employs the Priestley-Taylor algorithm because of its rigorously validated ability to replicate small-scale evapotranspiration differences between emergent vegetation and open water areas (German 2000, Shoemaker and Sumner 2006) and its direct, functional relationship to meteorological variables. The algorithm requires cell type (ridge or slough), water elevation relative to soil elevation, incoming solar radiation, and air temperature as inputs and provides an estimate of ET (length per unit time) that has been verified to reproduce actual measured ET to within 15% for daily sums (German 2000). The data sets for incoming solar radiation and air temperature in 1996 from German's site 3 were linearly resampled to the time step of the model and applied to the Priestley-Taylor ET formulation (data sets *available online*).⁴ For cells containing sawgrass, the calculated ET was supplied by first preferentially extracting water down to wilting point (θ_{wp}) in the vadose zone, if present (e.g., Rodriguez-Iturbe and Porporato 2004),

$$\varepsilon = \max \left\{ 0, \text{ET} - \frac{H_{vz} - \theta_{\text{wp}} n [z - z_{\text{dat}} - \min(h, z - z_{\text{dat}})]}{dt} \right\} \quad (8)$$

and then reducing water table in accordance with S_2 :

$$S_2 = (1 - \theta_{\text{wp}})n. \quad (9)$$

Note that the storage coefficient S_2 is analogous to S_y , defined in terms of field capacity (θ_{fc}) as $S_y = (1 - \theta_{\text{fc}})n$.

The only term now remaining to be parameterized in the water balance (Eq. 6) is the "new water" term, due to inputs from precipitation and runoff. In this simulation, precipitation occurs at a spatially constant rate, \bar{P} . In contrast, runoff can vary spatially. Runoff occurs in PeatAccrete during periods of rewetting after a dry-down, when water table mounds intersect the peat surface at elevations higher than the free water surface (see Fig. 6C). Further additions of water from precipitation cause water to overtop the ridge and drain

⁴ (<http://sofia.usgs.gov/projects/evapotrans/>)

laterally to the lower free water surface. The runoff term is positive for cells receiving water in excess of direct precipitation and negative for cells that lose water to other parts of the model domain. Thus, the sum $\bar{P} + \bar{R}$ is the net rate of addition of water to a cell that ultimately comes from precipitation. In pore water cells the rate of change of head due to precipitation is a function of the available pore space in the vadose zone, so that $S_3 = S_{\text{rise}}$.

As previously stated, the amount of water lost from cells in the pore water domain to a lower free water surface is nonzero only when the amount of precipitation in a time step exceeds available pore space in the vadose zone:

$$\bar{R}_{\text{pw}} = -\max\left[0, \bar{P} - \frac{n(z - z_{\text{dat}} - h) - H_{\text{vz}}}{dt}\right]. \quad (11)$$

Runoff originating from topographically higher cells is evenly distributed across the free water surface:

$$\bar{R}_{\text{sw}} = \frac{\int_{\text{pw}} \bar{R}_{\text{pw}} dx}{\int_{\text{sw}} dx} \quad (12)$$

where the numerator is integrated over the pore water domain and the denominator is integrated over the surface water domain.

To quantify each term of the water balance, we first obtain the balance of precipitation and runoff for the surface water domain by substituting the derivative of Eq. 5 into the left-hand side of Eq. 6 and solving for the term $S_3^{-1}(\bar{P} + \bar{R}_{\text{sw}})$. The numerical value of this term, together with Eqs. 11–12, now constitute three equations in three unknowns, enabling solution for the remaining dependent variables.

Vadose zone water content

Vadose zone water content may increase or decrease by all of the processes affecting the water table. Generally, reductions in water table cause an increase in vadose zone water content because of partial drainage, whereas a rising water table assimilates the vadose zone into the saturated zone. Furthermore, evapotranspiration can withdraw water from the vadose zone in excess of the water drained by gravity. The conservation equation for vadose zone water content is as follows:

$$-\frac{\partial H_{\text{vz}}}{\partial t} = \left(\frac{n - S_1}{S_1}\right) K \frac{\partial}{\partial x} \left(h \frac{\partial h}{\partial x}\right) - \left(\frac{n - S_2}{S_2}\right) \varepsilon + \varepsilon_{\text{vz}} + \left(\frac{n - S_3}{S_3}\right) (\bar{P} + \bar{R}). \quad (13)$$

In effect, Eq. 13 produces an approximation of a capillary fringe, in which the saturated zone transitions above to a zone at field capacity and finally to a moisture-

depleted zone at wilting point. Eq. 13 is analogous to Eq. 6, but with opposite sign and an additional term, ε_{vz} , which represents the withdrawal of water from an existing vadose zone to wilting point by evapotranspiration. ε_{vz} does not appear in Eq. 6 because, in the PeatAccrete simulations, withdrawals from the vadose zone do not effect a decrease in water table. As suggested by Eq. 8, ε_{vz} is formulated as follows:

$$\varepsilon_{\text{vz}} = \min\left\{\text{ET}, \frac{H_{\text{vz}} - \theta_{\text{wp}} n [z - z_{\text{dat}} - \min(h, z - z_{\text{dat}})]}{dt}\right\}. \quad (14)$$

TP concentration

The long-term time rate of change of TP concentration is governed by dispersion, ET, lateral advection, advection perpendicular to the model domain by downstream flow, rainfall, runoff, and sequestration in peat:

$$\frac{\partial C}{\partial t} = D_c \frac{\partial^2 C}{\partial x^2} - \frac{C}{H_{\text{tot}}} \frac{\partial \tilde{V}}{\partial t} + \frac{1}{H_{\text{tot}}} \frac{\partial \tilde{M}}{\partial t} \quad (15)$$

where \tilde{M} and \tilde{V} are the mass of P and volume of water per unit area. Short-term sequestration of P in live standing vegetation is not simulated. D_c is the dispersion coefficient for P in water, calculated as an average of dispersivity in surface water and pore water (Appendix B), weighted by the height of the equivalent column of open water. Over the range of velocities simulated (Appendix B), D_c is assumed not to vary with velocity. H_{tot} is the equivalent height of a water column with a cross-sectional area equal to that of the domain cell, formed from all water within the cell:

$$H_{\text{tot}} = n \cdot \min(z - z_{\text{dat}}, h) + H_{\text{vz}} + \max(h - z + z_{\text{dat}}, 0) \quad (16)$$

where the first term is the saturated portion of pore water, the second term is the unsaturated portion of pore water, and the third term is surface water.

Expanding Eq. 15, the time rate of change of water volume per unit area is written as the sum of the change in volume due to lateral flow, ET, precipitation, and runoff, respectively:

$$\frac{\partial \tilde{V}}{\partial t} = S_y \left(\frac{\partial h}{\partial t}\right)_{\text{lat}} - \text{ET} + \bar{P} + \bar{R}. \quad (17)$$

Second, the time rate of change of mass per unit area can be expanded into a sum of a lateral advection term, “new water” input, through-flow advection, and peat sequestration term, respectively:

$$\begin{aligned} \frac{\partial \tilde{M}}{\partial t} = & K \frac{\partial}{\partial x} \left(C \times h \frac{\partial h}{\partial x} \right) + C_{bg}(\bar{P} + \bar{R}) + (C - C_{bg}) \\ & \times \frac{v_{sw} \max(h - z + z_{dat}, 0) + v_{pw} n \min(z - z_{dat}, h)}{dy} \\ & - a_n \text{NPA} \end{aligned} \quad (18)$$

where dy is the unit thickness of the model cell perpendicular to the domain, and v_{sw} and v_{pw} are the downstream velocities of surface water and pore water, respectively. Since this model simulates a ridge head, through-flow replaces local concentrations with background TP concentrations (C_{bg}) from upstream. Lastly, a_n is a binding constant governing TP sequestration in peat or release from peat during periods when low water levels result in net peat oxidation. The value of a_n varies with the TP concentration of the water and was obtained from observations of the rate of accumulation of TP in peat along the WCA-2A transect (Craft and Richardson 1993b, Reddy et al. 1993, Kadlec 1994), to which we fit a logarithmic curve using least-squares regression (Appendix D). Based on this data, the rate of peat accretion along the transect, and TP along the transect, a_n was calculated as a function of TP in water, as displayed in Appendix D.

Periodic boundary conditions are imposed for lateral transfers that extend across the entire model domain. For lateral advective transport in pore water during periods when both a below-ground water table and free water surface are present, specified concentrations equal to TP concentration in the well-mixed surface water are imposed on false nodes at the edges of the pore water domain.

Model solution and sensitivity

PeatAccrete solves the governing equations with a forward difference, staggered grid scheme, in which some variables are calculated at cell boundaries whereas others are calculated at cell centers to improve numerical accuracy (Fornberg 1990). Initial conditions consist of a spatially uniform P concentration set equal to the background concentration and a surface-water level specified by Eq. 6 for $t = 0$. We initialized the model domain with a rectangular or sinusoidal proto-ridge with a maximum elevation above the fixed threshold for sawgrass growth. Spatial and time steps, listed in Appendix B, were checked for stability and convergence ($\Delta\text{NPA} < 1\%$ with further change in spatial/time step). We evaluated the sensitivity of the simulated net rate of peat accretion at the center and edge of ridges to model parameters and present the results in Appendix F.

MODEL RESULTS AND DISCUSSION

Sensitivity test results

Based on sensitivity analyses (Appendix F), ridge growth rate is most sensitive to background P concentration, followed by amplitude of the annual water level

fluctuations and hydraulic conductivity. These variables each lead to a change in the rate of NPA of at least 0.05 mm peat/yr over the expected range of parameter variation. Porosity, specific yield, background flow velocity, wilting point, P dispersivity, and the threshold elevation for sawgrass growth are less sensitive parameters over the expected range of variation.

Model output

Fig. 6 shows typical model results for the evolution of peat topography over approximately 274 years of simulation (A and B) and for the evolution of TP and water level over one year of simulation (C and D), using redox formulation B1 (Appendix E). Temporal changes in TP and water depth (from 6000 to 6800 $\mu\text{g P/m}^3$ for long-term simulations and 0 to 1.5 m, respectively) occur seasonally due to evapotranspiration and precipitation. The shape of TP and water table profiles also change interannually over ~ 274 years of simulation when $D_{sed} \neq 0$, reflecting the progressively more rounded morphology of the ridge (Fig. 6B). In contrast, when $D_{sed} = 0 \text{ m}^2/\text{d}$, the shape of the ridge and TP profiles remain approximately constant over the long term (Fig. 6A).

Inability of Peat Accrete to reproduce a stable characteristic ridge width and wavelength

Water table mounds that result from relatively low evapotranspiration on ridges compared to open-water evaporation (German 2000) form underneath ridges during the dry season (Fig. 6C). During these times some evaporative concentration of P within ridges occurs but does not significantly elevate ridge TP concentrations over slough TP. The predicted increase in TP from slough to ridge (12%) lies within the 95% confidence intervals of two independently observed values of percentage increase in TP from slough to ridge within the RSL. Ross et al. (2006) observed a mean elevation of ridge soil TP over slough soil TP (assumed proportional to pore water TP in accordance with Pan et al. [2000]) of 13%, while our measurements of pore water TP (L. G. Larsen, *unpublished data*) within the best-preserved portion of the RSL indicate a mean dry-season difference of 14%. These results contrast with Rietkerk et al.'s simulation of the nutrient accumulation mechanism in bogs (2004), where cones of depression under transpiring vegetation draw nutrients away from open-water areas, restricting outward expansion and causing vegetation patches to reach equilibrium widths.

Instead, the present numerical experiments reveal that a differential peat accretion feedback alone cannot control ridge width. For example, when we experimentally increase ridge width from 30 m to 70 m, net rates of peat accretion at ridge edges do not vary significantly, changing by less than $1 \times 10^{-3} \text{ mm/yr}$. Due to the limited spatiotemporal variability in TP in these oligotrophic model runs (representative of the pre-drainage Everglades), changes in ridge NPA are dominantly correlated with changes in water table

elevation (Fig. 6D). Thus, the lack of response in NPA arises directly from the lack of change in the general shape of water table mounds under ridge edges as ridge width changes.

In the absence of negative feedback between ridge width and NPA rates at ridge edges, ridges tend to expand into sloughs over time in our simulations. This gradual expansion occurs because gravitational erosion spreads some of the sediment originating from ridge tops in a diffusion-like process. Without gravitational erosion, ridge edges remain stable as the result of a static threshold elevation within the ridge/slough transition zone below which sawgrass cannot grow because of unfavorable inundation depths and duration. In contrast, with a diffusive erosion process, some of the sediment from ridge tops is redistributed to transition areas and sloughs, slightly increasing their local elevations and allowing sawgrass to expand laterally. Subsequently, the newly colonized regions are subject to higher rates of NPA, causing ridges to continue expanding upward and ultimately outward.

Clearly, because paleoecological evidence indicates that ridge widths remained stable over millennia given relatively constant climatic conditions (Willard et al. 2001, Bernhardt et al. 2004), the mechanisms and feedbacks simulated in PeatAccrete are incomplete representations of reality. In the natural system, it is likely that a feedback not simulated in this model counteracts the tendency for ridge expansion. It is less likely that diffusion-like gravitational erosion simply does not occur. Since peat is formed from detritus, a portion originates as loosely consolidated material prior to its compaction. This material, as mentioned in *Development of a conceptual model for the origin and stability of the Everglades RSL: Differences between the RSL and classical anabranching streams*, is relatively prone to entrainment through bioturbation, shear, and thermal overturn. During its original settling to the bed from its point of origin in the water column or following an entrainment event, this detrital material would be subject to gravitational transport. Indeed, preliminary evidence in support of this process lies in a biochemical characterization of floc in Everglades National Park sloughs that revealed a strong sawgrass signature (Neto et al. 2006).

Because our numerical simulation of differential peat accretion and gravitational transfer of sediment could not reproduce laterally stable ridges, we conclude that these feedback processes alone are insufficient to produce historic RSL morphology. Instead, our conceptual model leads to the prediction that the tendency for ridges to expand outwards is counteracted by flow redistributing sediment from sloughs and ridge/slough transition zones to sawgrass regions. To some extent, this process completes a bi-directional exchange, in which some of the ridge sediment transported to sloughs by gravitational transfer would be redistributed to ridges by the flow. Again, preliminary evidence for this bidirec-

tional exchange arises from Neto et al. (2006), who found greater sawgrass influence in the floc organic matter within sloughs than in the underlying peat sediment.

In addition to providing lateral stability, feedback between a sediment redistribution process, landscape morphology, and flow could also explain the attainment of a characteristic ridge width, which was not produced with the PeatAccrete simulation. If sediment redistribution by flow is insufficient to counteract ridge expansion, gradual ridge widening across the landscape would result in narrower sloughs, promoting slightly higher average depths, flows, and shear stresses, until the tendency for ridge expansion was again in balance with sediment redistribution (Fig. 4).

Another discrepancy between PeatAccrete model results and the historic RSL lies in the inability of PeatAccrete to effect landscape adjustment to a characteristic wavelength. To determine whether a field of closely-spaced, sinusoidal proto-ridges would evolve to a mature state with a different characteristic wavelength, we ran a simulation in which we initiated the model domain with proto-ridges of amplitude 15 cm and period 2 m. These characteristics are consistent with the geometry of longitudinal bedforms formed by secondary circulation processes in rivers, coastal areas, and estuaries (Karcz 1981, Allen 1982), which scale with water depth (Richards 1982). Instead, within 10 000 days, this simulated field of proto-ridges evolved into a flat, uniform surface. Thus, even when coupled to secondary circulation processes, which are common in wetland environments (Nepf and Koch 1999), the differential peat accretion mechanism lacks a process for ridge initiation and wavelength evolution.

Overall, discrepancies between the PeatAccrete simulation and the historic RSL provide the rationale for moving forward with experimental characterization and comprehensive numerical simulation of local flow and sediment transport in the RSL.

Evolution of stable elevation differences between ridge and slough

Though the feedback processes simulated with PeatAccrete could not capture all of the important characteristics of the pre-drainage RSL, they could reproduce some key aspects of historic landscape morphology, such as the evolution of a stable elevation difference between ridge and slough. This evolution can be observed from Fig. 7, which shows a family of NPA vs. ridge elevation curves associated with specific groupings of parameter values (Appendix E). NPA values were averaged over the second year of a simulation of an initially flat proto-ridge. While the sensitivity of the model to redox-depth relations is apparent, several mechanistic conclusions arise from an examination of this figure. First, in all model formulations, a stable equilibrium ridge height exists relative to sloughs, denoted by an "S" in Fig. 7. At this equilibrium the average NPA rates on ridge and slough are

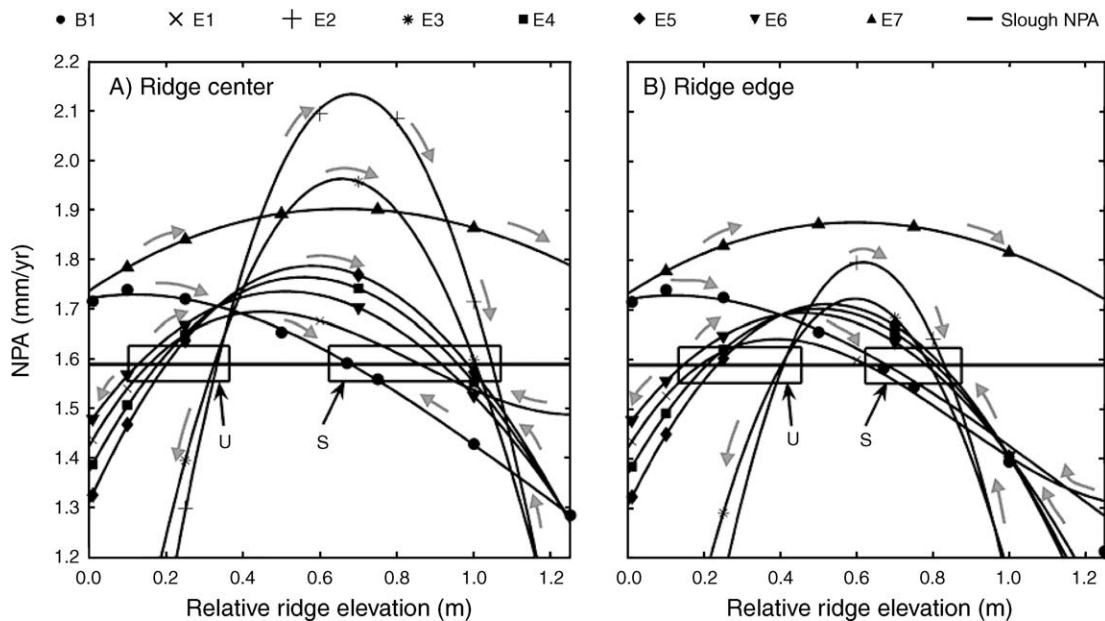


FIG. 7. Net peat accretion (NPA) vs. ridge elevation at (A) ridge center and (B) ridge edge for different possible depth/redox potential relationships (Appendix E) for the oligotrophic Everglades (Table 3). Data points represent individual simulation results, grouped by their association with a unique set of parameter values. Smooth curves are cubic least-squares regressions for each set of simulation results. The relative ridge elevation for each point is the elevation at which the simulation was initialized, and NPA was determined from the second year of simulation. Note that curves do not directly show temporal evolution of ridges, but temporal evolution is implied by the gray arrows indicating the direction of ridge growth (relative to slough growth) over time. Boxes indicate the loci where the family of curves cross the mean rate of NPA in sloughs, at which the rate of NPA on ridges and sloughs is equivalent. The box labeled “U” corresponds to the family of unstable equilibrium points, which physically correspond to required initiation heights for ridge growth under this differential peat accretion feedback mechanism. The box labeled “S” corresponds to the family of stable equilibrium points, which physically correspond to equilibrium ridge heights. Ridges initiated anywhere to the left of “U” approach the stable equilibrium height “S” with respect to slough bottoms, whereas ridges initiated to the left of “U” subside and become indistinguishable from the slough.

equivalent. This stability arises directly from the shape of the response curve of sawgrass NPA to changes in water level, as predicted earlier. When the ridge is displaced downward from its equilibrium elevation, the effective hydroperiod increases, and mean rates of NPA increase (Fig. 5) until the equilibrium relative elevation difference between ridge and slough is again attained, and vice versa. The attainment of an equilibrium height under this mechanism is consistent with the finding that differential rates of peat accretion in bogs cause hummocks to reach an equilibrium height that can be accurately predicted with a model (Nungesser 2003). While caution should be exercised in any quantitative interpretations of the model, most of the redox potential/depth formulations predicted an equilibrium ridge height above sloughs in the 0.6–1.0 m range, which is consistent with historical observations (Science Coordination Team 2003). Other ranges of equilibrium heights could be attained by adjusting the redox-potential–depth relationship.

Fig. 7 also predicts a ridge initiation height for many formulations (e.g., E1–E6). Proto-ridges below this threshold elevation will accrete peat more slowly than the slough bottom and subside, whereas proto-ridges above this threshold will accumulate peat more rapidly

than the slough bottom and approach the stable equilibrium. Dynamically, the initiation height is an unstable equilibrium point, denoted in Fig. 7 by “U.” Thus, the model suggests that some other process (e.g., sediment deposition, tussock formation) needs to initiate ridges. It is also likely that biological or geochemical factors not accounted for in the model (such as a minimum amount of time the peat surface needs to be exposed to air for sawgrass to germinate) play a role in determining an initiation height or preventing the growth of sawgrass.

While PeatAccrete predicts the attainment of an equilibrium ridge height, the numerical value of that height differs laterally across the ridge, with ridge centers attaining a higher equilibrium height than ridge edges (Fig. 7), leading to a rounded morphology that reflects the shape of the dry-season water table mounds (Fig. 6B), consistent with the shape of raised bogs (Ingram 1982). However, anecdotal observations (Science Coordination Team 2003) point toward roughly flat ridges in the pre-drainage Everglades, and even topographic surveys conducted in the best-preserved portion of RSL in WCA-3A (Appendix G) do not show the roughly 20-cm difference between ridge center and edge that the model predicts, lending support to the

TABLE 3. PeatAccrete simulation results from P enrichment, increased/decreased hydroperiod amplitude, and increased/decreased redox potential experiments.

Experiment	Redox potential–depth relationship	Max. NPA, center (mm/yr)	Initiation height, center (m)	Equilibrium height, center (m)	Equilibrium height, edge (m)
No change	B1	1.73	0	0.68	0.67
P enrichment	B1	1.88	0	0.91	0.87
Decreased hydroperiod amplitude	B1	1.79	0	0.48	0.50
Increased hydroperiod amplitude	B1	1.64	0	0.74	0.66
Decreased redox potential	B1	1.75	0	0.84	0.78
No change	E6	1.74	0.13	0.92	0.78
P enrichment	E6	1.87	0	1.06	0.93
Decreased hydroperiod amplitude	E6	1.92	0	0.79	0.73
Increased hydroperiod amplitude	E6	1.52	0	0–ridge drowns	0
Decreased redox potential	E6	1.89	0.11	1.22	1.05

Notes: Cases of redox potential–depth relationship are described in Appendix E. NPA indicates net peat accretion.

hypothesis that flow redistributes sediment from sloughs to ridge edges. Reducing lateral erosion by setting D_{sed} near zero can also result in relatively flat ridges (Fig. 6A).

Model interpretation of RSL degradation

By perturbing model parameters in PeatAccrete, effects of select anthropogenic changes on landscape morphology via the differential peat accretion feedback mechanism and gravitational erosion can be simulated. From the agreement between characteristics of the historic Everglades and results from simulations run with inputs consistent with the pre-drainage Everglades, it appears that the simulated feedback processes dominate the vertical dimensionality of the landscape (i.e., the attainment of a stable equilibrium elevation difference between ridges and sloughs). Characteristics of the transition zone between ridge and slough are expected to be governed by another process. The topographic flattening that has been observed in the Everglades may be explained either by vertical phenomena (i.e., ridges flattening or sloughs filling in) or by lateral phenomena (i.e., ridges expanding). Perturbations to the PeatAccrete model can provide insight into some of the potential causes of degradation of the former type, while a complete numerical simulation would be necessary to fully quantify the dominant factors causing RSL degradation.

Even without fully simulating the dual feedback processes that we propose regulate landscape morphology in the RSL, PeatAccrete model results imply the importance of vertical landscape phenomena relative to lateral phenomena. Anabranching river-type feedback processes are expected to regulate ridge width, but in the absence of sediment transport by flowing water, the PeatAccrete model results depicted in Fig. 6B show that ridge edges expand into sloughs at the rate of only 1–2 m per century, assuming that sawgrass can colonize peat at a threshold elevation of 10–20 cm above slough bottoms. Compared to the 100-m-scale spacing of ridges, this order-of-magnitude expansion rate is insufficient to fully explain landscape degradation over the

past century, indicating that processes causing disturbance to vertical landscape processes (i.e., the differential peat accretion feedback mechanism) likely contribute significantly to landscape degradation. As we will describe, ridges may decrease in elevation relative to sloughs and sloughs may increase in elevation relative to ridges as a result of hydrologic and water quality changes consistent with anthropogenic impacts to the Everglades over the past century. These changes may have further contributed to the widespread disappearance of sloughs by facilitating the emergence of new sawgrass ridges within former slough environments.

PeatAccrete predicts that under temporally constant input parameter values (Appendix B), an equilibrium ridge elevation with respect to sloughs evolves. Sensitivity tests (Appendix F) indicate that perturbations to certain input parameters can cause the location of the equilibrium ridge elevation to shift, resulting in taller or shorter ridges. Furthermore, perturbations to input parameters may also alter the location or existence of the unstable equilibrium point (Fig. 7) corresponding to the minimum initial height of proto-ridges that will mature to a stable ridge at the equilibrium height under the differential peat accretion feedback mechanism. Using PeatAccrete, we examined effects of changes to input parameters consistent with the major anthropogenic influences over the past century: P enrichment, altered hydroperiod amplitude, and altered redox-potential–depth relations. We performed these numerical experiments on two different base cases from Appendix E: B1 and E6. In the P enrichment experiments, background concentrations of P were increased from 6 $\mu\text{g/L}$ to 8 $\mu\text{g/L}$. The altered hydroperiod experiments perturbed the amplitude of surface water stage from a base value of 1.5 m to 1.0 m and 2.0 m while maintaining the same minimum water level. Finally, we explored the effects of anthropogenically lowered redox potentials, which are associated with eutrophication processes and sulfate contamination from agriculture (Bates et al. 2001). Anthropogenically lowered redox conditions would be manifested as a

downward shift in the depth required to maintain a particular redox potential. We explored the effects of a downward shift of 10 cm, which is associated with the regression coefficients for the NPA–depth relationship listed in Appendix E for cases CRP1 and CRP2.

Results from all anthropogenic modification experiments are reported in Table 3. Lowered redox potentials, P enrichment, and increased hydroperiod amplitude/higher mean water levels all have similar impacts on ridge morphology in that they increase equilibrium ridge height with respect to slough bottoms, resulting in taller ridges. None of these perturbations, then, can contribute to a flattening of RSL topography by decreasing ridge elevations, unless increased NPA on ridges reflects a similar increase in the supply of unconsolidated sediment subject to lateral spreading by gravitational erosion. In this case, sediment supply may overwhelm the ability of the system to transport sediment, leading to slough infilling and/or ridge expansion. A decreased hydroperiod amplitude/lower mean water level, on the other hand, can contribute to topographic flattening by decreasing ridge elevations with respect to sloughs. Decreased equilibrium ridge elevations, however, cannot explain the complete loss of topographic heterogeneity and colonization of sloughs by sawgrass that has been observed in many portions of the RSL, indicating that slough infilling processes must also be occurring.

PeatAccrete predicts that several factors may lead to replacement of slough with ridge vegetation. Model results indicate that increased background P concentrations and reduced hydroperiod amplitudes could contribute to slough infilling and landscape degradation by decreasing the initiation height required for ridge growth, thereby facilitating the emergence of new ridges. At this stage in model development, PeatAccrete does not simulate changes in NPA within sloughs in response to external drivers, although we recognize that a number of factors could affect autochthonous NPA rates in sloughs, stimulating infilling (summarized in Table 2). For example, the assumption of constant NPA may be violated under sustained P enrichment or altered redox conditions. If perturbations are not sufficient to induce a change in species assemblages, Table 2 indicates that low redox potentials/high water levels will likely induce higher slough NPA. Due to increased decomposition rates, P enrichment alone may not induce slough infilling, but when coupled to lower redox potentials and/or a shift in vegetation to a higher abundance of emergent species, higher NPA will likely result. Sustained high redox potential/low water level may also shift the balance of slough vegetation to emergents, increasing productivity, decreasing decomposition, and increasing NPA. If such vegetation shifts occur, anabranching river-type feedbacks could further contribute to slough infilling through enhanced sedimentation around macrophyte stems and roots relative to the former deep-water slough. Finally, allogenic processes

(i.e., sediment transport) may contribute to rates of NPA in sloughs. If sediment entrainment within sloughs was a significant process historically, the mean rate of NPA assigned to sloughs in the model would have implicitly incorporated this process. A present-day decrease in sediment entrainment would therefore cause a higher relative NPA in sloughs than that employed in PeatAccrete, possibly contributing to infilling.

To summarize, PeatAccrete model results show that decreased mean water levels may decrease ridge elevations, diminishing the relief between ridge and slough. Results also indicate that the emergence of new ridges due to a downward shift in ridge initiation heights resulting from P enrichment or lower redox potentials may further contribute to the widespread disappearance of sloughs. Though not directly simulated in PeatAccrete, greater rates of NPA in sloughs resulting from decreased redox potentials, P enrichment, a shift in slough communities to emergent species, and allogenic processes such as diminished entrainment of sediment may also lead to topographic flattening. Thus, the widespread P enrichment, decreased water levels, and sulfate contamination leading to more reduced redox potentials that have affected portions of the Everglades over the past century may have all served as drivers of landscape degradation. Decreases in flow velocity likely also contributed to ridge widening, but not at a rate sufficient to completely overtake sloughs in the past century. Further work will be necessary to quantify whether decreased flows have decreased sediment entrainment within sloughs to the extent that slough NPA is sufficiently increased to permit sawgrass colonization.

SUMMARY

Whereas the morphology of boreal bogs results from feedback between differential peat accretion rates governed by nutrient concentration and water level, and the morphology of anabranching rivers results from feedback between sediment supply, flow rates, and sediment deposition, it is apparent that both feedbacks must be involved in the maintenance of stable landscape heterogeneity in the RSL. Specifically, based on a synthesis of the literature, anabranching river theory can explain the initial pattern formation of the RSL, the evolution of stable, characteristic ridge widths and wavelengths, and, likely, the flat cross-sectional profiles of ridges. Meanwhile, PeatAccrete model results indicate that nutrient concentration and water level govern the equilibrium height difference between ridge and slough. Historically, the landscape adjusted to a morphology in which the capacity for sloughs to transport organic sediment downstream and to ridges balanced in situ organic matter production and gravitational erosion such that rates of NPA were spatially constant.

Perturbations to either the differential peat accretion or anabranching river-type feedback mechanism can contribute to the topographic flattening that is prevalent

in degraded portions of the Everglades RSL. Predicted rates of ridge expansion in the absence of sediment transport are an order of magnitude slower than the rate of slough disappearance in portions of the landscape, indicating that disturbances to the vertical peat accretion processes likely play a significant role in landscape degradation. The differential peat accretion feedback mechanism is most sensitive to P concentration, hydroperiod amplitude/mean water level, and soil redox potential, in descending order, with decreased mean water levels resulting in lower equilibrium ridge heights relative to slough. To explain widespread slough disappearance over the past century, it is necessary to invoke slough infilling processes. P enrichment and decreased redox potential may contribute to slough infilling by facilitating the emergence of new ridges and increasing rates of peat accretion within sloughs. Decreased entrainment of slough sediment resulting from decreased flow may further increase the effective NPA within sloughs.

Both the conceptual and numerical model provide insight into restoration issues, for they indicate that if natural surface water depths, durations, and flow velocities are restored in areas of the landscape with some remaining topographic heterogeneity, it is likely that the differential peat accretion mechanism will eventually produce an stable, equilibrium landscape reminiscent of, if not identical to, the historical landscape. However, due to relatively high rates of NPA and sediment capture by vegetation stems in areas where sawgrass monocultures are prevalent and topographic heterogeneity has been lost, it is unlikely that hydrologic management can regenerate sloughs, unless sloughs are seeded by fire, drowning, or mowing. We also emphasize the importance of maintaining unenriched water chemistry with restored flows and hydroperiods, for, as PeatAccrete model results show, P enrichment leads to lower ridge initiation heights, allowing sawgrass to grow on some former slough bottom locations. By extension, P enrichment may also lead to lower redox conditions and/or slough species shifts, thereby decreasing decomposition rates in sloughs, increasing productivity, and stimulating infilling.

In the short term, the RSL appears more sensitive to changes in water level and redox potential than to changes in flow, due to the relatively long time scales of ridge expansion in the complete absence of sediment transport. Pragmatically, reinstatement of natural surface water depths, durations, and redox potentials may thus more effectively halt landscape degradation in the short term than restoration of pre-drainage flow velocities. However, in the long term, flows that induce sediment transport will likely be necessary to halt gradual ridge widening processes and possibly to restore the historic balance between ridge and slough NPA.

Recognition of the applicability of the anabranching river theory and differential peat accretion mechanism

to the RSL highlights future research priorities to arrive at a more quantitative understanding of landscape functioning. Improved knowledge of the relationship between water depth and redox potential, as well as of the specific multivariate relationship between P concentration, hydrology, and NPA rates in ridges and sloughs can allow for quantitative use of the PeatAccrete model. A greater understanding of biological and geochemical controls on sawgrass growth initiation and restriction is also needed. Finally, to quantify the role that anabranching river-type feedbacks play in the RSL, future research should focus on shear stresses and turbulence intensities required for sediment entrainment and transport, as well as on sediment capture efficiency by emergent vegetation under different flow regimes. With this information, a comprehensive, landscape-scale numerical model can be developed that will allow for more accurate predictions of landscape response to changes in ecosystem drivers.

This paper presents a new framework for analysis of the RSL and highlights two simple feedback mechanisms that likely govern landscape biogeomorphology. Both the anabranching river feedback and differential peat accretion feedback are expected to similarly govern the morphology of peatlands elsewhere with significant unidirectional flow, high seasonality, and shallow slopes/vegetation assemblages sufficient to prohibit the development of cross-gradient patterning.

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APPENDIX A

Review of factors affecting sediment supply and net peat accretion in the Everglades (*Ecological Archives* M077-017-A1).

APPENDIX B

PeatAccrete model parameter values and sources (*Ecological Archives* M077-017-A2).

APPENDIX C

Sawgrass total biomass production vs. soil redox potential (*Ecological Archives* M077-017-A3).

APPENDIX D

Development of empirical model relations and constants for PeatAccrete (*Ecological Archives* M077-017-A4).

APPENDIX E

Depth/redox potential cases evaluated in model and corresponding regression coefficients for depth effect, $f(h - z)$ (*Ecological Archives* M077-017-A5).

APPENDIX F

Sensitivity analysis of model parameters (*Ecological Archives* M077-017-A6).

APPENDIX G

Peat surface topography across two ridge/slough transects in the best-preserved portion of the ridge and slough landscape in WCA-3A (*Ecological Archives* M077-017-A7).