

HYDROLOGIC CONTROL ON ECOSYSTEM METABOLISM:  
LOCAL PROCESSES AND LANDSCAPE DYNAMICS IN THE EVERGLADES  
RIDGE-SLOUGH

By

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To Science!

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Danielle Leyanne Watts

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Tropical and sub-tropical peatlands represent a globally important carbon store where persistent higher temperatures release carbon budgets from this control and render other environmental factors more influential to ecosystem carbon budgets. The ridge-slough mosaic in the Everglades is a lotic subtropical peatland that has undergone significant ecological change in the 20<sup>th</sup> century response to both hydrologic drainage and impoundment. These changes are reflected in a degradation of the metrics associated with patch stability and self-organized patterning, primarily the vertical differentiation of peat elevations. The de-coupling of the peat topography from the limestone suggests autogenic controls maintain ridge and slough differentiation, although it does not speak to the particular geometry of ridge-slough patterning.

Here, I investigate local and regional variation in hydrologic controls on carbon dynamics, and hence peat accretion dynamics, in this landscape. I do so via investigations into soil and ecosystem carbon exchange using closed chamber methods across a hydrologic gradient in Water Conservation Area 3. I further investigate the role ridge vegetation plays in inducing evapotranspiration scale-dependent feedbacks to

nutrient availability. The culmination is a model that explores what is known about the carbon budget and evaluates the conditions for vertical differentiation between ridge and slough configurations. Results indicate that 1) the landscape-scale modifications to hydrology have altered carbon cycling in the region; 2) the central portions of the Everglades retain a potential for long term carbon accretion; 3) peat elevation differences and a highly connected water table create conditions for convergent flow of water, and hence a nutrient subsidy, to ridges that is scaled to patch size; and 4) despite a higher peat accretion potential in ridges, the long-term maintenance of peat elevation differences is induced by interannual hydrologic variability.

## CHAPTER 1 INTRODUCTION

### **Patterned Peatlands**

Peatlands are estimated to cover around 3% of the world's total land area, making up approximately 50% of all wetlands, and storing around 25% of the world's terrestrial carbon (Wigley and Schimel 2000). These peatlands are found in nearly every part of the world, from the extensive peatlands in the arctic and boreal regions, to tropical peatlands in Indonesia, Latin America, Africa, and the Caribbean. Peatlands are of increasing interest due to both their potential for long-term carbon storage (Page and others 2002; Jaenicke and others 2008) and their role in our understanding of long-term ecosystem equilibria (Clymo and others 1998; Rietkerk and others 2004). The value of peatlands derives from the burial of incompletely decomposed plant material under water logged conditions leading to carbon accumulation lasting for thousands of years. For example, radio carbon dating of sub-coastal peatlands in Borneo suggests they started accumulating peat around 27,000 years ago (Page and others 2004). The biological and hydrological interactions that lead to peat accretion - where productivity (P) that exceeds decomposition (or respiration, R) - lead to myriad types of peatlands and peatland configurations which can have substantial influence on regional water patterns (e.g. Watters and Stanley 2006), biodiversity, and large-scale C fixation.

Many peatlands are a matrix of multiple ecosystems, forming a regular spatial pattern in communities and peat characteristics; examples include the Great Vasyugan Bog in Siberia, Glacial Lake Agassiz Peatland, Minnesota, and the Everglades, Florida (Figure 1-1). Each patch type is a stable ecosystem arrangement given local environmental conditions. Patterned peatlands occur where conditions allow for a single

regional peat accretion rate to be achieved under different ecosystem configurations and where each configuration is self-inhibitory at a larger distance. Importantly, the regional peat accretion rate may be zero (i.e., the peatland complex is at neutral long-term carbon equilibrium), or may be positive (i.e., the peatland elevation is increasing; Clymo and others 1998; Brady 2002). Regardless of the accretion rate, the different ecosystem configurations generally consist of a higher production, higher respiration state and a lower production, lower respiration state that form distinct microtopography with each patch type occupying different elevation modes.

The ridge-slough patterned peatland in the Everglades provides an excellent model system for testing the hypothesis that the dominant ecosystems in a patterned peatland represent alternative configurations to achieve carbon equilibrium with the regional landscape. Further, the presence of a hydrologic gradient from modern hydrologic modification of large portions of the Everglades allows for tests of deviations from this equilibrium. The existence of multiple peat accretion equilibria has been proposed (SCT 2003; Larsen and others 2007) but never explicitly tested in this landscape.

Successful restoration of the Everglades ridge-slough will require a quantification of the hydrologic conditions under which elevation differences and patterning between ridges and sloughs can be maintained. The recent (~100 years) drainage and impoundment of the ridge-slough landscape provides a living laboratory for the control hydrology has on carbon dynamics with some areas being much drier than historical conditions and others much wetter. Since restoration success is predicated on 'getting the hydrology right', the hydrologic gradient present in the Everglades provides both an

opportunity for understanding alternative state stability in a subtropical wetland and a unique opportunity to study the drivers behind state stability loss. Enumerating the rates of productivity and respiration as a function of local and regional hydrology is of intrinsic restoration value. The Comprehensive Everglades Restoration Plan (CERP) has several performance measures related to the ridge-slough landscape, including the stability of the ridge-slough vegetative patterning, inundation patterns, with differing inundations of ridges and sloughs explicitly considered, and sheetflow measures, including timing and distribution of flows and flow volume and continuity. All of these performance measures necessarily consider the maintenance of elevation differences between ridges and sloughs as a component of successful restoration.

The overall objective of this dissertation is to investigate the carbon dynamics of the two dominant patch types in the ridge-slough patterned landscape along a gradient of hydrologic modification. To achieve this objective, I plan to test whether the two states in the best conserved Everglades are in equilibrium, and investigate the degree to which net autotrophy has been lost with hydrologic modification. I will do this via investigations into how respiration and primary productivity respond to hydrologic drivers, both in observation and by simulation modeling. The combined outcomes of these studies will be able to provide guidance about the hydrologic conditions necessary for the maintenance of elevation differences between ridges and sloughs.

## **Research Questions**

### **Ridges and Sloughs as Alternative Carbon Accretion Equilibria**

There are multiple lines of evidence that lead to the hypothesis that ridges and sloughs represent alternative carbon accretion equilibria. Ridges and sloughs appear to have existed as distinct communities for around 2,700 years (Bernhardt and Willard

2009). That the two communities have differing hydroperiod requirements and water depths suggests that the communities have also had differing peat elevations for the same length of time. Further, historic accounts of ridge-slough elevation differences suggest that ridges were 1 to 3 feet (30 to 91 cm) higher than sloughs (McVoy and others 2011), with an abrupt transition zone between patches.

In order to maintain long-term positive peat accretion rates and elevation differences, there are three hypothesized solutions to the carbon budget (Figure 1-2). Under historic hydrologic conditions, locations with elevations different from an equilibrium level are driven towards one of those equilibria by changes in peat accretion rates. For example, shallow water conditions will generally increase productivity on ridges in response to increased oxygen availability. However, oxygen availability also increases respiration rates, canceling out or surpassing the incremental increases in productivity. With lowered water levels, peat oxidation brings the soil elevation back to equilibrium. Similarly, sloughs at lower elevation than the equilibrium slough elevation will tend to accumulate peat more rapidly due to reduced exposure probability. The third intermediate configuration is unstable, because small environmental perturbations change the ratios of productivity to respiration (P:R) such that the system ends up driven to one of the stable configurations (i.e., ridge or slough). Note that while R is drawn in Figure 1-2 as a linear relationship with hydrologic conditions, the relationship need not be linear as long as it is monotonic.

The hypothesis proposing ridges and sloughs as alternative solutions to landscape peat accretion equilibrium invokes a homeostatic feedback between soil accretion, hydroperiod and soil redox. Increased peat accretion shortens hydroperiod

and increases soil redox potential, in turn inhibiting peat accretion via accelerated respiration. Higher peat accretion potential in ridges is ultimately offset by increased peat exposure caused by being situated higher in the water column. As ridge elevation increases, hydroperiod decreases (approx. 310 days in the best conserved areas; Watts and others 2010), exposing peat in ridges to longer and more frequent periods of oxidation. Sloughs in contrast are rarely exposed (approx. 350+ day hydroperiod), at least where hydrologic conditions are thought to best approximate pre-drainage conditions (Givnish and others 2007; Watts and others 2010). The balance of these positive and negative feedbacks produces two alternative attractors (high productivity-high respiration and low productivity-low respiration; Figure 1-2) whose similar net peat accretion explains the extended stability (>1000 years; Bernhardt and Willard 2009) of landscape patch configuration.

Nutrients reinforce and even induce patch differentiation in some patterned peatlands (e.g. Rietkerk and others 2004), and are inexorably linked to productivity differences between adjacent patches. The mechanism leading to higher nutrient availability in the higher-elevation patch is the convective transport of nutrients, induced by belowground hydraulic flow towards areas with greater transpiration. This mechanism results in a positive feedback between nutrients and plant biomass. A two-patch condition arises because the convergent flow of nutrients leads to nutrient limitation at some critical scale. The convective transport of nutrients, specifically phosphorus, in the Everglades has been modeled as an autogenic process helping to explain patch differentiation for tree islands (Ross and others 2006). A similar process may occur between ridges and sloughs, as suggested by the observation of higher soil

nutrient concentrations coinciding with the highest elevations where soil elevation bimodality is observed (Cohen and others 2009).

Demonstrating multiple peat accretion equilibria would provide mechanistic evidence for the existence of alternative stable states in the ridge-slough region, and aid in understanding the hydrologic requirements for landscape maintenance. The hydrologic gradient present in WCA 3A allows for an excellent natural experiment for these hypotheses. That is, directionality at the landscape-scale can be inferred from carbon budgets spanning the drained areas to the impounded areas. Further, such a study would give us the hydrologic regime within which both ridge and slough patches are stable at the point scale. This information would be vital to management and restoration strategies, where the goal is to maintain the historic ridge-slough patterning. It is evident that our understanding of the processes that create and maintain patterning in the central Everglades is incomplete. Regardless of the mechanisms consideration of the scale of their action and interaction is an important unknown.

### **Recent Hydrologic Modification and the Ridge-Slough Landscape**

The remarkable leveling of the peat surface under both drained and impounded conditions (Watts and others 2010) in the Everglades is clear evidence that recent (100 year) anthropogenic alterations in the regional hydrology have changed the underlying processes governing ridges and sloughs. The strong control hydrology has over peat accretion suggests that some of the leveling can be ascribed to altered carbon budgets. The draining of peatlands, where more of the peat experiences oxidation, can lead to a rate of subsidence that vegetative productivity cannot compensate for (examples include Galloway and others 1999; Gambolati and others 2006; Schipper and McLeod 2006). The loss of elevation differences between ridges and sloughs may be further

exacerbated by observed changes in community structure in the Everglades; deep-water sloughs are replaced by emergent prairie vegetation, which has higher productivity. Drained portions of the landscape are therefore experiencing the stress of excess respiration on ridges at the same times as increased productivity in the former sloughs.

The loss of bimodality in peat elevations with hydrologic impoundment likely has more to do with changes in the carbon balance on ridges than with changes in sloughs. Slough vegetation does not change markedly with impoundment, presumably because most of the species are adapted to permanently inundated conditions. In contrast, sawgrass is not well adapted to permanent deep inundation, and exhibits evidence of physiological stress and eventually patches dieback under deeper water conditions. Localized persistence of sawgrass in impounded areas is presumed to be due to observed upward extension of rhizome, a strategy that places the meristem at a depth that may periodically become exposed, but limits the lateral expansion of each individual. The result is the observed 'moth eaten' landscape (Figure 1-1D), which can be linked to the loss of the productive sawgrass. This upward extension cannot compensate for deeper and longer inundation, and bimodality in peat elevations is lost.

We lack both the historic (pre-20<sup>th</sup> century hydrologic modification) and modern carbon budgets necessary to evaluate the degree to which the landscape has degraded. The loss of landscape pattern has been inferred on many occasions by observing changes in community structure and vegetative patterns over time (examples include Wu and others 1997; Givnish and others 2007; Zweig and Kitchens 2008). State stability is inferred by robust vegetative patterning in these studies. The limitation of this

approach, however, is the implicit over-emphasizing of the role of productivity in this landscape; the role of respiration in regulating the ridge-slough pattern is as yet poorly understood (although see Debusk and Reddy 2003 for a laboratory study). An explicit consideration of the carbon budgets of ridges and sloughs along a gradient of hydrologic modification is the next step to understanding the underlying causes of pattern loss in the Everglades.

### **Research Aim**

In order to address the current gap in knowledge in the role of ecosystem carbon exchange in regulating microtopography in the Everglades, the following aim is formulated:

The aim of the dissertation is to investigate whether locally endogenous carbon budgets are sufficient to explain the divergence of elevations between ridges and sloughs.

### **Research Questions**

In order to reach the aim of the dissertation, the research can be divided into investigations of the following research questions:

1. Does respiration demonstrate a monotonic and inverse relationship to water depths, as described in Figure 1-2?
2. Do observations of ecosystem productivity corroborate the predictions from the s-curve relationship described in Figure 1-2?
3. Can productivity-induced differences in evapotranspiration reinforce patch differentiation in the ridge-slough?
4. What are the long-term implications of considering patches from the point-scale of Figure 1-2?

## **Research Approach**

### **Synergy Through Model and Measurement**

In this dissertation, a combination of empirical and modeling approaches is adopted. The empirical parts consist of field investigations of ecosystem scale carbon and water dynamics along a hydrologic gradient of regional drained through impounded hydrologic conditions. I use the a priori hypotheses generated by Figure 1-2, which differs fundamentally from hypotheses generated by data interpretation (Belyea and Lancaster 2002). Strong inference in ecology is criticized as assuming mutually exclusive competing hypotheses, where real ecosystems often exhibit properties of multiple competing hypotheses (i.e. non-exclusionary mechanisms; e.g. Quinn and Dunham 1983; Roughgarden 1983; Scheffer 1999). I am therefore cognizant throughout this dissertation that pattern mechanisms in the Everglades may not be exclusionary and that competing hypotheses may act at different times, scales, and further, that investigations into what maintains the Everglades ridge-slough may not be the same phenomena that gave rise to the Everglades ridge-slough initially.

The investigations in point-scale phenomena comprise of field measurements of instantaneous carbon fluxes and small-scale variability in diel water table in Water Conservation Area 3A. The spatial and temporal scales of Everglades patch dynamics preclude the sorts of manipulative experiments that can identify direct cause-effect relationships. Therefore, field measurements along a hydrologic gradient are chosen instead, with the aim of identifying whether variation in these variables is consistent with theoretical models. The sampling is along the hydrologic gradient described in Watts and others (2010), using 2x4km landscape blocks identified as Drained, Conserved 1

and 2, and Impounded. Each landscape block has distinct characteristics with regard to hydrograph, vegetative prevalence, and microtopography.

Modeling, both statistical and simulation, is used throughout this manuscript. The aims of all of the models are to investigate the implications of measured relationships to larger scales, primarily temporal. The integration of the simulations throughout provides synergy between the measured data and the larger scale of the research questions.

### **Manuscript Outline**

In Chapters 2 and 3, I investigate the ecosystem carbon dynamics using closed chambers equipped with an infra-red gas analyzer. Chapters 2 and 3 therefore answer the first two research questions about the relationships of ecosystem carbon dynamics with water levels.

In Chapter 4 I investigate the hypothesis that higher-elevation community (here, ridges) can induce convergent flow of water and nutrients to that patch. Until now, nutrient accumulation induced by patch differences in evapotranspiration has only been demonstrated in northern peatlands. I infer the potential of a subsidy of nutrients to ridges by investigating the connectivity of the water table as it recedes below the soil surface on ridges.

In Chapter 5 I test the theoretical predictions of Figure 1-2 at longer time scales. The model asks whether point-level processes can explain the microtopographic properties of the modern Everglades. The implication is if they cannot, then contagion properties induced by the spatial scale of patterning in the Everglades is necessary to re-create microtopographic separation between ridges and sloughs.

Finally, in Chapter 6 I synthesize the findings and discuss their implications for the future of the ridge-slough Everglades.

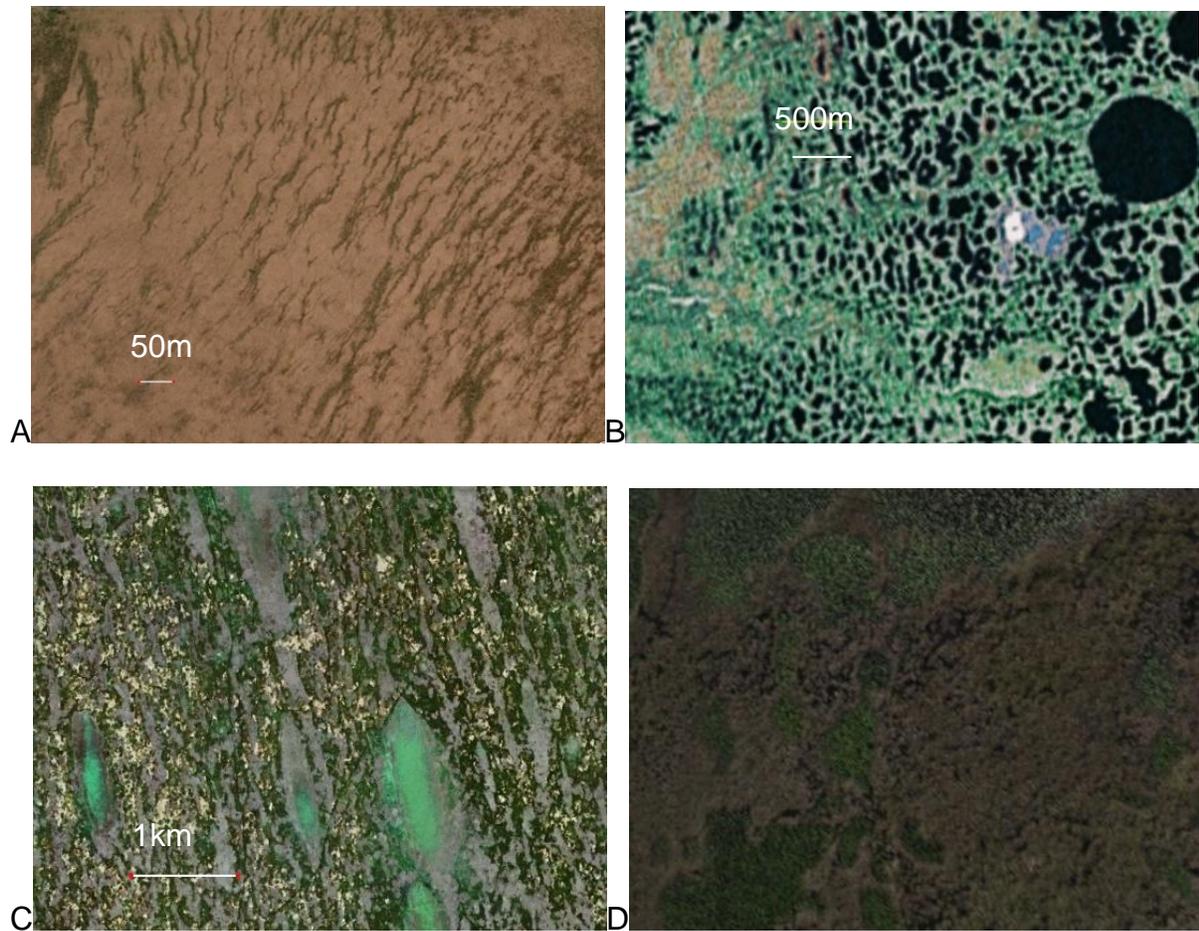


Figure 1-1. Patterned peatlands are a matrix of communities with corresponding differing peat elevations. Examples include A) Lake Agassiz bogs in Minnesota (USA), B) string bogs in the Yuganskiy Nature Reserve, Siberia, and C) the ridge-slough-tree island complex in the greater Everglades area, Florida (WCA 3AS shown). D) Hydrologic impoundment is associated with a “moth-eaten” characteristic of ridges (photo courtesy of UF Small UAV program). Ridge vegetation is pale brown, slough is green (*N. odorata* leaves) and black is open water (altitude 100 m). Figures A) B) and C) generated with SPOT imagery viewed with Google Earth (Google, Inc., Mountain view, CA, USA).

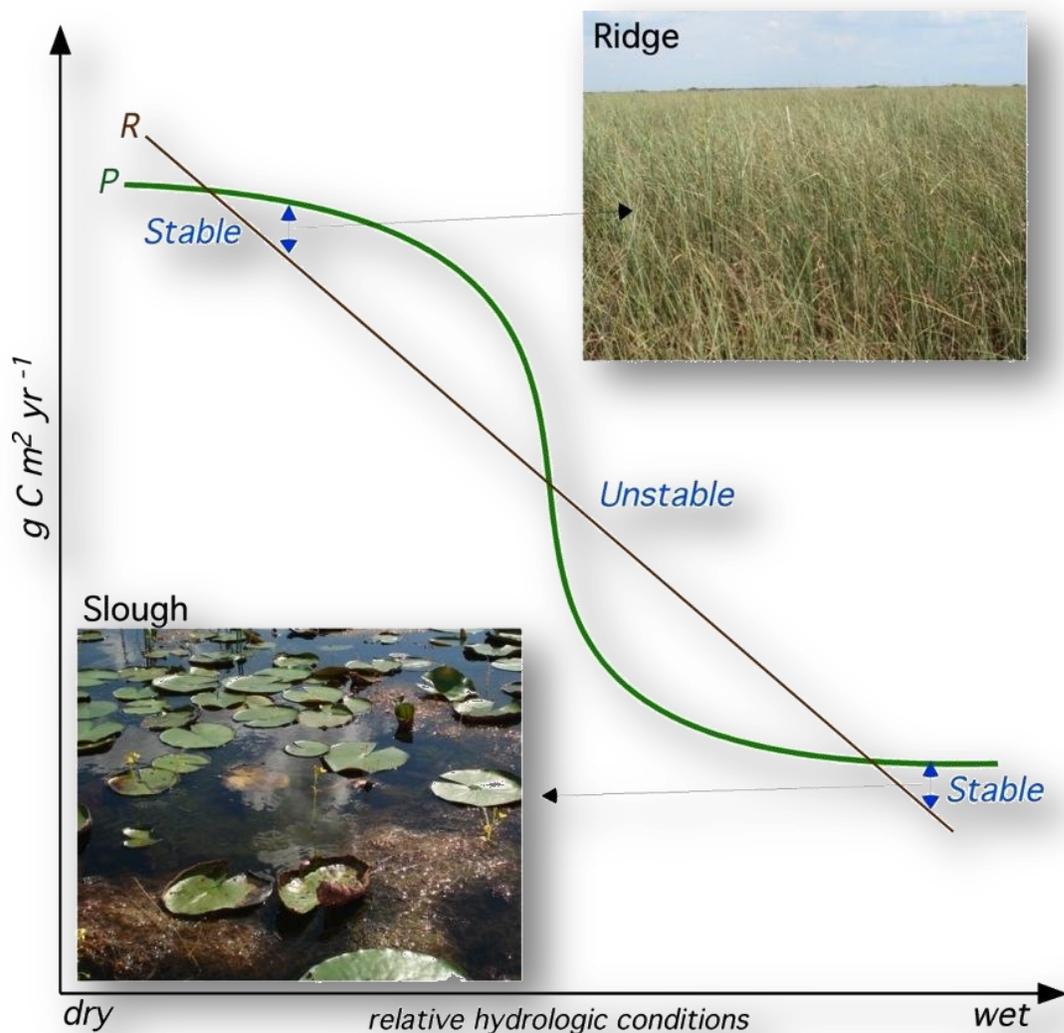


Figure 1-2. Hypothesized relationship between hydrologic conditions and carbon in the Everglades ridge-slough landscape. There is a range of water depths ideal for ridges and sloughs, where the ecosystem carbon balance will move towards the equilibrium state over any time period. At some intermediate level of hydrologic conditions, the vulnerability of the state to even small changes in hydrologic conditions leads to a lack of long-term stability; a point falling in this region will likely shift to either a ridge or slough state. The arrows between R and P represent three configurations to achieve a nominal landscape peat accretion rate. Images courtesy of D. Watts.

## CHAPTER 2 HYDROLOGIC CONTROLS ON CO<sub>2</sub> RESPIRATION IN A SUBTROPICAL PATTERNED PEATLAND

Peatlands are a globally important terrestrial carbon store (Wigley and Schimel 2000) and are under increasing risk due to anthropogenic change. These anthropogenic changes may be in the form of increased temperatures, artificially modified water tables, increased drought and fire risk, and altered timing and frequency of precipitation (1991; Oechel and others 1993; Maltby and Immirzi 1993; Hooijer and others 2006; Limpens and others 2008; Ise and others 2008; Gorham). Although many studies have qualitatively considered the role water levels have on peatland carbon fluxes, only recently have water table dynamics been explicitly considered in modeling carbon fluxes (Dimitrov and others 2010; Sulman and others 2012). Relatively few studies have evaluated how soil carbon efflux changes with anthropogenically altered regional water tables (Jauhiainen and others 2008).

Peatland carbon dynamics in both northern and tropical peatlands have been shown to be sensitive to water table variation (Alm and others 1999; Vasander and Jauhiainen 2001; Chimner 2004), although the magnitude of the effect has varied by ecosystem. While lower water table generally increases respiration rates, some experimental studies have found either no change with altered water levels (Updegraff and others 2001) or reduced carbon flux under saturated conditions compared to both flooded and non-flooded conditions (Debusk and Reddy 2003). A seasonal shift between temperature and water table control on respiration further complicates the water table response (Bubier and others 2003). Moreover, the effect of water table likely depends on the characteristics of the peat such as degree of decomposition and fiber content (Dimitrov and others 2010), potentially indicating community-level differences

independent of exogenous controls. Subtropical and tropical peatlands are subjected to higher annual temperatures and thus have the potential for greater carbon effluxes (Chimner and others 2004); persistent high temperatures may be associated with reduced sensitivity to variance in temperature and possibly greater sensitivity to altered water tables (Jauhiainen and others 2008).

The Everglades ridge-slough landscape is one such subtropical peatland. Long-term peat accretion rates in the Everglades prior to the modern era of severe hydrologic modification were relatively low (0.1 to 0.6 mm yr<sup>-1</sup> accretion; Bernhardt and Willard 2009), lower than rates observed in other tropical peatlands (Sorensen 1993; Page and others 2004) but similar to those of temperate systems (0.2 to 1 mm yr<sup>-1</sup>; Aaby and Tauber 1975) and boreal and subarctic peatlands (0.2 to 0.8 mm yr<sup>-1</sup>; Gorham 1991). The peat micro-topography is distinctly patterned in the well-conserved portions of the landscape, hypothesized to be the result of feedback relationships between carbon dynamics and hydrology (Larsen and others 2007; Watts and others 2010; Cohen and others 2011). The remarkable loss of the peat microtopography under both drained and impounded conditions (Watts and others 2010) in the Everglades is evidence that recent (100 year) anthropogenic alterations in the regional hydrology have changed the underlying processes governing landscape topographic variation. One hypothesized mechanism governing the degradation of the landscape involves the loss of soil carbon from oxidation due to lowered water tables (Larsen and others 2007; Watts and others 2010). In particular, Watts and others (2010) hypothesize that micro-topographic differences between the two predominant ecotypes (ridge, dominated

by *Cladium jamaicense* and a deeper-water slough), is maintained in part by an inverse but monotonic relationship between ecosystem respiration and hydrology.

The hypothesis of a monotonic relationship between ecosystem respiration and hydrology predicts a predominant control of hydrology over soil carbon mineralization. To test this hypothesis, my goals in this study were two-fold. First, I sought to determine controls on peat respiration, explicitly considering the dynamic water table, and contrasting the two dominant community types of the landscape. Second, I sought to understand these effects on respiration rates along a gradient of hydrologic modification from drained to impounded, encompassing those areas where the patterning and ridge-slough elevation differences are best conserved. Neither soil nor ecosystem respiration are accurate descriptions of measured fluxes for the purposes of this study. The presence of a biologically active water table means the carbon flux measured here contains aspects of both. In a wetland with primarily inundated conditions, the flux of interest for large-scale carbon dynamics is the amount of CO<sub>2</sub> that ultimately makes it out of the water column. Thus respiration here is denoted R<sub>aq</sub>, quantified as the CO<sub>2</sub>-C flux out of the combined soil and water portions of the ecosystem. Although organic matter mineralization in wetland soils involves multiple electron donor sources, the contribution of methane to total respiration is generally very low, as much as one to two orders of magnitude lower than CO<sub>2</sub> and with no apparent relationship to differences in water depths in the Everglades (Debusk and Reddy 2003). The relatively low methane fluxes are attributed to methane oxidation; methanotrophs can consume as much as 91% of maximum methane flux in these soils (King and others 1990). I therefore

focused measurements on soil/water CO<sub>2</sub> fluxes in Water Conservation Area (WCA) 3A in the central Everglades along a hydrologic gradient.

## **Methods**

### **Study Sites**

Most of the historical Everglades was a subtropical peatland overlaying limestone bedrock, with a maximum peat thickness of 2.7 to 3.3 m near Lake Okeechobee, thinning from north to south to an average ranging 0.3 to 1.5 m in the ridge-slough mosaic of the central and southern Everglades. The Everglades has a relatively low topographic relief (ca. 3 cm per km throughout Water Conservation Area (WCA) 3A), and local increases in elevation as low as 0.1 m can result in a 45% reduction in water depth and a 20% reduction in hydroperiod in some areas (David 1996). Precipitation is seasonal, with ca 70% of the rainfall between May and October and an average annual rainfall of 1.22 m (2002 to 2010 at site W11 from EDEN; <http://sofia.usgs.gov/eden/>). The rainfall is tracked by annual water levels, where the majority of outflow occurs in the rainy season.

In order to capture the effects of regional hydrology on soil respiration, four 2x4 km landscape sampling blocks were located throughout the southern Everglades (WCA 3A, oriented along historical flow lines; Figure 2-1). These landscape blocks are a part of a larger effort to monitor restoration activities as a part of the Central Everglades Restoration Project. More information on these landscape blocks can be found in Watts and others (2010); for the sake of brevity, I will describe only their key features here. WCA 3A spans hydrologic conditions from drained in the north to impounded in the south; its center is widely viewed as the best conserved ridge-slough landscape, which I

assume implies hydrologic drivers most similar to historical conditions (SCT 2003; Larsen and others 2007; Watts and others 2010).

The Drained site located in WCA 3AN (Figure 2-1) has a reduced median annual water depth as compared to the remaining sites in WCA 3AS (Table 2-1). This landscape block has lost nearly all vertical differentiation between ridge and slough soils, with replacement of the deep water slough community by emergent freshwater marsh vegetation.

The Conserved 1 landscape block (Figure 2-1) has evidence of some recent changes in ridges and sloughs including increased wet prairie prevalence, divergent land and water slope over the landscape block, and lower annual median water depths (Table 2-1). In contrast, the Conserved 2 block retains the strongest evidence of landscape patterning, with fidelity of communities to differing soil elevations (approx. 22 cm difference between community elevation modes). Wet prairies, likely transitional communities between deep water sloughs and sawgrass ridges, are absent from this block, suggesting hydrologic conditions remain favorable for deep water sloughs dominated by *Utricularia* spp and *Nymphaea odorata*.

The Impounded block has both the highest median water depth (Table 2-1) and nearly permanent inundation in all communities. A levee to the east of this landscape block has resulted in a re-routing of water from east to west that is then impounded against the east-west road corridor of Tamiami Trail. Elevation differences between ridges and sloughs are no longer as pronounced as in the conserved areas, and sawgrass ridges show marked signs of patchy local dieback, presumably from inundation stress.

## Data Collection

Respiration of the combined soil and water column was measured with a Li-6400 portable gas exchange system fitted with a 6400-09 soil CO<sub>2</sub> flux chamber (LiCor, Inc., Lincoln, NE). Sites were generally 8 paired ridges and sloughs in each landscape block. More measurements were taken in Drained and Conserved 1 when water tables were below the surface in both ridges and sloughs in order to obtain higher power for this critical period. Respiration measurements (total n = 544) were taken approximately bi-monthly between January 2009 and June 2011, with the timing of measurements primarily motivated by observing the full range of water levels observed in the Everglades. Due to the presence of water at all sites for at least part of the year, a modular collar was used to extend the CO<sub>2</sub> flux chamber above the water column, using the water present to form a seal. Measurements in 2009 were located on a soil base inserted 15 cm into the soil (installed in November of 2008) with the modular collar fitted overtop. Measurements from 2010 through 2011 were undertaken with the modular collar set atop the soil surface without insertion into the soil. Measurements of instantaneous flux rates were similar at the same water depth over all the years and a variance components analysis for 2009 respiration values showed little site effect (<0.1% of the total variance). I therefore infer the methodological change did not significantly alter measured flux rates, and prevented the trampling impacts of repeated site visitation that were already evident after the first year of measurements. Further, randomly selected sites in each of the landscape blocks allowed us to capture some of the spatial variability in respiration fluxes as a result of micro-topography. Water column depth was noted for each sample period, and head volume space calculated accordingly. Between 3 and 10 independent measurements were made at each site,

with the averages across these measurements reported. Chamber fluxes were sometimes suppressed because of high humidity or large changes in chamber temperature, or increased dramatically due to ebullition events. A linear function was used to extrapolate chamber CO<sub>2</sub> concentrations to rates, with an R<sup>2</sup><0.98 used to remove data altered by unfavorable conditions.

Simultaneous measurements of water column and soil temperature (at 10 cm below the water surface; separate soil and water temperature measurements commenced in 2010), and measurements of vegetative community species and cover within 1 m<sup>2</sup> were also performed. The vegetative community was then used to distinguish between slough and ridge communities in the same manner described by Watts and others (2010). As calcareous periphyton is present throughout the ecosystems sampled, the potential for changes in pH due to calcite dynamics to affect CO<sub>2</sub> efflux was a concern. Theoretically, high CO<sub>2</sub> in the chamber headspace could induce CO<sub>2</sub> to dissolve back into the water column. If this occurred, the pH of the water column could be sufficiently reduced to dissolve calcium carbonate that in turn would result in higher CO<sub>2</sub> respiration values. Increases of headspace CO<sub>2</sub> were limited to no more than 5 ppm above ambient CO<sub>2</sub> to reduce the likelihood of induced calcium dissolution. To further enumerate any such effect, pH was measured with an Accumet AP63 (Fisher Scientific, Pittsburg, PA) both within and adjacent (within 1 m) to the respiration chamber. To ensure calcium dissolution was not induced via higher partial pressure of CO<sub>2</sub>, the change in pH(ambient minus post-measurement pH) was compared to water depth and soil respiration.

## **Data Analysis**

A series of non-linear regression models were fitted to predict respiration as a function of pH, water depths, water column and soil temperature, and ecological community (ridge vs. slough as a fixed effect). Lacking a mechanistic reason for a particular model structure, both a negative exponential and a monomolecular (which approaches the lower asymptote, here K) models were evaluated for water depths. I used a non-linear least squares fitting method to test which environmental factors most strongly correlated with soil respiration in this system. Akaike's Information Criterion (AIC) was used to discriminate between predictive models. The best-fit model was then used to estimate annual flux rates for 2009 – 2011. Incorporating water elevations provided by the Everglades Depth Estimation Network (EDEN sites shown in Table 2-1; <http://sofia.usgs.gov/eden/>) and soil elevations Watts and others (2010) allowed us to estimate daily water depths for 473 points among the four landscape blocks. These daily water depths were used to extrapolate to daily fluxes and then summed for an estimated annual carbon efflux. To demonstrate the change in long-term soil respiration over the range of extant soil elevations I used this technique to create an average annual flux rate from 2000 to 2011 for the points in each landscape block (Figure 2-4).

## **Results**

### **Instantaneous Fluxes**

Hydrologic conditions varied substantially over the course of this study. In 2009 mean water levels fell only slightly below the 20 year average, 2010 was a chronically wet year, where the minimum water levels were in the 90<sup>th</sup> percentile, and 2011 was the driest year in the recent record (20 years) with a prolonged dry season (Figure 2-2). Mean annual air temperatures in South Florida ranged 23 to 24.5°C from 2009 to 2011

(FAWN; Fort Lauderdale station, 2 m above ground surface; <http://fawn.ifas.ufl.edu>) with only a single day over that time period where temperatures dropped to freezing (January 2011).

Carbon efflux ranged from 0.24 to 6.26 g CO<sub>2</sub>-C m<sup>-2</sup> d<sup>-1</sup> for sloughs and 0.18 to 6.72 g CO<sub>2</sub>-C m<sup>-2</sup> d<sup>-1</sup> for ridges. A notched box plot (McGill and others 1978) of instantaneous respiration rates revealed no landscape-block effect in instantaneous measured fluxes, nor did the residuals when accounting for water level and community effects. I infer that any block effects that may exist are small when compared to the temporal variation in instantaneous rates, and therefore used models without a block effect. Soil temperature was a poor predictor of carbon efflux ( $R^2 = 0.01$ , Figure 2-3A) with a negative fitted exponent. Carbon efflux was best predicted by water depth ( $R^2 = 0.51$ ,  $p < 0.01$ , Table 2, Figure 2-3B). Based on AIC, carbon efflux was best predicted by a model with community-specific parameterization. Both the exponential decay model and the model with an asymptotic structure had very similar goodness of fit. I used the asymptotic model for extrapolations, as this model incorporated fewer parameters. Including soil/water temperature did not improve the explanatory power of the models (Table 2-2, with water temperature shown); the same result was obtained using air and soil temperature (not shown). Residuals of the selected model did not deviate significantly from normality. I explored whether temperature effects emerge below a water depth threshold, but no evidence for any threshold behavior was found. For example, I continued to observe a much stronger relationship with water depth when water levels were less than 5 cm ( $R^2 = 0.44$ ) than temperature ( $R^2 = 0.2$ ), which remained true with water levels below 0 and -5 cm the soil surface. Notably, however,

the temperature exponent at shallow depths was positive, consistent with expectations. Soil and water temperature were weakly but positively related ( $r = 0.17$ ) for the times they were measured separately, and each were more weakly related to water depth ( $r = 0.10$  and  $0.04$ , respectively), to which I infer soil temperatures may be buffered by water depths but are essentially independent from surface water temperatures.

Water column pH increased on average during the measurements (ambient pH mean = 7.38, var. = 0.07; post-measurement mean = 7.41, var. = 0.09;  $n = 157$ ), but was not normally distributed. A t-test performed on log-transformed ambient and post-measurement pH showed they were significantly different ( $p < 0.05$ ) but positively correlated ( $r = 0.77$ ). I was unable to establish a relationship between pH and soil  $\text{CO}_2$  respiration rates untransformed data. The residual respiration rates (de-trended for water depth and community effect) did have a weak but significant positive relationship with the ambient pH (linear model  $p < 0.01$ ,  $R^2 = 0.084$ ) and post-measurement pH (linear model  $p < 0.01$ ,  $R^2 = 0.1$ ), but had no significant relationship to the change in pH (linear model  $p > 0.1$ ,  $R^2 = 0.0$ ). This suggests that while pH may affect respiration rates, capping of the water column did not significantly alter  $\text{CO}_2$  fluxes.

### **Model Extrapolation**

I estimated annual respiration for the three years of measurements (Table 2-3) modeling carbon effluxes as a function of water depth. The largest estimated flux rate ( $825 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ ) was for Drained ridges in 2011, the record dry year. This year was 36% higher than in 2009 ( $607 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ ), the year of average precipitation, and 79% higher than for the wet year of 2010 ( $460 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ ), illustrating the dramatic effects of varying hydrologic conditions (Table 2-3). The magnitude of annual differences between communities was small with annual ridge respiration ranging 96 –

117% that of sloughs. The mean annual hydroperiods across the 3-year measurement period were longer for sloughs than ridges, ca. 77 days longer in Conserved 1, 60 days longer in Conserved 2, and 20 days longer in Impounded. The hydroperiod range was dramatic, with no difference in hydroperiods between communities for Impounded in 2010 to 136 days longer for sloughs than ridges in Conserved 2, 2011.

Figure 2-4 demonstrates the relationship between local soil elevation and extrapolated carbon efflux. The dashed lines indicate the long-term averaged carbon efflux (2000-2011) for the median soil elevations for ridges and sloughs in each landscape block. A larger difference in the averaged annual effluxes is observed where microtopography is also observed. The averaged extrapolation from 2000 to 2011 showed difference in long-term fluxes for median ridge and slough fluxes of 9, 50, 35, and 5 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup> from Drained through Impounded.

### **Discussion**

The estimated annual respiration rates I found in the Everglades peatland (Table 2-3) were substantially higher than northern bogs and mires (average 94 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Raich and others 1992) but lower than tropical moist forests (average 1260 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Raich and others 1992), secondary forests in South Kalimantan (1200 ± 430 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Inubushi and others 2003), and hummock and hollow swamps in Micronesia (with a 50/50 ratio of each, 1061 ± 83 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Jauhiainen and others 2005). Even the drained site did not reach the annual flux rates of other tropical systems that experience prolonged periods without inundation such as Sarawak (2130 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Melling and others 2005), and Indonesia (1993 to 2031 g CO<sub>2</sub>-C m<sup>-2</sup> yr<sup>-1</sup>; Jauhiainen and others 2008).

Water table variation appears to exert a stronger control on respiration than does temperature. The marked increase observed in flux rates as the water table dropped to and below the soil surface has been observed in other studies (Bubier and others 1998; Alm and others 1999; Vasaner and Jauhiainen 2001; Chimner 2004). Despite this precedent, I expected to also observe some temperature effect, as observed by Inglett and others (2011) in an incubation study of Everglades soils. The lack of a statistically discernible effect does not obviate the well established influence of temperature on respiration rates (Raich and others 1992), but does underscore the growing recognition that tropical and subtropical peat systems respond more strongly to water table (Chimner 2004; Jauhianen and others 2005; Jauhianen and others 2008). The absence of a significant temperature effect may be attributed to low temporal variability in air temperature and the thermal buffering capacity of standing water, as inferred by the low correlation between soil and water temperatures. Peatlands with relatively small water level fluctuations appear to be less controlled by hydrology (North Carolina: Bridgham and Richardson 1992; Micronesia and Hawaii: Chimner and others 2004; Sarawak, Malasia: Melling and others 2005) than those with larger fluctuations (Borneo swamps: Jauhiainen and others 2005; drained and restored peatlands in Indonesia: Jauhiainen and others 2008; Everglades ridge-slough: this study). This reinforces the emerging contention (Sulman and others 2012) that the carbon cycle in peatlands should be studied and modeled as tightly coupled with hydrologic dynamics and, as such, mediated by both exogenous flows and also small-scale local topographic variation.

If the peat soils in the Everglades were persistently moist rather than waterlogged, a temperature response may become prominent, as indicated by the

stronger control of temperature observed when water levels dropped below the soil surface. It is important to note, however, that low water table conditions in the Everglades generally occur during the coolest months. Were a low water table to occur during the warmest times of the year, the steep increase I observed in respiration may be larger. Under such conditions the vertical peat accumulation balance would be disrupted, and the vertical differentiation between ridges and sloughs would likely disappear as soil respiration rates eclipse productivity. Even assuming that the higher standing biomass stocks of sawgrass in the Everglades completely turns over annually to become source material for peat, extrapolated flux rates under drained hydrologic conditions suggest a rapid loss of peat with year-round drainage. For example, offsetting the hydrograph for 2011 in the driest site so that the water is at or below the soil surface year-round leads to estimated respiration rates of approximately  $2262 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$  for ridges. This respiration would be far in excess of any published primary productivity values in the literature (e.g.,  $1436 \pm 427 \text{ g C m}^{-2} \text{ yr}^{-1}$ , converted from a dry weight using an estimated leaf C of 48%; Daoust and Childers 1998). It is in this context that water management and climate change (reduced summer rainfall, increased potential evapotranspiration) need to be considered.

I observed high instantaneous flux rates that were comparable to other tropical peatlands when the water table dropped more than 50 cm below the soil surface. The maximum measured rate for Drained of  $280 \text{ mg CO}_2\text{-C m}^{-2}\text{h}^{-1}$  in 2011 was akin to  $\sim 132$  to  $166 \text{ mg CO}_2\text{-C m}^{-2}\text{h}^{-1}$  in hummocks and  $38$  to  $188 \text{ mg CO}_2\text{-C m}^{-2}\text{h}^{-1}$  in hollows of a tropical peat swamp (Jauhiainen and others 2005) and  $100$  to  $335 \text{ mg C m}^{-2}\text{h}^{-1}$  forested peatland in Malaysia (Melling and others 2005). The large water level drop and

resulting longer aeration of the typically saturated soils likely explains the large rise in soil carbon efflux in 2011. In contrast to the ca. 187 day hydroperiod in 2011 for this landscape block, the long-term average hydroperiod for ridges under hydrologically conserved conditions has been estimated to be ca. 310 days and ca. 292 days in the Drained area (2000 to 2008; Watts and others 2010, comparable to pre-1800's estimates of ~9 to 10 months; McVoy and others 2011). As described earlier, dramatic leveling of the peat surface has occurred in this part of the Everglades, with nearly a complete loss of vertical differentiation between communities (Watts and others 2010).

There are several possible explanations for the small but (statistically) significant differences in carbon flux rates. In wetlands with complex microtopography, differing water tables can lead to offsetting respiration responses (Dimitrov and others 2010). Vegetative source material can also lead to offset respiration rates, although the differences in community respiration rates resulted in annual fluxes differing by less than 20 g C for many year/hydrologic combinations (Table 2-3). This small difference is despite the higher recalcitrance of sawgrass vegetation compared to slough species (Amador and Jones 1997; Debusk and Reddy 1998; Vaithyanathan and Richardson 1998; Lewis 2005; Osborne and others 2007). Several factors may be at play resulting in such small community differences. First, it may be that soil material is made more of roots than leaf detritus and that root material between communities is similar in decomposition rate. Second, ridges also generally have higher concentrations of soil phosphorus in those areas where soil elevation bimodality has been maintained (Cohen and others 2009). Since phosphorus is the key limiting nutrient in the Everglades (Noe and others 2001), C mineralization may be releasing organically bound phosphorus and

acting as a positive feedback, enhancing soil respiration (Debusk and Reddy 2003) in ridges. Third, there may be seasonal influences over soil respiration which this study did not cover. Community-specific phenology may play a role during dry down not covered here, particularly in terms of the contribution of root respiration. For example, the deeper water vegetation senesces during the dry season and may reduce root respiration relative to the ridge vegetation. There may also be lagged effects during dry downs caused by the length of time the soil was exposed, inducing a qualitative difference in fluxes I was unable to observe in my point measurements.

The logistical challenge of partitioning soil and water column respiration resulted in measurements that were integrations of the two. The contribution from the water column to total respiration may be important in sloughs, giving the appearance of similar  $R_{aq}$  C efflux between communities when there is standing water. There is far greater abundance of submerged aquatic vegetation and algal communities in sloughs than in ridges. The ubiquitous nature of submerged vegetation and extensive algal and periphyton mats in sloughs means my measurements at least partially incorporated respiratory losses from these communities. Periphyton assemblages can dominate slough productivity in the Everglades (McCormick and Stevenson 1998; Iwaniec and others 2006), although these assemblages have been measured as a net carbon sink (Iwaniec and others 2006). Total aquatic metabolism indicates that the sloughs are a net carbon source across a variety of environmental and community factors (Hagerthey and others 2010). However, much of the respiration from the water column appears driven by sediment carbon mineralization rather than aquatic vegetation and periphyton respiration (Belanger and others 1989; Hagerthey and others 2010).

Although CH<sub>4</sub> is an important green house gas emitted by wetlands, it is not a large part of carbon fluxes in the ridge-slough Everglades. The Everglades is a weak source of atmospheric methane, with total system releases estimated below 0.5 Tg CH<sub>4</sub> yr<sup>-1</sup> (Burke and others 1988). Relatively low rates of CH<sub>4</sub> production (Bachoon and Jones 1992), combined with little to no relationship with temperature (Harriss and others 1988; Bachoon and Jones 1992) and water depth (Debusk and Reddy 1992), along with high rates of methane oxidation (King and others 1990) suggests that this pathway is not significant for carbon mineralization. Although based on laboratory studies of Everglades peat from central WCA 2A, potential methane fluxes appears to be between 0 and 8% of total carbon efflux, with an average of 2% across a range of water depths (-15 to 10 cm; Debusk and Reddy 1992). Further, CH<sub>4</sub> release appears to decrease with deeper water levels (Debusk and Reddy 1992), although it is possible that the release of gaseous carbon becomes dominated by ebullition events with deeper water (Burke and others 1988).

Linking hydrology to carbon budgets in the Everglades remains an important step in understanding landscape degradation. Both the Drained and Conserved 1 landscape blocks have lost significant portions of their peat profile (peat depths average 56.9 and 57.8 cm, respectively) compared to Conserved 2 and Impounded (118.8 and 113.8 cm, respectively; Watts unpublished data), suggesting much of the soil legacy carbon has been mineralized in northern areas. The draining of peatlands can lead to rates of oxidation and subsidence that vegetative productivity cannot compensate for (Wösten and others 1997; Galloway and others 1999; Furukawa and others 2005; Gambolati and others 2006; Schipper and McLeod 2006). Indeed, oxidized peat throughout the

Everglades is estimated to have released 12,500 kg CO<sub>2</sub> per ha of drained soil, with total C outflow on order of 10 million tons (Smil 1985). The higher peat bulk density in this region suggests some amount of subsidence is occurring alongside oxidation (Bruland and others 2006). Certainly the control hydrology has over peat accretion suggests the leveling of the peat surface can be ascribed to altered carbon budgets.

This study supports the hypothesis of monotonic changes in respiration with water depth, as outlined by Watts and others (2010). This hypothesis suggests that the long-term stability of landscape rests in nearly equivalent peat accretion rates between ridges and sloughs— a condition only possible if discontinuous productivity is balanced by an inverse but monotonic relationship between respiration and hydrologic conditions (presumably a balance of water levels and hydroperiod). Community differences in annual flux rates induced by differences in soil elevations (and hence, hydrologic conditions) between ridges and sloughs evaporates with hydrologic modification (Figure 2-4), with over-all respiration rates higher with drainage and lower with hydrologic impoundment. While the magnitude of these changes is small when compared to instantaneous variation in CO<sub>2</sub> efflux, the summed values suggest large differences in peat accumulation and/or deflation rates. This study also aids in predicting the amount of net primary productivity necessary for peat accretion in the region. Enumerating the rates of carbon uptake and release in relation to hydrologic modification is clearly important for establishing the hydrologic conditions necessary for landscape peat accretion.

Table 2-1. General attributes for each landscape block. Metrics are from Watts and others (2010). Coordinates are of the center of the landscape block.

	% Slough	% WP	% Ridge	Number of points	Median soil elevation (cm)	Median water depth (cm)	Latitude	Longitude	EDEN water level gage*
Drained	--	52.3	47.7	130	280.8	12.8	26.21788	-80.7380	Site 62
Conserved 1	28.9	17.0	54.1	135	249.9	18.1	26.08815	-80.7355	Eden5
Conserved 2	47.4	--	52.6	95	227.1	32.0	25.98338	-80.6970	W11
Impounded	69.9	2.7	27.4	113	190.4	54.2	25.82245	-80.7283	Site 65

\* Everglades Depth Estimation Network (EDEN) water level gages are from <http://sofia.usgs.gov/eden>.

Table 2-2. Parameters for respiration models.

Model	Community	<sup>§</sup> K	<sup>§</sup> a	<sup>§</sup> b	<sup>§</sup> c	<sup>*</sup> R <sup>2</sup>	AIC
$Cflux = K \times e^{b \times temp}$	NA	2.17 <sup>***</sup>		-0.017 <sup>**</sup>		0.011	
$Cflux = K \times e^{-a \times wd} + c$	NA	0.876 <sup>***</sup>	0.025 <sup>***</sup>		0.77 <sup>***</sup>	0.494	1239
<sup>1</sup> $Cflux = K_i \times (1 + e^{-a_i \times wd})$	Ridge Slough	0.791 <sup>***</sup> 0.826 <sup>***</sup>	0.029 0.022			0.513	1220
$Cflux = K_i \times e^{-a_i \times wd} + c_i$	Ridge Slough	0.744 <sup>***</sup> 1.23 <sup>***</sup>	0.031 <sup>***</sup> 0.012 <sup>***</sup>		0.83 <sup>***</sup> 0.51	0.516	1221
$Cflux = K_i \times e^{-a_i \times wd} \times e^{b_i \times temp} + c_i$	Ridge Slough	1.23 <sup>**</sup> 0.936 <sup>*</sup>	0.034 <sup>***</sup> 0.017 <sup>***</sup>	0.029 -0.011	0.89 <sup>***</sup> 0.51	0.519	1222

<sup>§</sup>Significance codes: \*\*\*p<0.001, \*\*p<0.01, \*p<0.05

<sup>1</sup>The selected model for subsequent extrapolation.

<sup>\*</sup>R<sup>2</sup> shown is  $Cflux_{observed} \sim f(Cflux_{extrapolated})$ .

Table 2-3. Extrapolated annual  $R_{aq}$  CO<sub>2</sub>-C and hydrologic characteristics for the median elevation for the dominant communities in each landscape block over the three years of measurement. Annual estimates were generated using soil elevations from Watts and others (2010) and water elevations in Figure 2-2.

		2009			2010			2011		
	Community*	Median Water Depth (cm)	Hydro-Period (d)	gCO <sub>2</sub> -C	Median Water Depth (cm)	Hydro-Period (d)	gCO <sub>2</sub> -C	Median Water Depth (cm)	Hydro-Period (d)	gCO <sub>2</sub> -C
Drained	R	10.2	248	607	20.0	347	460	-1.0	187	825
	WP	14.5	266	581	24.3	362	487	3.3	207	705
Cons.1	R	13.9	277	513	19.4	344	467	3.8	206	567
	S/WP	29.4	357	470	34.9	363	445	19.3	337	500
Cons. 2	R	30.2	315	452	24.6	365	427	6.3	209	553
	S	49.3	360	421	43.8	365	410	25.5	345	473
Impounded	R	47.6	354	386	43.3	365	370	24.8	280	482
	S	61.8	364	396	57.5	365	385	39.0	328	454

\*R = Ridge; S = Slough; WP = Wet prairie

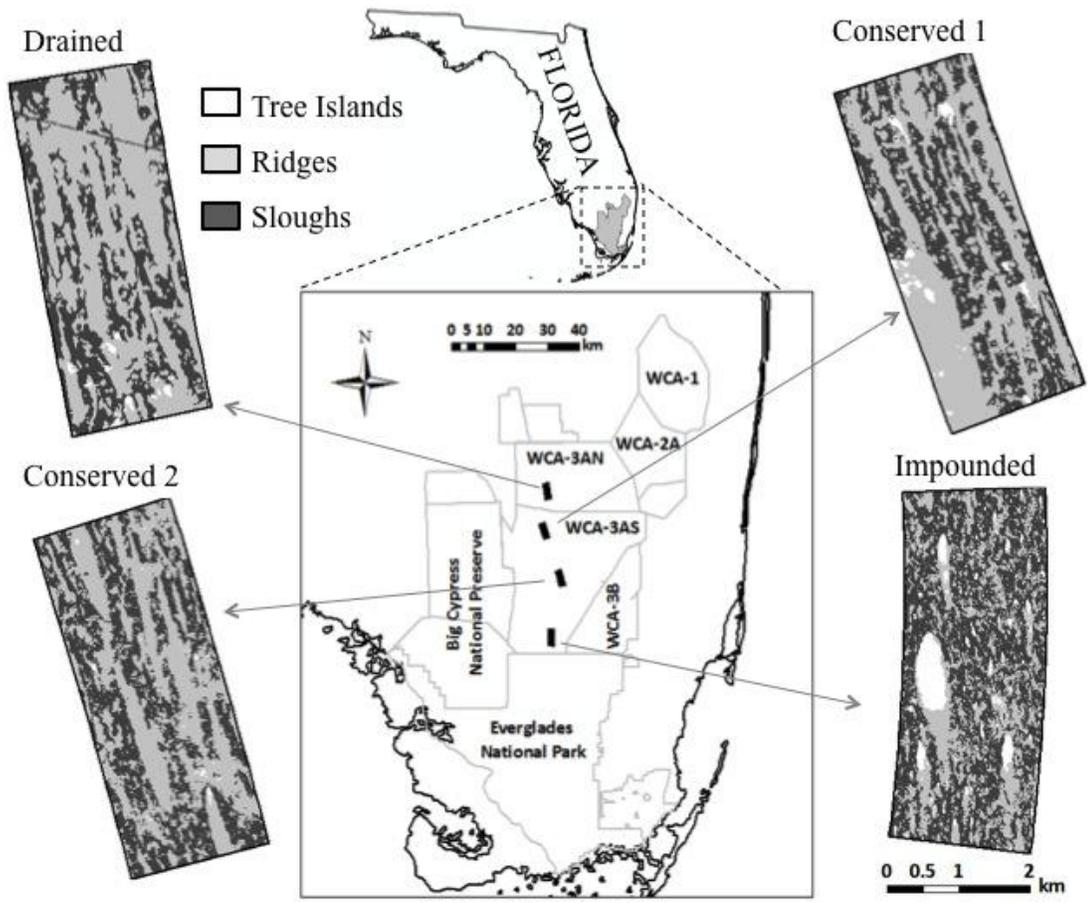


Figure 2-1. Location of 2 x 4 km landscape blocks in Water Conservation Area 3A (WCA 3A) for paired ridge-slough sampling.

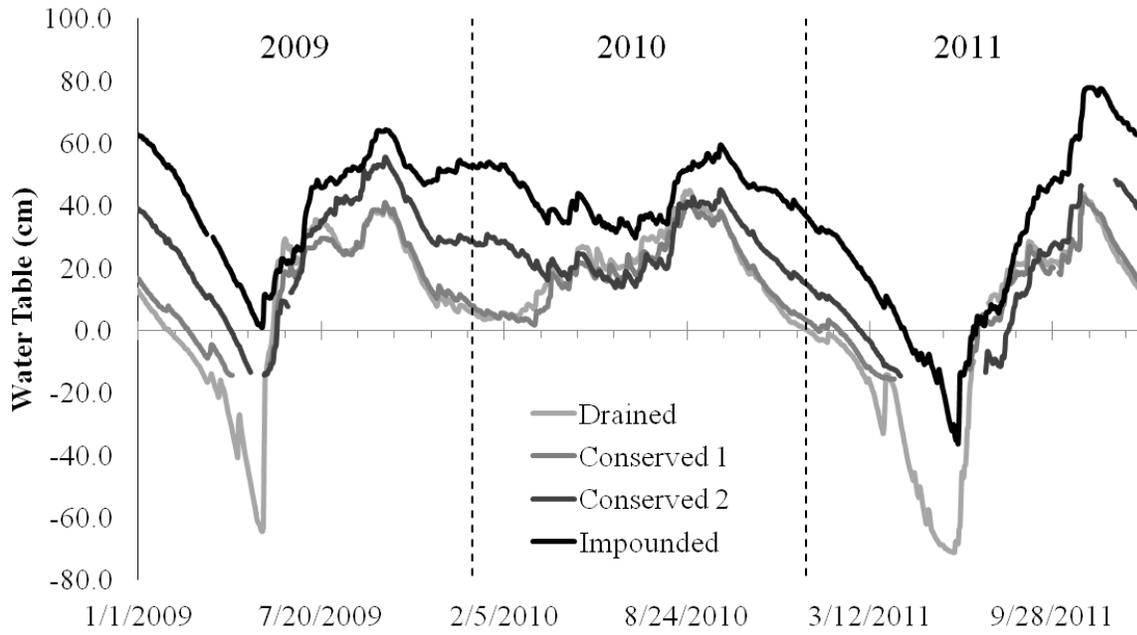


Figure 2-2. Water depths at the median ridge peat elevation (from Watts and others 2010) for 2009-2011. Mean slough water depths would be -6, -19, -22, and -10 cm for each of the respective landscape blocks (Drained to Impounded).

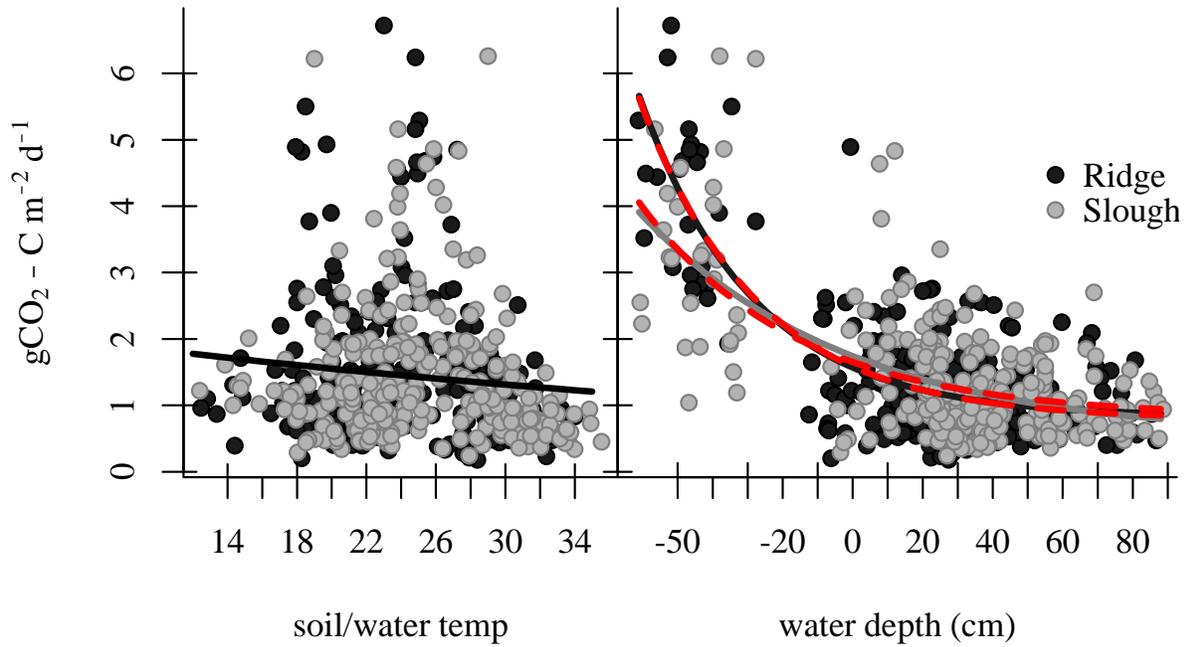


Figure 2-3. Soil temperature (water temperature when inundated) is a poor predictor of respiration whereas water depths are the better predictor of respiration (best-fit models shown). Solid lines are exponential models; dashed red lines are the asymptote models. Parameter values are in Table 2-2.

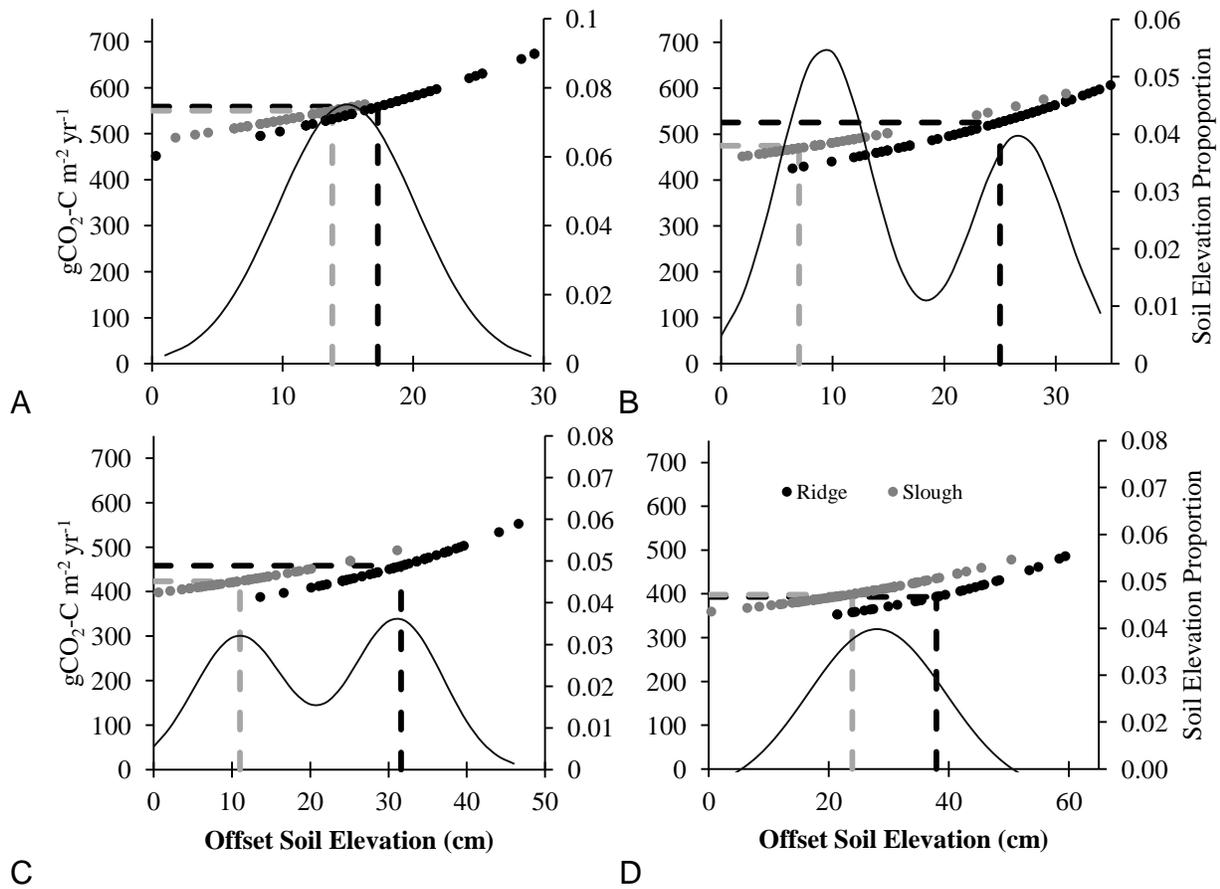


Figure 2-4. 11-year average CO<sub>2</sub>-C flux for soil elevations from Watts and others (2010) extrapolated from the asymptotic model. Panels correspond to A) Drained, B) Conserved 1, C) Conserved 2, and D) Impounded sites. Dashed lines indicate the median elevations for *a-priori* defined ridges and slough/wet prairies. Solid lines are the soil elevation probability density function, offset to the lowest landscape position.

### CHAPTER 3 NET ECOSYSTEM PRODUCTIVITY IN THE EVERGLADES RIDGE-SLOUGH

The carbon storage of peatlands is controlled by the presence of water and its impact on the balance between carbon uptake and loss. Research on boreal to tropical peatlands has increasingly focused on incorporating water table dynamics into ecosystem carbon budgets (examples include Dimitrov and others 2010; Sulman and others 2012; Jauhiainen and others 2008). I previously demonstrate that water column and soil respiration fluxes in the Everglades, a subtropical peatland, are predominantly controlled by water levels. In this work, I seek to expand on that finding to better understand the role of hydrologic variation in controlling totally ecosystem respiration and primary production.

The ridge-slough Everglades is a component of the largest restoration project yet initiated globally but restoration efforts are constrained by insufficient information on the feedbacks between hydrology and peat accretion. The peat portions of the landscape are patterned in both patch phenology and microtopography (e.g., Wu and others 2006; Watts and others 2010). This patterning must be driven at least in part by local carbon budgets, as microtopographic variation in the peat surface is not reflected in the underlying limestone topography (Lewis 2005; Givnish and others 2007). Much of the original ridge-slough landscape has been dramatically altered by 20th century changes to nutrient loading and hydrology, with changes to vegetative and periphyton communities, degradation of landscape patterning, and a loss of microtopography. Large expanses of Water Conservation Area 3A North (WCA 3AN) and Everglades National Park demonstrate such change in pattern metrics that the prognosis for rapid restoration remains in doubt (Watts and others 2010).

My overarching hypothesis is that ridges and sloughs represent two alternative ecosystem configurations that achieve the same long-term carbon accretion rate. The principal evidence in support of this hypothesis is that peat surface differentiation between adjacent ridges and sloughs is maintained without continual divergence (SCT 2003; Ross and others 2006; Larsen and others 2007; Cohen and others 2011). This hypothesis invokes a homeostatic feedback between soil accretion, hydroperiod and soil redox. Lowered water levels are associated with higher production and increased productivity in ridges that is ultimately inhibited by shortened hydroperiod and increased soil redox potential. Any higher peat accretion potential in ridges is ultimately offset by increased peat exposure. In contrast, sloughs situated lower in the water column have lowered peat accretion potential (via lowered productivity) but are balanced by lowered respiratory potential under anoxic conditions. The balance of these positive and negative feedbacks produces two alternative attractors (high productivity-high respiration and low productivity-low respiration) whose similar net peat accretion could explain the extended stability (>1000 years; Bernhardt and Willard 2009) of landscape patch configuration.

The remarkable leveling of the peat surface under both drained and impounded conditions (Watts and others 2010) in the Everglades is clear evidence that modern changes to the regional hydrology have changed the underlying processes governing ridges and sloughs. The control hydrology has over peat accretion suggests much of the leveling can be ascribed to altered carbon budgets. Drainage, where more of the peat experiences oxidation, can lead to a rate of subsidence that vegetative productivity cannot compensate for (examples include Galloway and others 1999; Gambolati and

others 2006; Schipper and McLeod 2006). The loss of elevation differences between ridges and sloughs is further exacerbated by changes in community structure; deep-water sloughs are replaced by more productive emergent prairie vegetation. Drained portions of the landscape are therefore experiencing the stress of excess respiration on ridges coinciding with increased productivity in the former sloughs.

The hydrologic gradient in the central Everglades of drained to impounded hydrologic conditions provides an opportunity to quantify carbon responses to changes in regional drivers. As both drainage and impoundment are associated with changes in community structure and soil microtopography, presumably the ecosystem carbon balances have also been altered such that equivalent carbon budgets are no longer plausible. In this study I measured net ecosystem productivity (NEP) and ecosystem respiration ( $R_{\text{eco}}$ ) using large, closed-system chambers for a year in ridges and sloughs across a range of hydrologic conditions in WCA 3A. I use the net  $\text{CO}_2$  uptake as a proxy for net ecosystem productivity (NEP), but acknowledge there are alternative losses of carbon that are not explored in this study, including non-biological oxidation (particularly photolysis) and carbon losses through DOC (dissolved organic carbon) transport. The purpose was to determine a) the role water levels plays in mediating  $\text{CO}_2$  fluxes over the course of a year, b) compare NEP between ridge and slough communities to test for carbon budgets equivalency, and c) evaluate a) and b) across a landscape-hydrologic gradient from drained to impounded conditions. This study adds to our understanding of  $\text{CO}_2$  dynamics in subtropical wetlands as well as aids in evaluating the potential for long-term peat accretion in the Everglades.

## Methods

### Site Description

The South Florida ridge and slough landscape is a major component of the once-contiguous Everglades system that started in the Kissimmee chain of lakes and Kissimmee River and flowed to Florida Bay. It is a predominantly surface-flowing fen that consists of two dominant patch types, elevated ridges and deep water sloughs organized in strikingly non-random pattern. Ridges comprise approximately 50% of the landscape and are distinctly elongated in the direction of flow. Sloughs form the remaining landscape matrix are, in the best conserved areas, longitudinally connected to create flowpaths for water, solutes, and organisms through the landscape. Peat accumulation began roughly 3,000 years before present over a limestone basin. Peat accretion appears to have been discontinuous, linked to major climatic events in history and tracking sea level rise over that period (Bernhardt and Willard 2009). Peat thicknesses historically ranged from 2.7 to 3.3 m at the northern end near Lake Okeechobee, thinning to 0.3 to 1.5 m in the central and southern Everglades.

Plant communities are dominated by *Cladium jamaicense* on ridges and *Nymphaea odorata* and *Utricularia* spp. in sloughs. Ridges are generally monotypic, with occasional small amounts of *Justicia angustifolia* and *Cephalanthus occidentalis*. Slough communities are considerably more variable, with assemblages specific to local water levels (Busch and others 1998; Givnish and others 2007; Zweig and Kitchens 2008). Chronically lower water table in sloughs leads to abundant emergent vegetation such as *Eleocharis* spp, *Panicum* spp, *Rhynchospora* spp, *Cyperus* spp, among others—often referred to as wet prairies. Ubiquitous throughout this region is the presence of a periphyton community whose productivity and competition is altered by water levels,

water nutrient status, and light penetration (McCormick and Stevenson 1998; Hagerthey and others 2008). Microtopographic differentiation of soil elevation is consistent in the regions considered hydrologically conserved, with a mean 22 cm difference between ridges and sloughs (Watts and others 2010). A loss of this differentiation has been associated with both drainage and impoundment, and co-occurs with a loss of slough communities and expansion of ridges (drainage) or a lowered prevalence of ridge communities (impoundment). These changes are reflected in the metrics of patterning, including altered patch geometry, loss of patch anisotropy, reduced autocorrelation at near-neighbor distances, and more (Wu and others 2006; Watts and others 2010).

Precipitation is seasonal, with 70% of the rainfall occurring between May and October and an average annual rainfall of 1.22 meters (2002-2010 at site W11 from EDEN; <http://sofia.usgs.gov/eden/>). As rainfall is the primary source of water, rainfall is tracked by annual water levels with the majority of outflow occurring in the wet season. Although the hydrology is dominated by sheetflow, water velocities are generally below  $5 \text{ cm s}^{-1}$  (Leonard and others 2006). There is relatively little seasonal variation in air temperature; freezing temperatures are only rarely reached (Duever and others 1997), and summers temperatures are often within  $10^{\circ}\text{C}$  of winter temperatures.

The Everglades is now highly compartmentalized and the loss of ridge-slough patterning that has ensued as a result of both drainage and impoundment is dramatic. The largest and best-conserved remnant landscape is found in WCA 3A, covering an area of roughly  $2,370 \text{ km}^2$ . This area has been drained by the construction of canals at the northern end and impounded by levees on the southern end. Landscape sampling blocks had been established by Watts and others (2010) and were used in this study in

WCA 3A along a hydrologic gradient designated Drained, Conserved 1, Conserved 2, and Impounded. Selected sites within each landscape block were randomly chosen as paired ridges and sloughs. Random site selection was designed to avoid the incremental compaction and canopy disturbance associated with repeated measurements at the same site.

### **Environmental Data**

Environmental data came from several sources. Precipitation and water elevation data was obtained from nearest EDEN made available by the Everglades Depth Estimation Network (EDEN; <http://sofia.usgs.gov/eden/>): EDEN Site 62 for Drained; Eden5 for Conserved 1; W11 for Conserved 2; Site 65 for Impounded. Air temperature and photosynthetically active radiation (PAR) for model extrapolations was obtained from site 3AS3WX via the South Florida Water Management District's data base DBHYDRO (<http://www.sfwmd.gov/>), located approximately 12 km southwest of the Drained landscape block.

### **CO<sub>2</sub> Flux Measurements**

Closed chambers (non-steady state) are widely used for quantifying carbon fluxes between ecosystems and the atmosphere due to portability and ease of operation in remote conditions. I built chambers similar to chambers constructed for use in other peatlands (Alm and others 1997; Tuittila and others 1999; Bubier and others 2002; Nykanen and others 2003; Burrows and others 2004; Laine and others 2006). Two Lexan chambers were constructed so they can be placed over sawgrass (in one case), and slough vegetation (in the other) with minimal canopy disturbance. Two chambers were needed to minimize headspace volume when assessing NEP in sloughs (volume~0.35 m<sup>3</sup>), and to accommodate sawgrass height on dense ridges (volume~0.5

m<sup>3</sup>). I used a dynamic chamber technique for CO<sub>2</sub> flux, using a Li-6400 portable infrared gas analyzer (LiCor, Inc., Lincoln, NE). CO<sub>2</sub> fluxes were measured pre-dawn through 1 PM whenever possible to capture potential temperature controls on CO<sub>2</sub> flux. Each measurement under ambient light conditions was followed by covering the chamber with a shade clothe for a R<sub>eco</sub> (ecosystem respiration) under dark conditions. CO<sub>2</sub> concentrations in the chamber were monitored for 3 to 15 minutes. The measurement length was dictated by the rate of increase in gas fluxes and intended to minimize chamber interior environmental changes such as changes in relative humidity and increases in temperature. However, storms, wind, and heavy condensation shortened or precluded measurements on several occasions.

Measurements commenced on 7/8/2011 and ended on 6/11/2012, with the start dates dictated by when all landscape blocks were accessible by airboat. Sampling was intended to be monthly in each landscape block, although weather and logistics at times precluded such sampling. PAR (in  $\mu\text{mol s}^{-1} \text{m}^{-2}$ ), water depths, and water surface and soil surface temperature were monitored during each sampling period. Species cover was noted both within the chambers and outside to encompass a 1 m<sup>2</sup> plot for each sampling period.

While temperature changes of the soil and atmosphere beneath the chamber are a potential source of error (Wagner and Reicosky 1992), the buffering effect of water on temperature changes due to standing water present during most of the year at nearly all sites likely reduced this potential source of error. In particular, the warmest time of the year coincides with the warmest, when temperature buffering would be most necessary.

Error due to the suppression of natural pressure fluctuations was reduced with the inclusion of a vent as described by Hutchinson and Mosier (1981).

The change in CO<sub>2</sub> concentrations with time during each measurement was regressed linearly (e.g., Xu and Qi 2001; Bubier and others 2002; Wang and others 2006; among many others) with the intention to reduce under-estimation of CO<sub>2</sub> fluxes caused by headspace concentration increases and reductions during measurement. Chamber conditions were occasionally altered by high humidity, heat, and pressure changes induced by wind gusts. A standard of a regression fitting the data with an R<sup>2</sup> of at least 0.98 was used to remove data when conditions were not favorable for measurement.

### Data Analyses

I used the convention of uptake as positive and emission via respiration as negative. Using the rectangular hyperbola (Thornley and Johnson 1990), the relationship between NEP and PAR is described as

$$NEP = \frac{\alpha + NEP_{max} \times PAR}{\alpha \times PAR + NEP_{max}} + R_{eco}$$

where NEP is NEE under full light with the chamber uncovered,  $\alpha$  is the initial slope of the rectangular hyperbola, also called the apparent quantum yield,  $NEP_{max}$  is the asymptotic approach to NEP, and  $R_{eco}$  is the y-axis intercept, or dark respiration. This relationship was used to fill measurement gaps and to estimate total annual CO<sub>2</sub> fluxes. I further compared the basic rectangular hyperbola fitted function to ones that allows  $R_{eco}$ ,  $NEP_{max}$ , and both flux parameters to be scaled by an influence of water depths such that full model looks like:

$$NEP = \frac{\alpha \times NEP_{max} \times e^{c \times wd} \times PAR}{\alpha \times PAR + NEP_{max} \times e^{c \times wd}} + R_{eco} \times e^{b \times wd}$$

where  $b$  and  $c$  are water depth scalars for  $R_{\text{eco}}$  and  $NEP_{\text{max}}$ , respectively. As the response of both uptake (NEP, as the response of both GPP and  $R_{\text{eco}}$ ) and release ( $R_{\text{eco}}$ ) may be expected to act differently with response to water, model fitting includes the addition of each scaling relationship separately and in combination.

I tested for site level and community effects via an analysis of variance (ANOVA), testing for differences in daytime NEP and ecosystem respiration. I did this both on the raw data and after de-trending for the light response. To determine which ancillary environmental measurements are most important for capturing measured variance (including landscape block, community, PAR, air and soil/water temperature and relative community) I used a tree regression to inform how I divided the data for model extrapolations. I further evaluated the rectangular hyperbola models across seasons, dividing the data into rising water (wet season 2011, or 7/8/2011 to 11/2/2011), falling water (dry season 2011, or 11/3/2011 to 5/17/2012), and the beginning of the following wet season (wet season 2012, or 5/18/2012 to 7/19/2012).

I used Akaike's Information Criterion (AIC) to compare between models as a test for whether treating the dynamic water table explicitly increases the predictive power of the model. A criterion of 4 AIC values was used to discriminate between models. As calculating an  $R^2$  of direct model fits is inappropriate for non-linear models, I use a proxy of fit by comparing the predicted values from the model to the measured values; the subsequent  $R^2$  is a measure of how well the predicted data correlated to the measured data.

The best-fit model was then used to estimate annual flux rates for the period of the measurements (incorporating water elevations; each hydrograph was offset for the

center of the landscape block, Figure 3-2) and soil elevation from the sites measured in Watts and others (2010). Extrapolations for all models were done from 7/20/2011 to 7/19/2012, the timing of which was dictated by when hydrologic data were available at all sites. By subtracting the median soil elevation for each community from the water elevation hydrographs, I constructed a water depth hydrograph for the most commonly observed conditions for ridges and sloughs in each landscape block. To evaluate these fluxes in terms of their significance for peat accretion, I converted the summed annual estimated fluxes for each community/landscape block to a *potential* peat elevation increase using soil values of an average bulk density of  $0.13 \text{ g cm}^{-3}$  and soil %C of 0.405 from Bruland and others (2006).

## **Results**

### **Climate and Environment**

Rainfall was higher during the observation period than the long-term average, with 1528 mm near Drained, 1528 mm near Conserved 1, 1707 mm near Conserved 2, and 1677 mm near Impounded (Figure 3-1A). This hydrologic year was unusual, demonstrating both a recovery from a deep drought as well as an early onset to the 2012 wet season (Figure 3-1B, Table 3-1). The beginning of the rise of the water table was a month or longer earlier than the long term (18-year) average across all sites. One key effect of the deep drought was a long delay before the water table reached the soil surface in the central part of WCA 3A. Another key effect was in the near complete lack of vegetation in the sloughs at the end of the dry season. Vegetation often totaling less than 5% of measured plots (see Figure 3-2), recovering to 25-100% cover by the peak of the wet season. Drained water levels started and ended more than 20 cm below the long-term average (18-year). A similar relationship was observed in Conserved 1,

although the ending water levels were closer to the long-term median values. In contrast, Conserved 2 started nearly 30 cm below the long-term median value, and ended in the upper 75-90<sup>th</sup> percentile of water levels, with a similar relationship observed in Impounded.

### **Instantaneous Fluxes**

There were clear differences in the measured community respiration ( $R_{\text{eco}}$ , indicated by positive values; Figure 3-4), with slough values averaging less than half those of ridge values. Although absolute  $\text{CO}_2$  flux values differ when comparing community (ridge vs. slough), sawgrass cover (*C. jamaicense*; greater or less than 45%), or landscape sampling unit, a clear seasonal response was not observed (Figure 3-3). There were some general differences by season, where slough respiration rates averaged 1.12 (wet season 2011), 0.67 (dry season 2011-2012), and 0.53 (wet season 2012)  $\text{mg CO}_2\text{-C m}^{-2} \text{min}^{-1}$ . Ridge respiration rates averaged 2.53, 1.57, and 1.75  $\text{mg CO}_2\text{-C m}^{-2} \text{min}^{-1}$  for the wet season, dry season, and commencement of the following wet season. Thus  $R_{\text{eco}}$  was still high early in the study, but thereafter settles into a relative constant value, where the similarity of which could have been induced by the unusually stable hydrologic conditions that persisted in the later portions of this study.

Rates of respiratory loss across the hydrologic year were greatest on ridges and smallest in sloughs (Figures 3-3, 3-4), with no significant difference among landscape units ( $p > 0.25$ ). The measured daytime NEP ( $\text{PAR} > 125 \mu\text{mol s}^{-1} \text{m}^{-2}$ ) ranged from -0.10 to -9.15 and 1.10 to -5.26  $\text{mg CO}_2\text{-C m}^{-2} \text{min}^{-1}$  for ridges and sloughs, respectively. Thus all the ridge sites showed net  $\text{CO}_2$  uptake at PAR levels greater than  $125 \mu\text{mol s}^{-1} \text{m}^{-2}$ , whereas slough sites demonstrated more variability across a broad range of PAR (Figure 3-4A). A tree regression suggested that after light levels and

community effects, the percent of ridge cover (at the 45% threshold) controlled the variance in flux measurements. I therefore used this threshold to compare flux rates (Figure 3-4 B-C; Figure 3-5A), and observed that while there was considerable overlap in flux rates, both  $R_{eco}$  and NEP were generally lower for the lower sawgrass area coverage. I was unable to establish a landscape block effect, in respiration or in NEP, or once de-trended for light (ANOVA,  $p > 0.05$ ). Tree regressions also did not demonstrate a landscape block effect, thus landscape position was not included in subsequent analyses.

## Models

Model fits for the rectangular hyperbola are shown in Table 3-2. Only models with significant parameters ( $p < 0.05$ ) are shown; where multiple models were significant, the model used for subsequent extrapolations is marked with an asterisk. The inclusion of parameters that permit inference of water level effects on both  $NEP_{max}$  and  $R_{eco}$  (water depth scalars  $b$  and  $c$ ) did not improve the model fit for ridges but did for sloughs in the global data set. Taking the residuals of global data sets, there was no significant relationship (linear;  $p > 0.05$ ) for water depth (ridges only), temperature (air), or soil temperature (water temperature, if inundated).

Dividing ridge measurements into two categories based on sawgrass cover improves model fit (as indicated by the proxy of an  $R^2$  of the predicted as a function of measured values; model curve fit is demonstrated in Figure 3-5). The observations of generally higher  $R_{eco}$  and NEP for  $>45\%$  sawgrass cover than for the lower is reflected in the model parameters. The consequences for fitting the rectangular hyperbola independently to different sawgrass covers is significant, with  $\alpha$  nearly 1.9 times higher,  $NEP_{max}$  nearly 1.7 times higher, and  $R_{eco}$  1.6 times higher with the greater sawgrass

cover (>45% sawgrass cover; Table 3-2). Interestingly, the inclusion of water depth scaling parameters for both  $NEP_{max}$  and  $R_{eco}$  was significant for the lower cover data, but not for the higher (Table 3-2). Monthly extrapolations for the division of sawgrass are shown in Figure 3-7A.

Model fits differed when dividing the data into hydrological seasons (wet 2011, dry 2011, and wet 2012; Table 3-2). The addition of water depth scaling variables do not improve ridge models for seasonal responses, but does improve slough models across all seasons (Table 3-2). Notably, however, there is low sample density during the early post-dawn hours across the entire data set due to condensation during this time. This low sampling density results in non-significant quantum yield values for the wet 2012-time period ( $p>0.1$ ). Monthly extrapolations for the seasonal models are shown in Figure 3-3B-D for the Drained, Conserved 2, and Impounded sites (Conserved 1 not shown due to similarity to Conserved 2).

The potential for  $CO_2$  uptake larger than the potential for loss was captured by the higher parameter values for  $NEP_{max}$  relative to  $R_{eco}$  (Table 3-3). To compare total ecosystem respiration to water column respiration I evaluated the  $R_{eco}$  in relation to the estimated  $R_{aq}$  (Chapter 2). The calculated  $R_{aq}$  ranged anywhere from an average of 31% of the  $R_{eco}$  rates to 90% (Impounded and Conserved 1, respectively) in ridges, but were generally higher than  $R_{eco}$  in sloughs (ranging from equal to nearly 2.5 times higher, Impounded and Conserved 2, respectively; Figure 3-6).

### **Annual Fluxes**

Summed monthly slough NEP estimates ranged between net autotrophy and net heterotrophy across all the landscape blocks. The greatest net heterotrophy occurring during the dry season for the Drained site (Figure 3-7). Despite larger respiratory losses

on ridges, ridges were net autotrophic after September. Unfortunately I lacked sufficient data to divide sawgrass into both seasonal responses and sawgrass cover, so I must evaluate model behavior for sawgrass density and seasonality on ridges separately. The conclusion of large carbon uptake by Impounded ridge communities with low vegetative cover (Table 3-3) may not follow real patterns— observations of sawgrass cover <50% were not observed in the field in the Impounded site. The greatest potential for carbon uptake (and respiratory loss) is in the high biomass ridge, although all of the ridge models resulted in net annual carbon uptake across all of the hydrologic conditions. Sloughs demonstrated variability of a net annual loss (Drained) to net annual uptake (Conserved through Impounded).

The conversion of annual net carbon flux was converted to a potential peat accretion increase and is shown as parenthetical notation in Table 3-3. In general, the potential for incremental peat increase was higher for ridges than sloughs, ranging from 1.8 to 7.6 mm yr<sup>-1</sup> in ridges and -0.4 to 1.6 mm yr<sup>-1</sup> in sloughs.

### **Discussion**

The central portion of the Everglades ridge-slough landscape retains the capacity for carbon uptake to exceed carbon losses. Community specific rates differed however, in terms of productivity, respiration, and the balance of the two. Slough vegetative communities demonstrated variation with respect to hydrology, consistent with expectations in terms of the effects of drainage. However, ridge communities did not demonstrate a corresponding hydrologic sensitivity. Only low-density sawgrass communities demonstrated a hydrologic relationship with NEP. The annual carbon uptake values I observe for ridges were not outside the range of carbon inputs for peat production in other tropical peat systems. For example, Chimner and others (2005)

estimated carbon accumulation to be closer to  $300 \text{ g C m}^{-2} \text{ yr}^{-1}$  in peatlands of Hawaii and Micronesia, similar to estimates in Thailand of  $527 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Suzuki and others 1999). However, estimated annual  $R_{\text{eco}}$  values for ridges in the Everglades were considerably lower than values for a tropical peat swamp in Indonesia (Hirano and others 2007; averaging  $3866 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), and all of the fluxes were substantially smaller than those observed in a drained tropical peat swamp of Indonesia (Hiraono and others 2007).

The results here are similar to those found by Jimenez and others (2012) in a long-hydroperiod peat portion of Everglades National Park from 2008-2009. However, the two studies are not directly comparable as the eddy covariance method incorporates both ridge and slough communities in the area footprint. Their site in SRS had peat depths similar to my sites (0.6-1.0 m thick in SRS, 0.3-0.86 m thick in WCA 3AN, 0.5-1.5 m thick in WCA 3AS). Watts and others (2010) suggest this area of SRS is of intermediate hydrologic degradation due to low water levels; topographic variation between ridges and sloughs are reduced but not yet lost and much of the slough community has been replaced by shallower water marsh species. However, Jimenez and others (2012) estimate an annual net loss of carbon, in contrast to this study estimating an annual net uptake at all but the slough communities in the Drained landscape. Lowered water levels due to lowered precipitation the years they observed may further explain the gap between their measurements and this study; precipitation during the sampling 2011-2012 period was roughly 50% higher than what they observed in 2009. The higher precipitation likely contributed to my observed lowered respiration during the 2011 to 2012 sampling period.

The observed increased potential carbon uptake in sloughs from drained to impounded hydrologic conditions is consistent with the deeper-water species responses. For example, *Nymphaea odorata* does not exhibit physiological limitations up to water depths of 2 m (Sinden-Hempstead and Killingbeck 1996). *N. odorata* (syn. *N. tuberosa*) demonstrates a high rate of rhizome respiration under increasingly anaerobic conditions (Laing 1940), likely due to increased oxygenation of the rhizosphere via a thermo-osmotic transport mechanism (Grosse and others 1991). As *N. odorata* is a dominant species in the deep-water sloughs, it can be presumed that low water is a greater stressor for these communities than high water.

Annual estimates of ridge soil/water respiration ( $R_{aq}$ ) are roughly 1/3 to 1/2 of the modeled ecosystem respiration ( $R_{eco}$ ; Table 3-3). In contrast, slough  $R_{aq}$  is estimated to be larger than  $R_{eco}$ . The lack of emergent vegetation in sloughs means  $R_{aq}$  may be nearly equal to  $R_{eco}$  in this community. There are three plausible explanations for this disparity. First, measured fluxes are far more variable than the modeled fluxes. The difference between the two model results may well not be significant with respect to measured variance. Secondly, it is possible that the difference in chamber sizes between the one deployed for  $R_{aq}$  and the substantially larger one deployed in this study resulted in non-comparable flux measurements. Further, both measured and modeled  $R_{eco}$  follow predictions that would be made based on community phenology and abundance and seasonal responses. This suggesting whatever resulted in seemingly low respiratory fluxes in sloughs is systematic. Finally, I suggested earlier that this hydrologic year was unusual relative to others. Since slough vegetation was severely affected by the 2010-2011 dry season drought, it is plausible that root respiration was

severely diminished in proportion to the loss of vegetative cover– an important consideration as root respiration can be 30 to 70% of total soil respiration (Schlesinger 1977). It may be that the length and severity of the dry season dry down has a strong control on all respiration rates, as was observed in chapter 2 and has been observed in other tropical peatlands (e.g., Couwenberg and others 2010). I surmise I simply did not observe the high respiration conditions that may be present many other years in the Everglades, and the flux measurements presented here are representative of one of many annual hydrologic scenarios that occur in the Everglades.

As a relatively young peatland the Everglades landscape has not yet reached a steady state. Peat formation started around 5000 years ago in the northern portions of the Everglades, with the majority of the Everglades initiating peat formations 2000-3000 years ago (Gleason and Stone 1994). Pre-hydrologic modification peat accretion rates in the Everglades were relatively low (0.1 to 0.6 mm yr<sup>-1</sup> accretion; Bernhardt and Willard 2009). The results presented here demonstrate a significant potential for peat accretion throughout WCA 3A under modern hydrologic conditions. The peat accretion estimates using NEP from this study are generally similar to other measurements of peat accretion rates in the Everglades. Peat accretion rates in sawgrass communities using <sup>137</sup>Cs dating in WCA 3A (for years 1983 to 1989; Craft and Richardson 1993) ranged from 2.0 mm yr<sup>-1</sup> for a core in the drained area to 3.2 mm yr<sup>-1</sup> for a core in the southern impounded area. The peat accretion rates I estimate for low density ridges matches these numbers, but estimates using the entire data set suggests much larger potential for peat accretion for ridges overall. However, all of the peat accretion rates for sloughs were similar to values of 0.8-1.55 mm yr<sup>-1</sup> measured by McDowell and others

(1969), although those values were for peat cores taken at the far northern end of the historic Everglades in what would have been a sawgrass plain.

The conversion to a potential peat accretion is not a wholly accurate way of looking at peat accretion potential, because I lack dissolved and particulate organic carbon measurements, methane production, quantification of ebullition events, and known lags in carbon turnover, particularly via standing dead matter in sawgrass. Although it is an important green house gas emitted by wetlands, CH<sub>4</sub> does not appear to be a large part of carbon fluxes in the ridge-slough Everglades. Relatively low rates of CH<sub>4</sub> production (Bachoon and Jones 1992), combined with little to no relationship with temperature (Harriss and others 1988; Bachoon and Jones 1992) and water depth (Debusk and Reddy 1992), and high rates of methane oxidation (King and others 1990), suggest that CH<sub>4</sub> is not a significant carbon mineralization pathway with respect to carbon mass balance. Although based on laboratory studies of Everglades peat, potential methane fluxes appears to be between 0 and 8% of total carbon efflux, with an average of 2% across a range of water levels (-15 to 10 cm water level; un-enriched peat cores; Debusk and Reddy 1992; also see Inglett and others 2012). Using that average to estimate CH<sub>4</sub>-C would reduce net carbon uptake estimates by roughly 0 to 27 g C m<sup>-2</sup> yr<sup>-1</sup>.

There is a further loss of dissolved organic carbon (DOC) not covered by this study. A substantial portion of the DOC in the water column is photolysized (Qualls and Richardson 2003), which is likely included as a respiratory component of the NEP measurements under full light conditions. The proportion of DOC mineralized by microbes is fairly small (<10% over 6 months; Qualls and Richardson 2003), so the

respiration of DOC likely made up a very small proportion of the measured fluxes here. However, DOC production is also generally very low outside of the Everglades Agricultural Area, less than 6% of ecosystem productivity in WCA 2 in the un-enriched areas (Qualls and Richardson 2003). I can therefore estimate combined losses from DOC and CH<sub>4</sub> of roughly 20 to 50 gC m<sup>-2</sup> yr<sup>-1</sup> for ridges and 9 to 14 gC m<sup>-2</sup> yr<sup>-1</sup> for sloughs. While this still leaves a small excess of production in ridges, the balance for sloughs begins to approach carbon neutral.

Ebullition may be the source of a large loss of carbon to the atmosphere in many peatlands, and remains difficult to quantify. Observed ebullition in peatlands can be quite high, with estimates as high as 35,000 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> (Minnesota; Glaser and others 2004), 10 to 1666 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> (Canadian fen; Strack and others 2004), and single releasing events between 100,000 and 172,000 mg CH<sub>4</sub> m<sup>-2</sup> occurring within less than 4 hours (Comas and others 2008). Measurements in the Everglades peats suggest high potential carbon fluxes via bubbling; Chanton and others (1988) determined bubble compositions between 10 to 33% CH<sub>4</sub>, 56 to 75% N<sub>2</sub>, and 2 to 4% CO<sub>2</sub>. Rare, large ebullition events in Everglades peats can be as much as an order of magnitude larger than daily ebullition, and are highly temporally heterogeneous (Comas and Wright 2012).

It is also important to consider the role fire may play in regulating carbon dynamics. Although natural return intervals for the Everglades are unknown (Lockwood and others 2003), sawgrass burns well and frequently, both via lightning strikes and fire management. The presence of standing dead, which can be as much as 3 years old (Mark Clark, personal communication), means carbon losses are not just from a single

year's biomass production. Presuming there is a proportionate loss of standing dead for each of the three years before becoming litter or peat, the losses of aboveground biomass (living + dead) to fire could eclipse the annual carbon uptake for any given year. This loss would be restricted primarily to ridges, as emergent biomass is generally too low to carry a fire across sloughs, and standing water during most years in sloughs would diminish the risk of peat fires. I can estimate a fire return interval using a very simplified set of conditions. Assuming 1/3 of the production in any year is converted to peat in each of three subsequent years. The standing biomass would include  $\text{production}_{(t)} + 0.67 * \text{production}_{t-1} + 0.33 * \text{production}_{t-2}$ . Assuming fire would remove all the standing vegetative material resulting in a zeroed productivity for that year, a fire return interval of 0-11 years is sufficient to reduce all of the peat accretion values in Table 3-3 to a long-term average of 0 mm. In reality, if the majority of the source material for peat comes from roots then this calculation over estimates the control fire would have on peat production. This over estimation may be balanced by the occasional peat fire, which not only consumes above ground biomass but also would likely kill roots and remove surface peat layers. Regardless of these considerations, it can be presumed that carbon loss to fire, although episodic, is a substantial regulator of long-term carbon budgets.

Literature values for net aboveground primary productivity (NAPP) in the Everglades are shown in Table 3-4. Although NAPP and NEP are problematic to reconcile, it is constructive to observe that the annual NEP values are not dissimilar to observed values of NAPP across the Everglades, both for ridges and sloughs, for most studies. As suggested by this study, the potential for peat accretion is highest in ridges

and varies based on sawgrass density and stature. This provides some confidence in the estimates, although with the caution that different hydrologic years may result in dramatically different flux rates.

Ultimately, interannual variation in hydrology may induce equivalency in the community carbon budgets. As ridges are situated higher in the water column, they are also more likely to experience prolonged periods of oxidation during drier years. The hydroperiod in ridges can vary substantially in length from year to year. For example, the hydroperiod was 160 days longer in 2010 than 2011 for ridges. Ecosystem respiration for the low density sawgrass demonstrated increases with decreased water levels (Table 3-3). It is within reason to expect that drier years would produce similar results across all ridges, ultimately lessening the high rate of potential peat accretion in ridges.

### **Conclusions**

Despite substantial hydrologic modification to the Everglades, the central portion of the ridge-slough landscape has a carbon accretion potential with declines in that potential with lowered water levels. Carbon fluxes differ seasonally, and the rate for all carbon fluxes in ridges is related to sawgrass density. As expected, the potential for carbon accretion is substantially higher on ridges than sloughs. In order for ridges to have equivalent net carbon balances to sloughs requires a loss of carbon from sloughs that is not covered by this study, but does suggest that exogenous carbon inputs to maintain ridge elevations may not be necessary to maintain ridge and slough soil elevation differences.

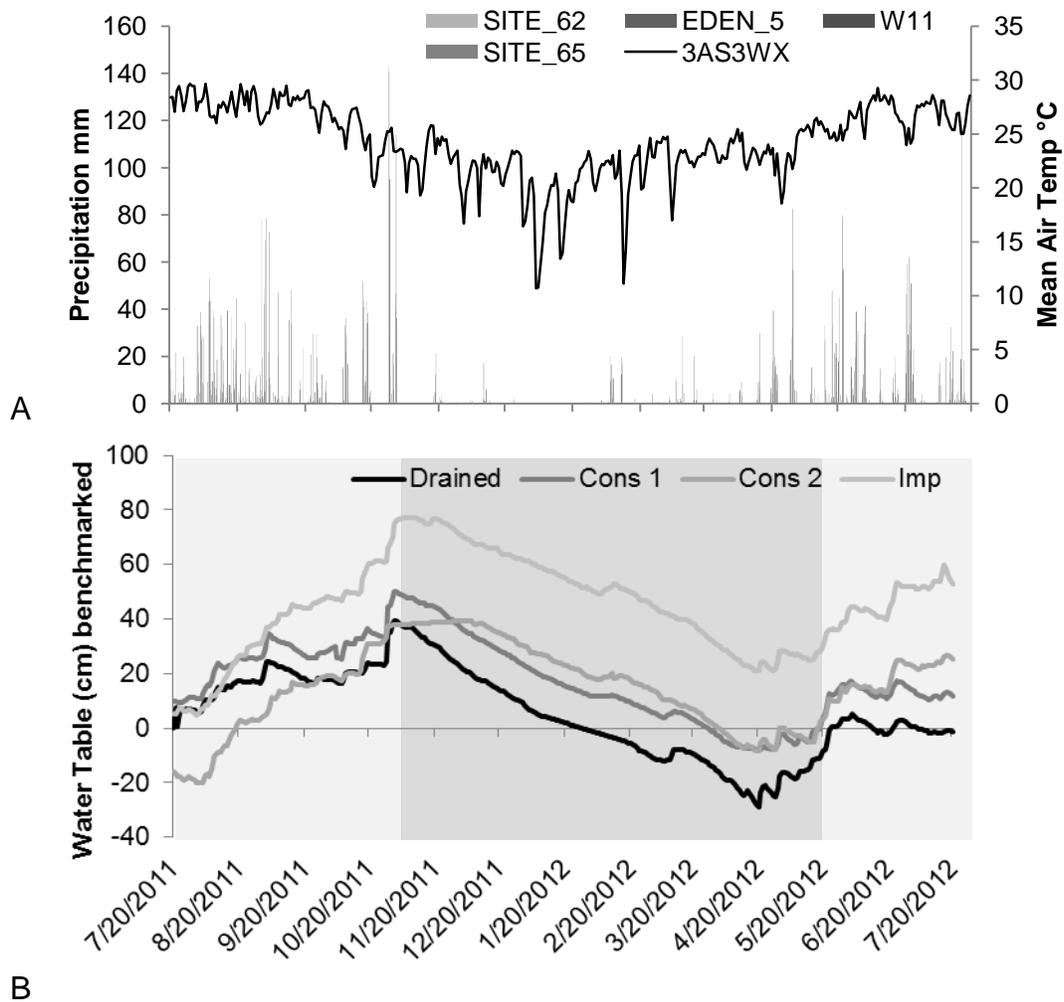


Figure 3-1. Environmental conditions during the period of study. A) Rainfall for the nearest meteorological stations, corresponding with Drained through Impounded and daily average air temperature from 3AS3WX. B) Water depths at the median ridge elevation (from Watts and others 2010) for hydrologic year 2011-2012. Mean slough water depths would be +6, +19, +22, and +10 cm for each of the respective landscape blocks. Shadings indicate (from left to right) wet season 2011, dry season, and the early commencement of the wet season, 2012.

Table 3-1. Hydrologic characteristics for each sampling block from  
7/20/2011-7/19/2012.

	Ridge water depths (cm)				Slough water depths (cm)			
	Min	Med	Max	Hydro- period	Min	Med	Max	Hydro- period
Drained	-28.8	3.3	39.5	193	-25.3	6.8	43.0	265
Conserved 1	-9.4	13.7	48.7	310	7.1	30.2	65.0	365
Conserved 2*	-20.9	15.6	38.9	269	0.0	36.3	60.0	365
Impounded	5.2	46.7	77.5	365	19.2	60.7	91.5	365

\*There is a lack of data at the peak of the hydrograph, so data is interpolated linearly between points; this likely results in an underestimation of the peak water depth for this site.



Figure 3-2. At the end of the 2011 dry season, sloughs were nearly devoid of vegetation. This picture was taken less than a kilometer off of Tamiami Trail in WCA 3AS, oriented north, in what is commonly considered the wettest portion of the Everglades. The sinusoidal trail is an alligator track. Photo courtesy of Danielle Watts.

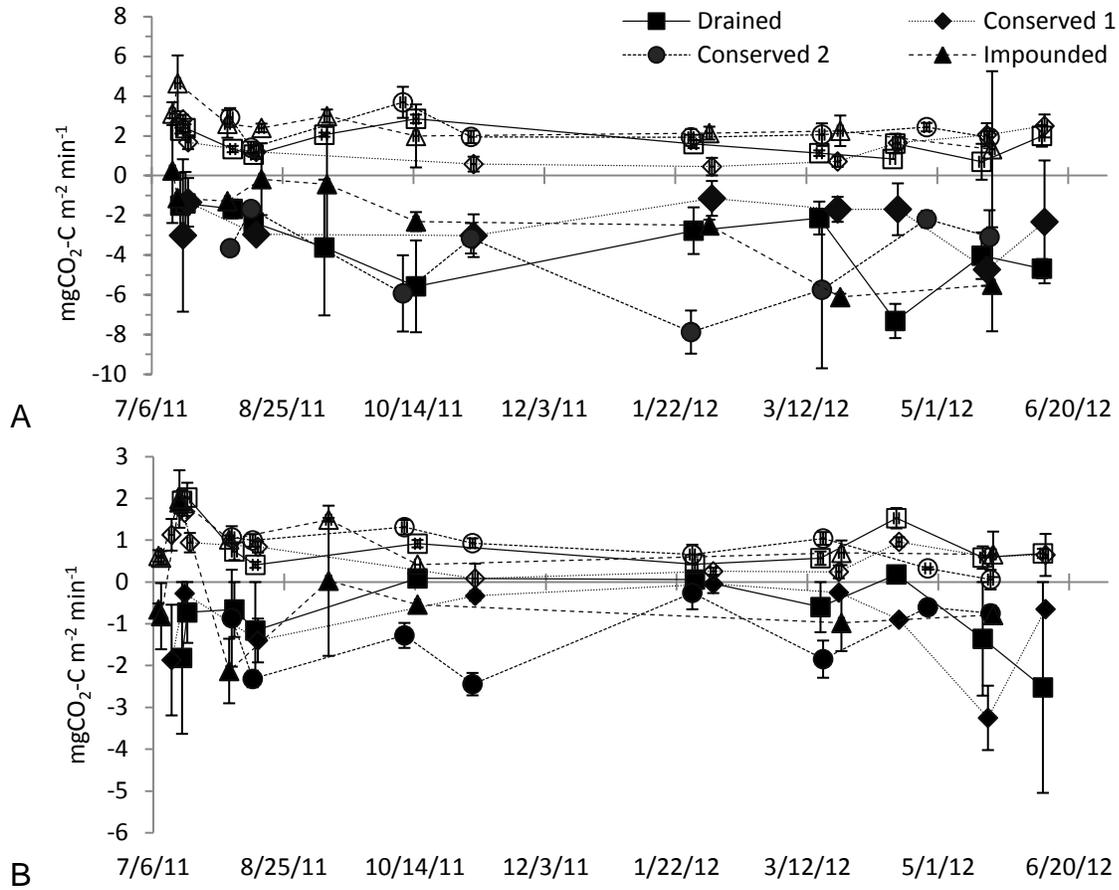


Figure 3-3. Daily average ( $\pm$  s.d. for each day/location) of daytime net CO<sub>2</sub> exchange (NEP, closed symbols) and total respiration (R<sub>eco</sub>, open symbols). A) Ridges and B) sloughs at sampled locations in WCA 3A.

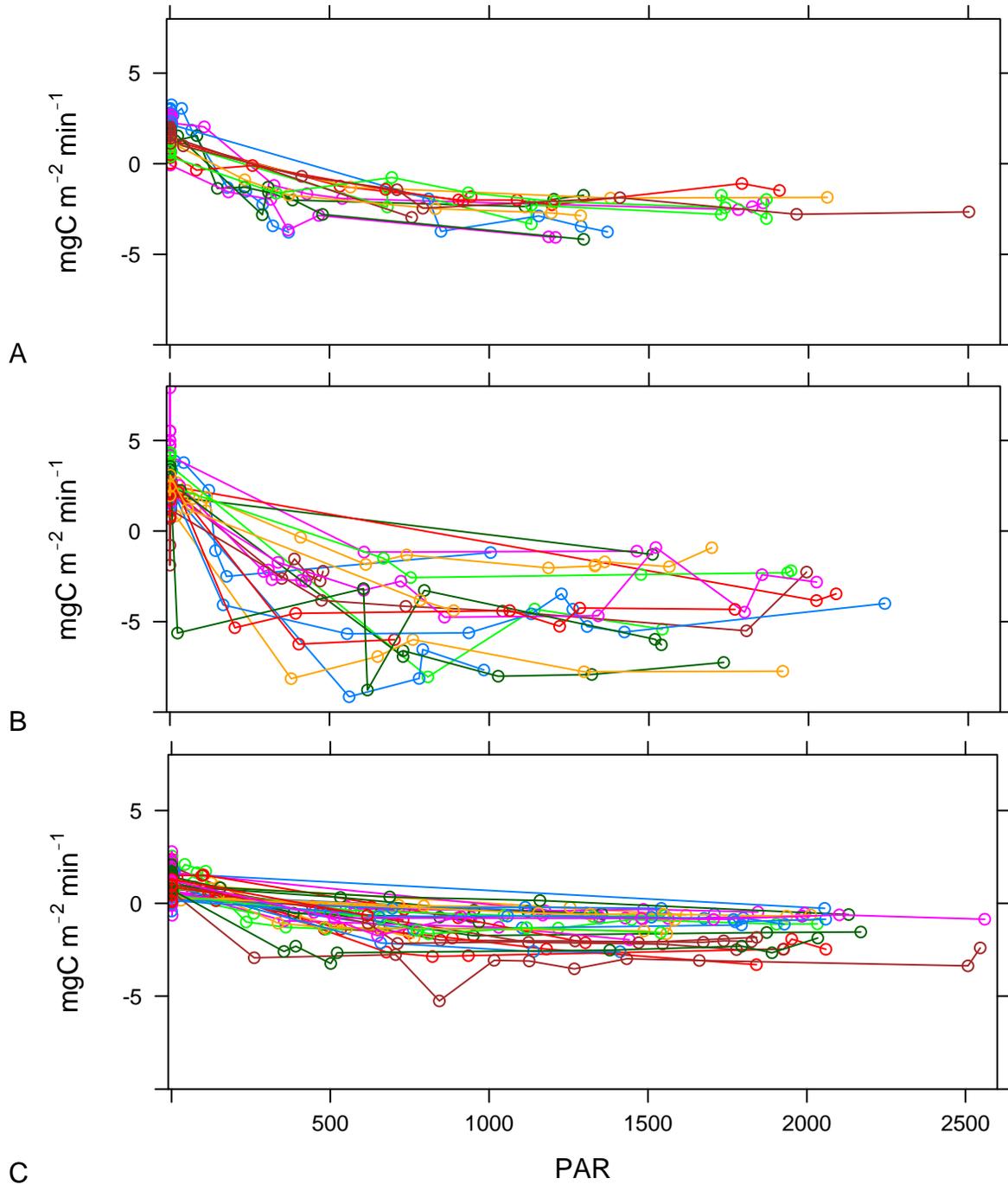


Figure 3-4. The variation in daily measured fluxes as a function of PAR (in  $\mu\text{mol s}^{-1} \text{m}^{-2}$ ). A) Ridges with sawgrass cover less than 50% and B) ridges with sawgrass cover equal to or greater than 50% and C) sloughs. Colors indicate different sampling sites/days.

Table 3-2. Parameters and model criteria for the rectangular hyperbola function (in mg CO<sub>2</sub>-C m<sup>-2</sup> min<sup>-1</sup>). Only models with significant parameters are shown. Parenthetical notation is the standard error of the estimate.

	$\alpha$	NEP <sub>max</sub>	R <sub>eco</sub>	R <sub>eco</sub> Scalar	NEP Scalar	AIC	R <sup>2§</sup>
<b>Ridge</b>							
Global Data	-0.041 (0.007)	-6.64 (0.27)	2.25 (0.11)	...	...	...	0.73
<i>C. jamaicense</i> <45% cover	-0.029 (0.006)	-4.66 (0.23)	1.62 (0.09)	...	...	424	0.83
	-0.030 (0.006)	-4.58 (0.25)	1.81 (0.09)	-0.0067 (0.001)	...	416*	0.84
	-0.030 (0.006)	-4.18 (0.25)	1.62 (0.09)	...	0.0047 (0.001)	416*	0.84
<i>C. jamaicense</i> >45% cover	-0.055 (0.014)	-7.77 (0.41)	2.59 (0.17)	...	...	...	0.75
Wet 2011	-0.038 (0.008)	-6.18 (0.33)	2.66 (0.12)	...	...	...	0.74
Dry 2011	-0.037 (0.012)	-6.73 (0.56)	1.67 (0.19)	...	...	...	0.73
Wet 2012	-0.173 (0.09)	-6.68 (0.38)	2.12 (0.28)	...	...	...	0.82
<b>Slough</b>							
Global Data	-0.011 (0.0024)	-2.79 (0.17)	0.92 (0.05)	...	...	925	0.66
	-0.010 (0.002)	-3.54 (0.34)	1.12 (0.10)	-0.0083 (0.003)	-0.0091 (0.003)	917*	0.67
Wet 2011	-0.011 (0.002)	-3.19 (0.21)	1.15 (0.06)	...	...	419	0.77
	-0.011 (0.003)	-3.95 (0.47)	1.15 (0.06)	...	-0.0086 (0.004)	416*	0.77
Dry 2011	-0.0048 (0.002)	-2.01 (0.39)	0.69 (0.07)	...	...	216	0.57
	-0.0048 (0.002)	-1.44 (0.30)	0.94 (0.09)	-0.018 (0.005)	0.0064 (0.004)	191*	0.66
Wet 2012	0.035 (0.031)	-2.25 (0.25)	0.51 (0.15)	...	...	187	0.67
	-0.079 (0.14)	-3.63 (0.42)	0.57 (0.14)	...	-0.014 (0.004)	170*	0.75*

§R<sup>2</sup> is for *predicted*~ *f(measured)*

\*Where more than one model had significant fits, the model for extrapolation is asterisked.

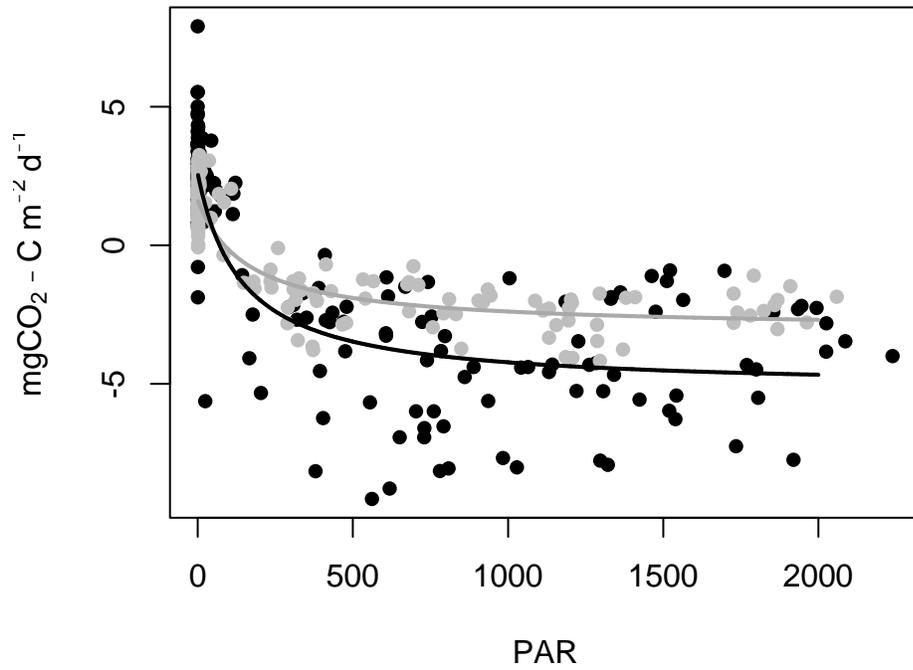


Figure 3-5. Ridge NEP and fitted model (model without water depth scalars; parameters in Table 3-2) for less than 45% sawgrass cover (grey circles) and more than 45% cover (black circles). PAR is in  $\mu\text{mol s}^{-1} \text{m}^{-2}$ .

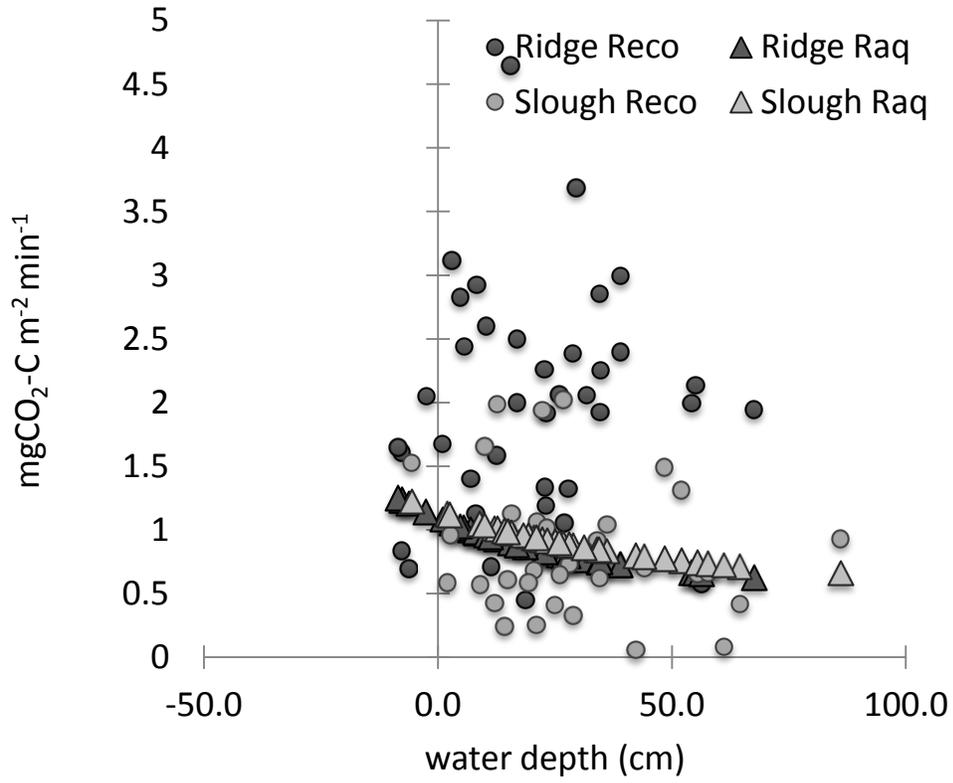


Figure 3-6. Measured ecosystem respiration (daily average,  $R_{\text{eco}}$ ) and modeled soil respiration ( $R_{\text{aq}}$ ) with relation to local water depths.

Table 3-3. Summed, modeled NEP and respiration for hydrologic year 2011-2012 ( $\text{g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ ). Numbers are for the median community elevation from Watts and others 2010 (sloughs and wet prairies combined as one community). Model parameters are in Table 3-2.  $R_{\text{aq}}$  is based on the asymptotic model in Chapter 2. Parenthetical notation indicates conversion to an approximate peat accretion increase in  $\text{mm yr}^{-1}$ .

NEP ( $\text{mm yr}^{-1}$ )	Ridge				Slough			
	Global	*Sawgrass <50%	Sawgrass >50%	Seasonal	Global	Seasonal		
Drained		-93 (1.8)	-113 (2.1)		-28 (0.5)	22 (-0.4)		
Conserved 1	-269	-158 (3.0)	-148 (2.8)	-400 (7.6)	-392 (7.4)	-50 (0.9)	-32 (0.6)	
Conserved 2	(5.1)	-147 (2.8)	-142 (2.7)			-51 (1.0)	-59 (1.1)	
Impounded		-310 (5.9)	-251 (4.8)			-62 (1.2)	-83 (1.6)	
<b>GPP</b>								
Drained			-968			-583	-467	
Conserved 1	-1453	-1017	-1003	-1766	-1462	-505	-423	
Conserved 2			-997			-498	-427	
Impounded			-1016			-429	-399	
<b>Respiration</b>								
	Global	Sawgrass <50%	Sawgrass >50%	Seasonal	$R_{\text{aq}}$	Global	Seasonal	$R_{\text{aq}}$
Drained		924			565	555	489	566
Conserved 1	1184	859	855	1366	1070	486	391	456
Conserved 2		869			500	447	368	449
Impounded		707			376	367	316	389

\*Since 2 models appeared to have equal goodness of fit, the first number is the model using a respiration scalar; the second is the model using the NEP scalar.

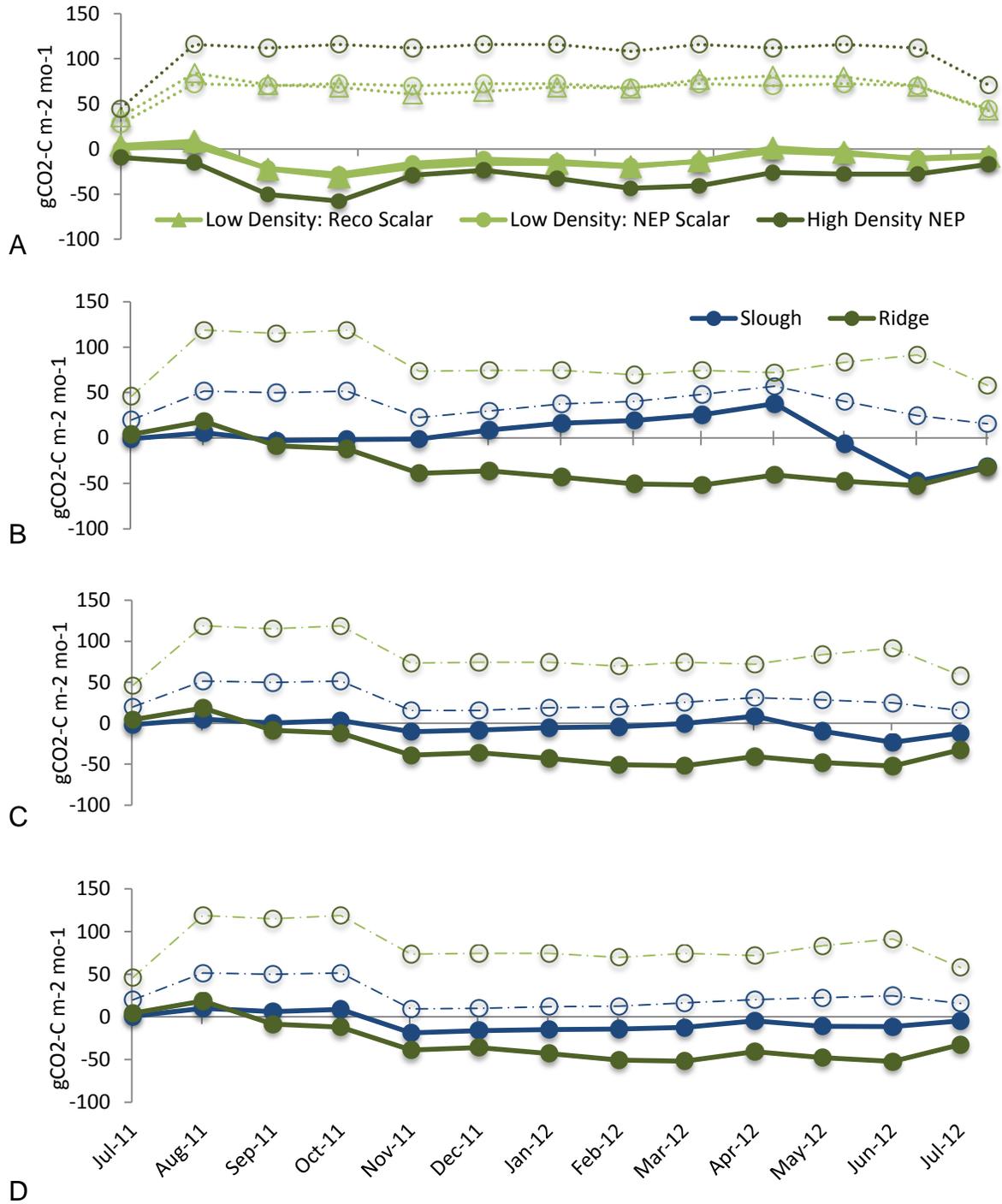


Figure 3-7. Seasonal variability in monthly C uptake and release. Extrapolations are for A) sawgrass density less than and greater than 45% (for Conserved 2), and seasonal models for B) Drained, C) Conserved 2, and D) Impounded. Parameters for the extrapolations are in Table 3-2.

Table 3-4. Literature values for ridge (or sawgrass community) and slough annual net aboveground primary productivity for the Everglades.

Community	Location	gC m <sup>-2</sup> yr <sup>-1</sup> *	Citation
Sawgrass		1436±427	Daoust and Childers 1998
Sawgrass		385-1457	Davis 1989
Sawgrass	Northern ENP	144-408	Daoust and Childers 1999
Wet Prairie	Northern ENP	14-65	Daoust and Childers 1999
Wet Prairie		196±77	Daoust and Childers 1998
Sawgrass	Shark River Slough	80-384	Ewe and others 2006
Tall Ridge	North WCA 3A	2062 ± 9	Lewis 2005
Sawgrass	Central WCA 3A	1760 ± 108	
	North ENP	2715 ± 48	
	Central ENP	1807 ± 202	
Short Ridge	North WCA 3A	1194 ± 77	Lewis 2005
Sawgrass	North ENP	525 ± 6	
	Central ENP	1674 ± 135	
Slough	North WCA 3A	808 ± 128	Lewis 2005
	Central WCA 3A	406 ± 195	
	North ENP	319 ± 103	
	Central ENP	728 ± 76	

\*g DW m<sup>-2</sup> yr<sup>-1</sup> was converted to gC m<sup>-2</sup> yr<sup>-1</sup> using an estimate of 48% C.

## CHAPTER 4 EVIDENCE FOR TRANSPIRATION-INDUCED NUTRIENT ACCUMULATION

The Everglades ridge-slough patterning organizes along hydrologic flow lines but the mechanisms underlying pattern origin and maintenance remain uncertain (SCT 2003; Larsen and others 2007; Cohen and others 2011). Most attention has focused on surface-flow phenomena with support for two mechanisms. Substantial empirical and modeling efforts to date offers some support for the first, wherein preferential deposition of particulates from sloughs to ridges occurs due to velocity differences between the communities during high flow events (sediment redistribution hypothesis; Larsen and others 2007; Larsen and others 2009; Larsen and Harvey 2010). A second mechanism proposes that ridges and sloughs organize to maintain landscape discharge competence so that sloughs self organize to route water (self-organizing canal hypothesis; Cohen and others 2011; Heffernan and others in press). Here we provide support for a third mechanism, where subsurface flow induced by differences in evapotranspiration leads to a subsidy of nutrients to ridges (Ross and others 2006; Cheng and others 2010).

Evapotranspiration gradients between communities can have significant influences on ecosystem and landscape water budgets, nutrient movement, and carbon accrual (McLaughlin and others 2012; Eppinga and others 2008; Mitsch and Gosslink 2011). Nutrient focusing induced by evapotranspiration differences between patch types has been demonstrated in both northern and subtropical peatlands (for example, Eppinga and others 2008; Nachabe and others 2005). In these cases, higher plant productivity in one patch coincides with higher ground elevation; higher evapotranspiration of this patch induces convergent flow of pore water with associated

nutrients towards the higher elevation from adjacent areas. This resource concentration supports the higher productivity in those patches but is critically limiting on a larger scale: As local focusing of water and nutrients is induced, there is a resulting distal inhibition where nutrient depletion in adjacent patches becomes limiting at larger scales. This combination of local activation and distal inhibition are referred to as scale dependent feedbacks (Eppinga and others 2008) and results in regular peatland surface patterning, although it is important to note that this self-organized patterning neither limited to peatlands nor is the only process demonstrated to lead to regular surface patterning (e.g., Rietkerk and others 2008).

The contention that the Everglades is a self-organized patterned landscape is largely the result of pattern metrics, both in patch geometry (Wu and others 2006) and soil elevation (Watts and others 2010), which demonstrate predictable degradation with altered hydrology (primarily water depths and hydroperiod). Notably, patterning is found in both vegetative communities (e.g., patch configuration—Wu and others 2006; species assemblages— Busch and others 1998; patch productivity—Daoust and Childers 1999; Ewe and others 2006, others) and soil elevation (Watts and others 2010). There is some evidence that both patterns are reflected in soil phosphorus concentrations with ridge TP ca. 100-150 mg kg<sup>-1</sup> higher in ridges than sloughs (Cohen and others 2009) and tree islands as much as an order of magnitude higher than the surrounding marsh (Ross and others 2006; Wetzel and others 2005). These observations have led to hypotheses of evapotranspiration gradients between patch types concentrating nutrient to higher elevations (Wetzel and others 2005; Ross and others 2006). Indeed, the mechanism has proved likely on many of the Everglades tree islands with observations

of diurnal reductions in water tables in the 1 to 3 cm range during the dry season and a predominance of groundwater recharge during the wet season (Ross and others 2006; Adamski 2009; Troxler and others 2009), although this resource concentration mechanism is likely only one of several working simultaneously on tree islands (Wetzel and others 2011).

Applying this hypothesis to pattern evolution in ridges and sloughs has been more problematic. In contrast to tree islands, the more productive, higher elevation sawgrass patches (ridges) are inundated for most of the year (ca. 310 days in the central Everglades), with even longer hydroperiods in sloughs (350+ days). Precipitation exceeds evapotranspiration in most years (German 2000), so a persistently higher head in ridges is unlikely. Further, the window of time for ridge transpiration to obtain soil water pulled through the peat matrix rather than accessing shallow surface water is short; in many years most ridges will be permanently inundated (Watts and others 2010; McVoy and others 2011). Deep and prolonged inundation during the typical wet season, which is also the typical growing season, should result in a chronic diffusion of any bio-available nutrients. There are, however, years with significantly longer and more severe dry seasons where an evapotranspiration mechanism could act more strongly. Even if a head gradient were not observed, equilibration of the water table between ridges and sloughs during the dry season would suggest a subsidy of water from sloughs to ridges. During those times when ridge soils are exposed, higher potential evapotranspiration must result in a subsidy of water to ridges from somewhere with the only likely source being inundated sloughs.

The objective of this study was to evaluate diurnal water table dynamics to assess an evapotranspiration-induced resource concentration on ridges. I do this via comparisons of diurnal water table dynamics between adjacent ridges and sloughs in Water Conservation Area 3A (WCA 3A). The hypothesis of a groundwater subsidy from sloughs to ridges implies amplified diurnal water table fluctuations in sloughs as the water table recedes from the soil surface in adjacent higher-elevation ridges. In this scenario the slough water table responds both to local evapotranspiration *and* demand for water from adjacent ridges. Under the scenario of a disconnected water table, the soil matrix amplifies diurnal changes to the water table in ridges but not sloughs. A connected water table suggests an amplified diurnal response of the water table in sloughs and a diminished response in ridges as ridge water demand is subsidized by adjacent sloughs. The equilibration of the water table would result in the ridge and slough water tables responding as the average of above and belowground signals, with the magnitude proportional to the relative abundance of ridges and sloughs.

## **Methods**

### **Data Collection**

Two sites of adjacent ridge and slough were chosen in WCA 3A (Figure 4-1). The Drained site is located in WCA 3AN (Figure 4-1, Table 4-1), designated as a drained area because of prolonged historically low water levels (Drained; Watts and others 2010). This area has shallow peat depths of less than a meter (Table 4-1). Vegetation cover at the Drained ridge was *Cladium jamaicense* (sawgrass) with epiphytic mats of periphyton. The slough was characteristic of a wet prairie, with periphyton, *Sagittaria lancifolia*, *Eleocharis* spp., *Bacopa caroliniana*, and *Panicum* spp.

The Conserved site (in the landscape unit referred to as Conserved 2 in Watts and others 2010) is located in the central portion of WCA 3AS (Figure 4-1, Table 4-1). Ridge vegetation was dense *Cladium jamaicense* with *Cephalanthus occidentalis* and sparse *Justicia angustifolia*. *Nymphaea odorata*, *Utricularia* spp., *Nymphoides aquatica*, and periphyton, with interspersed *Crinum* and *Eleocharis* spp, dominated the slough vegetation. The Conserved site has much deeper peats, averaging more than a meter deeper than those of the Drained site (Table 4-1).

Diurnal water table changes were measured in surface water wells installed in adjacent ridges and sloughs. The wells were constructed of Schedule 40 PVC pipe, screened above and below the soil surface. The installation depth was determined by the depth of peat to limestone bedrock (Table 4-1); anchoring to bedrock removes shrink-swell effects of the peat, the magnitude of which remains unknown. Total pressure was measured at 15-minute intervals using a total pressure transducer (Solinst Gold Leveloggers®, accuracy = 0.3 cm, resolution = 0.005 cm). A third dry well, open to atmospheric pressure, was installed near each ridge well and equipped with a barometric pressure transducer hung below the soil surface to account for temperature sensitivity described by McLaughlin and Cohen (2011). Total pressure was corrected for barometric pressure variation by barometric pressure transducers (Solinst Barologgers®, accuracy = 0.1 cm, resolution = 0.003 cm). Water depths were noted at 3 locations around each well averaged and converted to soil surface elevations using water elevation hydrographs at nearby Everglades Depth Estimation Network (EDEN) gauging stations. Probes were changed at Conserved on 2/26/2011 and Drained on 2/27/2011; readings were adjusted for a small offsets between probes (<0.5 cm). The

water table dropped below the sensors during the dry season at the Drained site (3/20/11 to 6/28/11 for the ridge well, 5/5/2011 to 6/28/11 for the slough well) and these data were excluded from analysis, as were days with rain (Figure 4-2).

### **Data Analysis**

A small but persistent drift (2.5 cm over the period of record) between the ridge and slough water level loggers rendered an analysis of head gradients impossible for the Conserved wells. However, the change over any single day was very small (~0.005 cm). As such, any analysis of diel variation was judged to be robust for subsequent analyses. This drift was not observed in the Drained site, so I evaluated water levels at this site for a persistent head difference between wells by comparing the difference in water stage.

In order to evaluate the presence of a lock-step response in water tables between ridges and sloughs I used an evapotranspiration: potential evapotranspiration (PET) relationship to infer groundwater exchange between ridges and sloughs. Evapotranspiration calculations are sensitive to the specific yield ( $S_y$ ) of either the vegetation, when water levels are above the soil surface, or of the soil matrix, when water levels are below the soil surface, with substantial differences in the specific yield between the two conditions. Thus evapotranspiration/PET should be between 0 and 1 when the water table is above the soil surface (where the specific yield approaches 1 due to the low displacement by marsh vegetation). Evapotranspiration/PET should increase in proportion to soil specific yield when the water table is below the soil surface (in response to the much lower specific yield of soil, here peat). If ridges and sloughs are hydrologically disconnected (i.e., no or little equilibration of the water table in response to higher evapotranspiration on ridges) then the slough

evapotranspiration/PET should remain between 0 and 1 during the critical time when ridges are dry but sloughs remain inundated. However, should evapotranspiration/PET in both communities act as a composite of ridge and slough conditions during this critical time then I can infer nearly instantaneous equilibration between ridges and sloughs. PET was estimated using the Hargreave's method (Hargreaves and Samani 1982), which incorporates length of day, air temperature, and monthly averaged incoming extraterrestrial radiation (<http://www.fao.org>). Meteorological data used to calculate PET was accessed via DBHYRO (<http://www.sfwmd.gov>). Air temperature and solar radiation data was accessed from S140W, located approximately 10.5 km from the Drained wells and from 3AS3WX, which is located roughly 15 km southwest of the Conserved wells.

I use this ratio method rather than directly measure evapotranspiration with specific yield for three reasons. First, the behavior of the groundwater is the variable of interest, and thus a relationship form is appropriate for this study. Moreover, there are considerable difficulties in accurately measuring specific yield, the most careful measurement of which may still miss the effects of hysteresis, air entrapment, microbial generation of gases, dissolution of gases, shrinking and swelling of the soil matrix, the effects of soil moisture, and capillary effects (examples include Duke 1972; Sophocleous 1985; Fayer and Hillel 1986a, 1986b; Choi and others 2003). A number of studies provide estimates of specific yield in the Everglades. For example, Gesch and others (2007) estimated porosities of 0.75 to 0.85 g cm<sup>-3</sup> for organic histosols in the Everglades, the high porosities in lines with specific yield values of 0.2 used by regional hydrologic models (Nair and others 2001; Wilsnack and others 2001), and strikingly

similar to the 0.22 calculated by Sumner (2007) for the Everglades. However, Sumner (2007) demonstrates out that estimating specific yield with simplified values above and below the soil surface creates large errors due to microtopography. Microtopography significantly influences realized specific yield (i.e. ESY) with a connected water table (also see McLaughlin and others 2011), where the water table in lower elevation areas are partially controlled by the ground water response to specific yield of higher elevation areas.

Evapotranspiration and exfiltration were calculated using two different methods using barometrically corrected water level data (Figure 4-3). White (1932) developed a method of analyzing groundwater fluctuations to determine use by plants, such that

$$ET = (\Delta h + \Delta G) \times Sy$$

where  $\Delta h$  is the change in water elevation at midnight between one day and the next (or,  $h_1 - h_2$ ) and  $\Delta G$  is the slope of ordinary least squares best-fit lines between nighttime water level and time and Sy is the specific yield (hereafter referred to as the White Method; Figure 4-3b). The diurnal period for the fitting of the slope was extended to 22:00-5:00 from 0:00-4:00 to improve the fit due to noise during low flux times of the year. This method was used when the  $R^2$  of the fitted slope fell between 0.15 and 0.85. Below 0.15, ET is considered to be negligible and essentially 0. A non-linear water table response occasionally caused the fit to be poor; on these occasions I instead used a method described by Hays (2003) as the draw down recharge method (hereafter referred to as the Hays Method). This method calculates evapotranspiration as

$$ET = h_1 - l + \frac{h_2 - l}{t_1} t_2 \times Sy$$

where  $h$  is the water level high,  $l$  is the water level low, and  $t_1$  and  $t_2$  are the lengths of time for night time recharge and daytime recharge, respectively (Figure 4-3a). The Hays method provides the average recharge rate during the diurnal cycle so that short-term alterations in rates (which lead to intermediate  $R^2$  values under the White method) do not affect the calculations. This method does not compensate for nighttime transpiration as the White Method does, and thus is a more conservative estimate for water use. The White Method, in comparison, considers recharge and daily changes in the water table, but assumes that recharge remains constant over any 24-hr period. Days where evapotranspiration values were artificially measured to be negative due to very low evapotranspiration fluxes were excluded. All such instances occurred during winter months when water was above the soil surface. Days with rainfall were also excluded; rainfall data came from gage-adjusted Next Generation Radar (NEXRAD) data from the U.S. National Weather Service, made available by the Everglades Depth Estimation Network (EDEN) via <http://sofia.usgs.gov/eden/nexrad.php>. Rainfall data for the Drained wells was obtained from EDEN site ID 3AN1W1, located 2.45 km (ridge) to 2.11 km (slough) away from the well locations. Rainfall data for the Conserved wells came from EDEN site ID Site\_64, located approximately 2.35 km from the wells.

I observed differing evapotranspiration/PET response during the 2011 wet season from 2010 values for the same water levels, with evapotranspiration/PET well over 1.0 for all dates after 8/1/2011; during the 2011 rise in the water table the diurnal variation in water levels is as high as 1.5 to 3 cm even after the water table rose above the soil surface across all of the wells. As this is inconsistent with all theoretical models of evapotranspiration/PET when  $S_y$  approaches 1, something systematic occurred either

to the sensors or to the local environment to dramatically increase the calculations. After careful evaluation of the barometric and temperature readings across all of the sensors, I conclude that the large diurnal signature is not consistent with errors due to sensor malfunction or drift nor is due to problematic calculations in evapotranspiration values. I am forced to conclude that there is an explanation not provided by available information (meteorological, stage, sensor, or vegetative) for these unusual readings. I therefore use only the data prior to 8/1/2011 for further evapotranspiration analysis. What remains unknown are regional water flows; marsh surface water velocity is not available but I infer from extended gate openings after 8/5/2011 at the southern end of WCA 3A that water flow may have been much higher during this time. Evapotranspiration calculations are generally problematic in flowing systems, thus accurate evapotranspiration calculations in the Everglades may only be possible when flow is negligible.

### **Subsidy Calculations**

Under the scenario of a rapidly equilibrating water table between ridges and sloughs,  $S_y$  and ESY (ecosystem specific yield) should diverge during the period of time when one ecosystem patch has the local  $S_y$  of peat (ridges) and the other has the  $S_y$  of open water (sloughs). Assuming that the full water demand is being met during this time, the observed change in water level in both ridges and sloughs should be PET/ESY, where ESY is approximated as

$$ESY = \frac{A_R \times Sy_p + A_S \times Sy_o}{A_R + A_S}$$

$A_R$  and  $A_S$  are the areas of each ridges and sloughs and  $Sy_o$  and  $Sy_p$  are the specific yields of open water and peat, respectively. This presumes that the observed diurnal change in water levels in sloughs is PET plus some loss of water to ridges, and the

diurnal change in water levels in ridges is  $PET/Sy_p$  minus some gain from sloughs. The implicit assumption is that all the atmospheric water demand is being met, such that evapotranspiration  $\times$   $ESY = PET$ . Therefore the subsidy of water from sloughs to ridges,  $Q$ , is then:

$$Q = PET \times A_R \times Sy_p \times \left( \frac{1}{Sy_p} - \frac{1}{ESY} \right)$$

which scales the volume of flow,  $Q$ , to water demand ( $PET$ ) by area of ridges ( $A_R$ ), adjusted for the landscape response to water demand. Ridge patch geometry data (area, perimeter) was obtained from Jing Yuan. For the sake of convenience, sloughs were assumed to be proportionate in size to the nearest ridges since sloughs are interconnected and therefore difficult to separate.  $Sy_p$  is estimated at 0.22, after Sumner (2009), and  $Sy_o$  was approximated as 1 for convenience, which may slightly over-approximate  $ESY$ .

The total number of days a year when induced lateral flow could occur were generated by subtracting the median soil elevation (from Watts and others 2010) for each patch type from the EDEN water elevations from 2002 to 2011. The days of interest were those days where the ridge soil would be exposed but slough still inundated. Individual points on the landscape may fall at the extremes of the variance in soil elevations, and thus experience differing hydroperiods. This calculation captures the most representative but not all landscape conditions. It is important to note that this gives a potential subsidy, only, and considers only the advective flow of phosphorus. To avoid concern about the disproportionate changes rainfall can create in diurnal water table fluctuations (e.g., Gerla 1992), calculations for extrapolated ground water flow were done only on days without rainfall. Estimating the potential advective flow of

phosphorus (P) to ridges on a per area basis was accomplished using values for soluble reactive phosphorus in the porewater, i.e., the bio-available phosphorus, of 6.54 ppb P for the Drained landscape and 8.88 ppb P for the Conserved landscape (Watts unpublished data).

## Results

I observed all the stage conditions of both communities inundated, ridges dry but sloughs inundated, and both communities dry (Figure 4-2). Recorded water depths in ridges were consistently lower than in the sloughs (on average  $9.7 \pm 0.54$  cm in Drained,  $18.0 \pm 0.95$  cm in Conserved), which aligned with the difference in soil elevation. The trend in the Drained head between wells was not consistent through time towards either ridges or sloughs. Focusing specifically on times when the water table is below the ridge soil surface, but above the slough surface, no persistent or enlarging head gradient was demonstrated, suggesting rapid lateral equilibration. Once the water table falls below the slough surface the difference in water table is generally less than 0.5 cm between wells. The average difference in water table between ridges and sloughs after ridge soil surface exposure is  $-0.07 (\pm 0.4)$  cm.

Figures 4-4 (Drained) and 4-5 (Conserved) demonstrate water elevations, relative to an arbitrary datum defined by the ridge well, for 3-day periods. The figures correspond to both wells inundated (Figures 4-4&5A), ridge soil surface exposed but slough inundated (Figures 4-4&5B), and the water table below the soil surface for both ridges and sloughs (Figures 4-4&5C). The diurnal response is small when both communities are inundated but becomes exaggerated as the water table falls below the soil surface across the landscape; this effect is larger for the Conserved site.

There was good agreement between the White and Hays methods for calculating evapotranspiration ( $R^2 = 0.86$  and  $0.77$  for the ridge and slough wells in Drained, and  $0.93$  and  $0.94$  for Conserved wells). Evapotranspiration/PET increased above 1 when the water dropped below the ridge soil surface for both sites (Figure 4-6). When both ridges and sloughs were dry, evapotranspiration/PET was consistently high for both the Drained ( $5.89 \pm 0.68$  and  $3.7 \pm 0.48$ , ridge and slough respectively) and Conserved locations ( $7.17 \pm 0.91$ ,  $8.75 \pm 1.77$ , ridge and slough, respectively). In comparison, evapotranspiration/PET was always significantly lower when both ridges and sloughs were inundated ( $0.79 \pm 0.48$ ,  $0.62 \pm 0.41$  for Drained ridge and slough,  $0.7 \pm 0.44$ ,  $1.03 \pm 0.35$  for Conserved ridge and slough). The behavior of evapotranspiration/PET was very different between sites during the critical period when the ridge soil was exposed but sloughs remained inundated. Consistent with expectations of instantaneous equilibration, the evapotranspiration/PET between the community types were correlated for both Conserved ( $0.7$ ) and Drained ( $0.93$ ) during the dry ridge/wet slough time period (Figure 4-6): Conserved evapotranspiration/PET for both communities demonstrated a dramatic increase starting when water depths on ridges reached 2 cm, with no significant difference between values for until sloughs also became dry ( $p < 0.05$ ,  $6.01 \pm 0.99$  and  $7.11 \pm 1.09$  for the ridge and slough). In contrast, the evapotranspiration/PET for both ridges and sloughs increased by roughly 0.37 per 1 cm drop in ridge daily water table until they reached the values when both ridges and sloughs were dry.

ESY was estimated as 0.57 for the Conserved landscape (Table 4-2). The Drained site had a larger ESY of 0.73 due to the lowered proportion of ridges to wet prairie (Table 4-2). Table 4-2 also shows values for Q, both in terms of total landscape

ridge area ( $Q_{\text{area}}$ ) and as a function of sum of all of the ridge perimeters ( $Q_{\text{perimeter}}$ ).

Because these values are summed across the landscape, they represent the average ridge condition for all landscape patches. What becomes strikingly obvious is that the shape of the ridges has large implications for the total volume of flow to those patches. Although a lower specific yield and longer period of time when ridge soil surfaces are exposed but sloughs inundated would suggest larger flow volumes to ridges at the Conserved site (as demonstrated by  $Q_{\text{area}}$ ), the skew of larger patches in Drained (and resultant smaller perimeter: area) results in values similar to that of the Conserved landscape. The influence of patch area on groundwater subsidy flow is demonstrated in Figure 4-8, where the subsidy per unit ridge perimeter ( $Q_{\text{perimeter}}$ ) is proportional to the size of the patch and thus power-function distributed, as patch size is also power-function distributed. Comparing the sum of the subsidy across years when data was available (Table 4-3) shows variability in  $Q_{\text{area}}$  and  $Q_{\text{perimeter}}$  between Drained and Conserved. The PET forcing differs by time of the year; PET forcing was quite low when the critical hydrologic conditions were met during winter months (e.g., Drained 2010, 2011) relative to years when the critical hydrologic conditions were met during summer months. Averaging across all of the years, the total subsidy to ridge edges ( $Q_{\text{perimeter}}$ ) was very similar between Drained and Conserved, despite the observation that, PET being equal between the two sites, flow would be much higher into ridge edges in Drained because of the perimeter:area influence. However, the annual subsidy of phosphorus, as a function of perimeter length, ultimately differed because estimated pore-water concentrations of P differed between the landscape units.

## Discussion

This study of diurnal variation in water levels supports the hypothesis that the underlying variability in soil phosphorus could be induced by evapotranspiration-induced convergent flow of water into ridges. Rather than demonstrate a persistent head towards ridges, as has been proposed in this landscape and demonstrated in other ecosystems, this study demonstrates groundwater-surface water connectivity can lead to convergent flow of groundwater to ridges during specific times of the year. Eppinga and others (2008) demonstrated a persistent head gradient from hollows towards ridges, driven by higher evapotranspiration rates there, which explained nutrient accumulation via pore water concentration below higher areas. Eppinga and others (2010) further demonstrated that this mechanism varied climatically, where high annual evapotranspiration relative to precipitation (evapotranspiration: precipitation >1) was indicative of redistribution of nutrients towards higher elevations whereas higher precipitation relative to evapotranspiration (evapotranspiration: precipitation <1) would lead to a flow of nutrients to lower elevations. I suggest there is a third alternative for climatic events, one that is specific to water table position. The Everglades has a precipitation: evapotranspiration greater than 1 for most years (German 2000), which is the major contributing factor to sheetflow hydrology across the historic Everglades. However, the exposure of the ridges while sloughs remain inundated leads to diurnal water responses that are clearly an intermediary between the conditions found in ridges and sloughs. The lack of a head gradient is therefore insufficient evidence to reject the hypothesis of a convergent ground water flow where there is strong hydrologic connectivity, microtopography, and a period of the year when the water table drops below the soil surface for the higher elevation areas.

Water levels did not vary independently during the critical time when ridges were exposed but sloughs were inundated. Moreover, the water elevation in the slough at the Conserved site behaves as if it is a mixture of peat and open water, which would only occur if the slough is hydrologically connected to the adjacent ridges. The difference in response between the Drained and Conserved sites is likely due to the probability density function of the soil elevations (see Watts and others 2010). Despite elevation differences between the adjacent ridge and slough at the Drained site the greater landscape is remarkably flat. This suggests gradual transitions between ridges and sloughs. A connected water table response would demonstrate a continuous change in realized specific yield until the entire landscape is dry. In contrast, the Conserved landscape is bimodal in soil elevations, with distinct and abrupt edges between the two communities. Under such a scenario a step-function response in ecosystem specific yield would be expected, consistent with Conserved observations. Both site responses are consistent with predictions posed by Sumner (2007), where landscape position and microtopography has a significant influence over ESY for lower elevation regions.

The assumption of a step in elevation between ridge and slough edges is a limitation of the approach here. The values presented in Table 4-3 assume all patches meet the median patch hydrologic conditions. The subsidies are going to be exaggerated to some degree for both sites, but more so in the Drained landscape. That the variance of ridge elevations is smaller than the variance of the elevations overall alleviates some of this concern for both landscapes.

The observed lateral water subsidy could provide the feedback that gives rise to power-function distributions in the Everglades (Yuan and others 2012). The

perimeter:area relationship with water demand leads to a larger subsidy to ridge edges with larger patch size (Figure 4-7). Power function distributions require a positive feedback that induces large patches to expand more rapidly than smaller patches. In other words, the feedbacks that induce patterning give rise to regular patterning. Power-functions of patch size needs a mechanism whose strength increases with patch size. The current hypotheses for the Everglades (sediment transport and self-organized canals) could create regular, linear features but lack a feedback that acts more strongly on larger patches. I note it is unlikely that the evapotranspiration mechanism alone is sufficient to explain the Everglades patterning; the length of time when convergent flow is most likely (Table 4-3) varies substantially from year to year. However, there remains power-law patch geometry in both landscapes despite strongly altered hydrology (Yuan and others 2012). This geometry in Drained suggests the phosphorus subsidy is still in play to some degree in that landscape.

As further evidence of convergent flow acting only as a reinforcing mechanism, the phosphorus availability on ridges is not as dramatically different from that of sloughs as compared to the third main Everglades patch, tree islands. Tree islands may have as much as an order of magnitude higher P in both pore water and soil compared to both sloughs and ridges (Ross and others 2006). The greater concentration of phosphorus in ridges compared to sloughs is far more subtle, and appears to be more associated with elevation than patch designation (Cohen and others 2009): The significance of the correlation between soil elevation and soil phosphorus is reduced when vertical relief between patches is lost.

I approximated the likely subsidy of phosphorus to ridges by multiplying the flow (Q) by the concentration of phosphorus in marsh pore waters yielding the values presented in Figure 4-8 and Table 4-3. Although likely an overestimation, it is useful to consider the scale of the subsidy to ridge edges, as the implication is this is the phosphorus that plays a role in driving ridge expansion. The year-to-year subsidy can differ by as much as an order of magnitude, and the potential subsidy is actually relatively small on an area basis. The values in Table 4-3 are essentially landscape-averaged values; small and large ridges would have proportionately smaller and larger subsidies per length of ridge edge. However, if we consider soil phosphorus in the upper 10 cm (3AN = 452 mg/kg TP; 3AS = 402 mg/kg TP; Bruland and others 2006), with peat accretion approximately 3 mm yr<sup>-1</sup> (Craft and Richardson 1993 measured 2 to 5 mm yr<sup>-1</sup> for ridges), then the annual subsidy of phosphorus to ridge edges is as much as to 4% (Drained) to 14% (Conserved) of the annual soil P storage.

The question remains whether convergent flow in large ridges would result in a horizontal transport of water. Although the total flow volumes are large, the actual flow for any length of ridge is small and the flow path long from ridge edge to center. Weaver and Speir (1960) measured horizontal hydraulic conductivity ranging 11.3 to 35.5 cm h<sup>-1</sup> for Everglades mucks in the upper 100 cm of peat, with remarkable similar vertical saturated conductivity ranging 15.2 to 42.1 cm h<sup>-1</sup>. Presumably the shorter vertical flow path results in some water be sourced from deeper peat; this suggests that some but not all of the increased phosphorus in ridge soils can be attributed to a subsidy of water from sloughs. Alternative mechanisms potentially generating greater phosphorus concentrations were not covered in this study and may complicate the phosphorus

narrative. Carbon mineralization during soil exposure releases both bound nutrients and carbon (Debusk and Reddy 2003), and the loss of carbon would lead to an apparent concentration of phosphorus without any exogenous subsidy. As this would be occurring during the same periods of the year when instantaneous ground/surface water equilibration would be significant for phosphorus movement, these two mechanisms may well act in concert. For phosphorus mass balance it may not matter the exact source of phosphorus, however, as both phosphorus sources would converge to the highest locations. Indeed, the mixture of sources of phosphorus, as well as the local activities of microbes, may explain the difference in marsh surface dissolved organic phosphorus (DOP;  $0.004 \text{ mL}^{-1}$ ) to that of porewater ( $0.013 \text{ mL}^{-1}$ ) observed in the nutrient un-enriched interior portions of WCA 2 (Qualls and Richardson 2003).

In this study I provide evidence for an evapotranspiration-induced convergent flow to ridges during critical times of the year when ridges are dry but sloughs remain inundated. There are several lines of evidence that would be predicted by the depth-dependent convergent flow to ridges. First, phosphorus availability should be greater on larger ridges, because the exerted water demand is proportionate to area. Second, during ridge dry-downs a phosphorus front should be observed on ridge edges, induced by convergent flow. The magnitude of that front should be larger on the edges of big ridges than those of smaller ridges. Third, the expansion of ridges in a bi-modal landscape should be faster than the expansion of small ridges. This would not be true in a drained landscape due to more favorable local hydrologic conditions at ridge edges; i.e. there is no need for a nutrient subsidy to overcome anoxic stress as there would where there are abrupt transitions between ridges and sloughs.

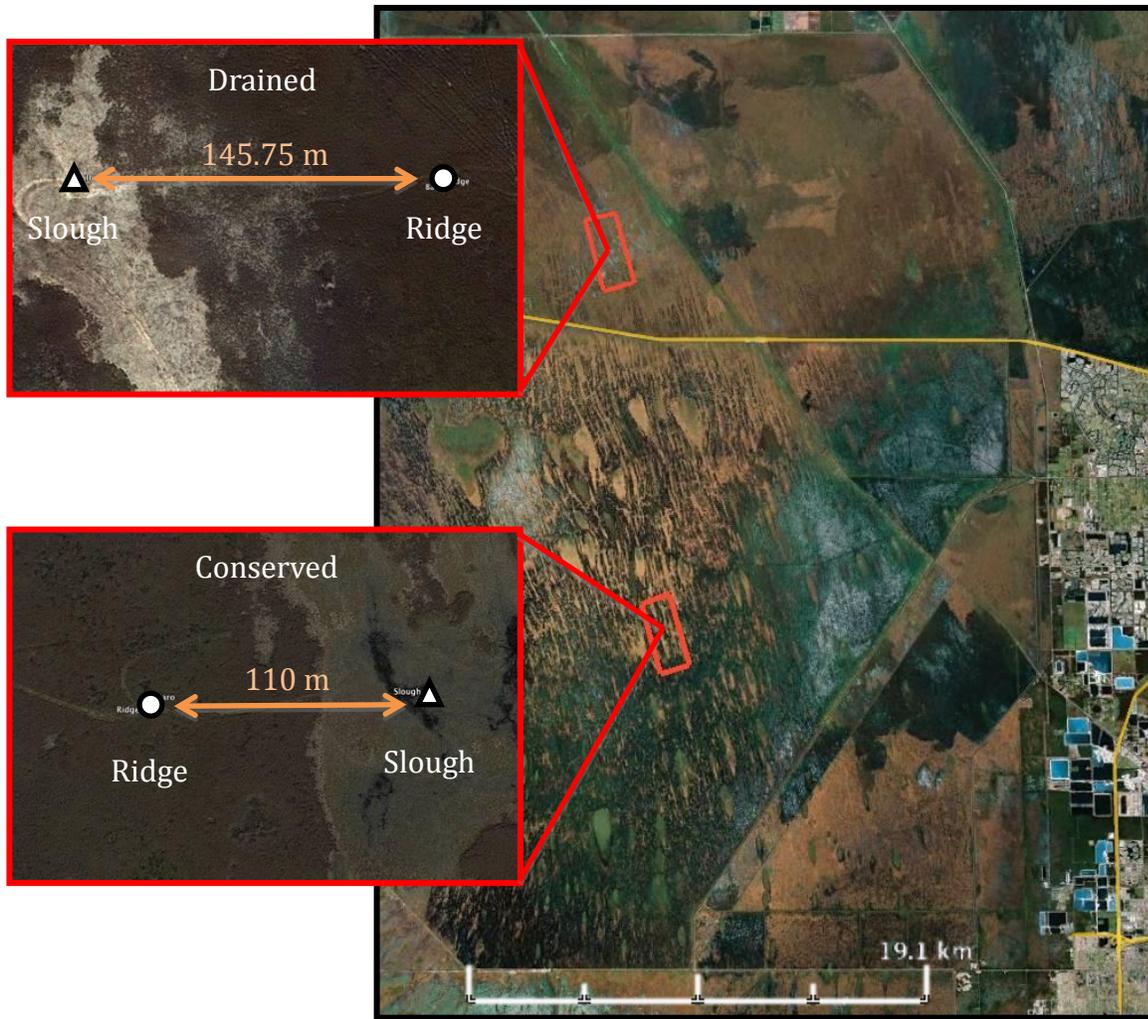


Figure 4-1. Locations of the wells in WCA 3AN (Drained) and 3AS (Conserved). Figure generated with SPOT imagery viewed with Google Earth (Google, Inc., Mountain view, CA, USA).

Table 4-1. Locations of the ground water wells.

	Ridge	Slough	Baro	Distance between R-S (m)	Date Length	Peat Thickness (cm)
Drained	-80.72755	-80.72901	-80.72750	151.75	11/2/2010	36.5-44.5
	26.20422	26.20419	26.20420		-3/17/12	
Conserved	-80.69190	-80.6908	-80.69190	109.98	11/3/10-	110-124
	25.96972	25.96974	25.96972		3/18/12	

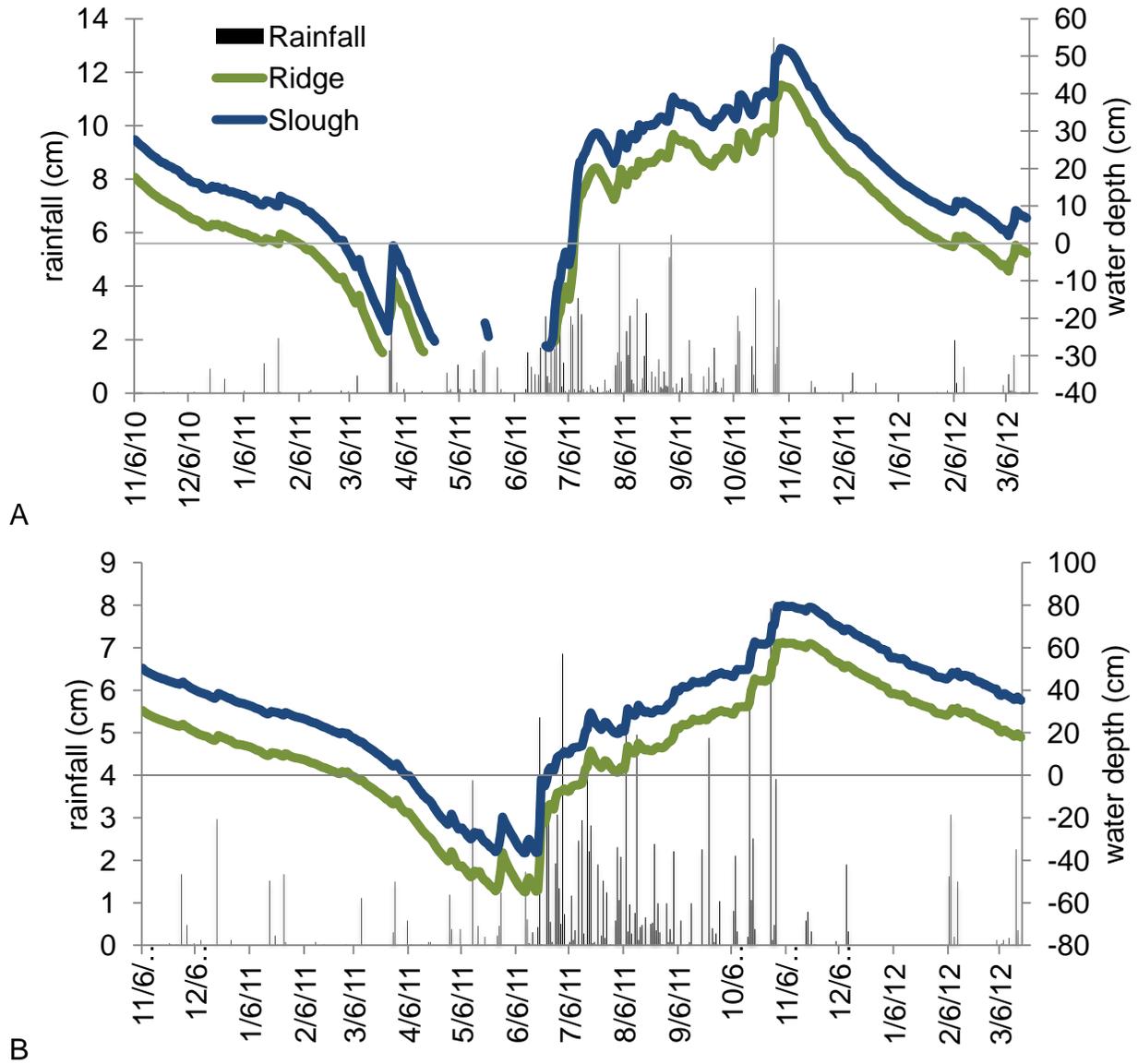


Figure 4-2. Daily average water depths and rainfall. A) Drained and B) Conserved for the period of record. The horizontal line represents the local soil elevation.

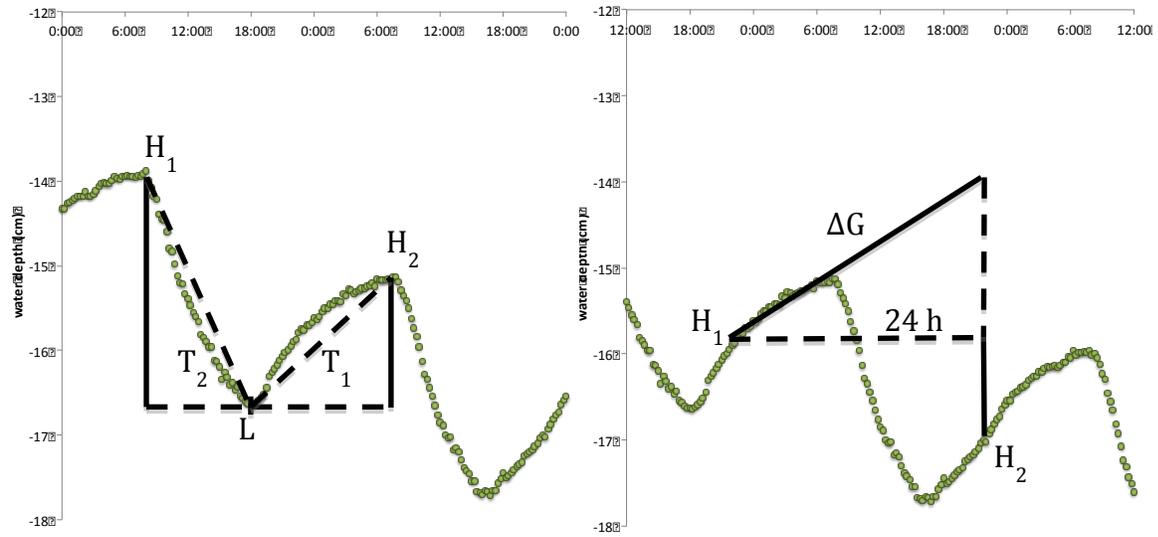


Figure 4-3. Schematic of evapotranspiration calculations. A) The Hays Method and B) The White Method.

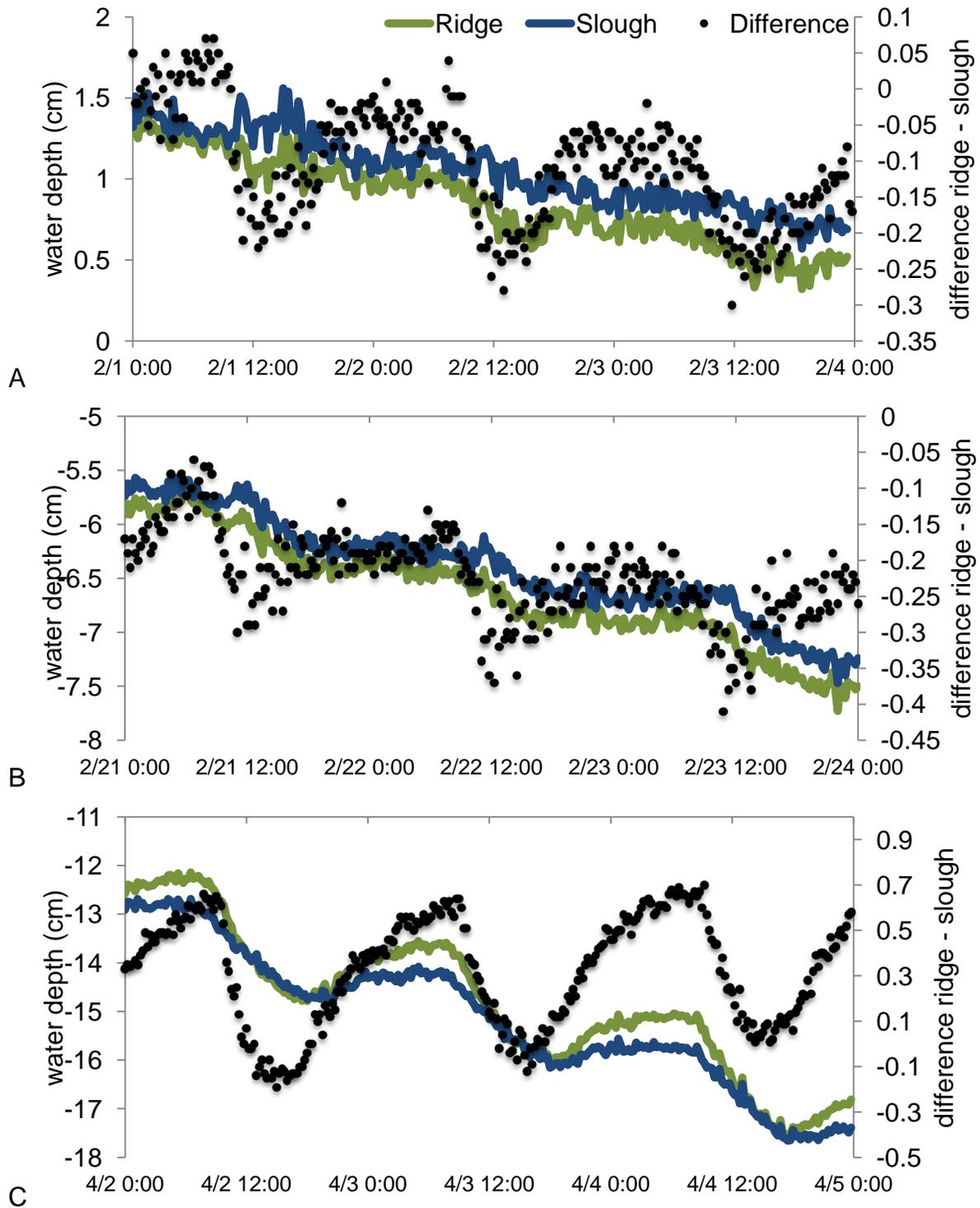


Figure 4-4. Water table position for Drained ridge and slough (relative to the ridge well) and the difference between the water tables for time periods. A) Both ridge and slough are inundated, B) ridge soil surface is exposed but the slough is inundated, and C) both ridge and slough surfaces are exposed.

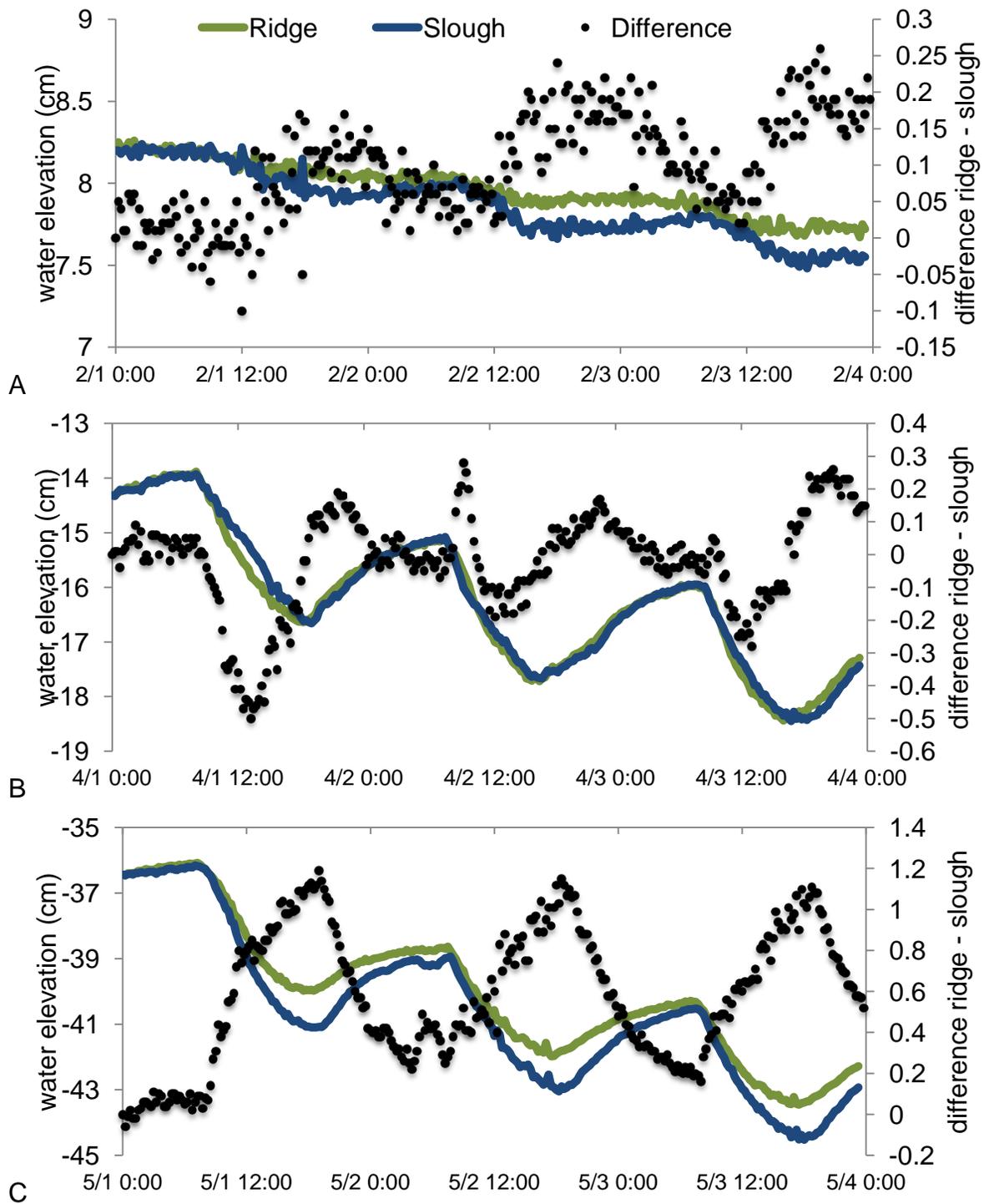


Figure 4-5. Water table position for Conserved ridge and slough (relative to the ridge well) and the difference between the water tables for time periods. A) Both ridge and slough are inundated, B) ridge soil surface is exposed but the slough is inundated, and C) both ridge and slough surfaces are exposed.

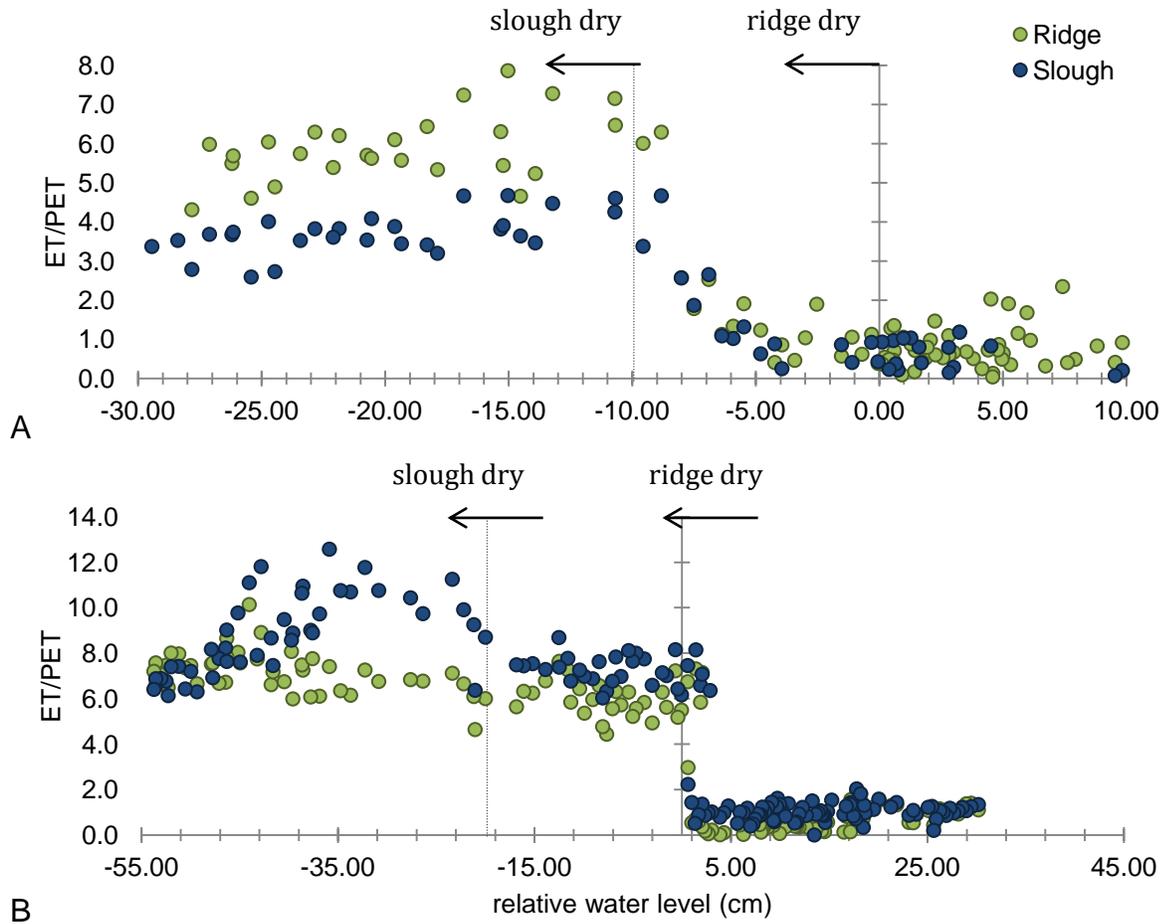


Figure 4-6. Evapotranspiration/PET relative to the water table position in the ridge well.  
 A) Drained and B) Conserved sites.

Table 4-2. Community area and water subsidies (averaged across days) to ridges (averaged across the landscape).

	Ridge:Slough*	Ridge Perimeter:Area	ESY	$Q_{Area}$ $m^3 m^{-2} d^{-1}$	$Q_{Perimeter}$ $m^3 m^{-1} d^{-1}$
Drained	0.53	0.030	0.73	0.0026	0.084
Conserved	1.21	0.032	0.57	0.0027	0.085

\*For the Drained landscape, sawgrass has expanded into slough/wet prairies such that the extent of sawgrass is quite a bit larger than the extent of ridges. Here “ridge” is restricted to communities dominated by sawgrass.

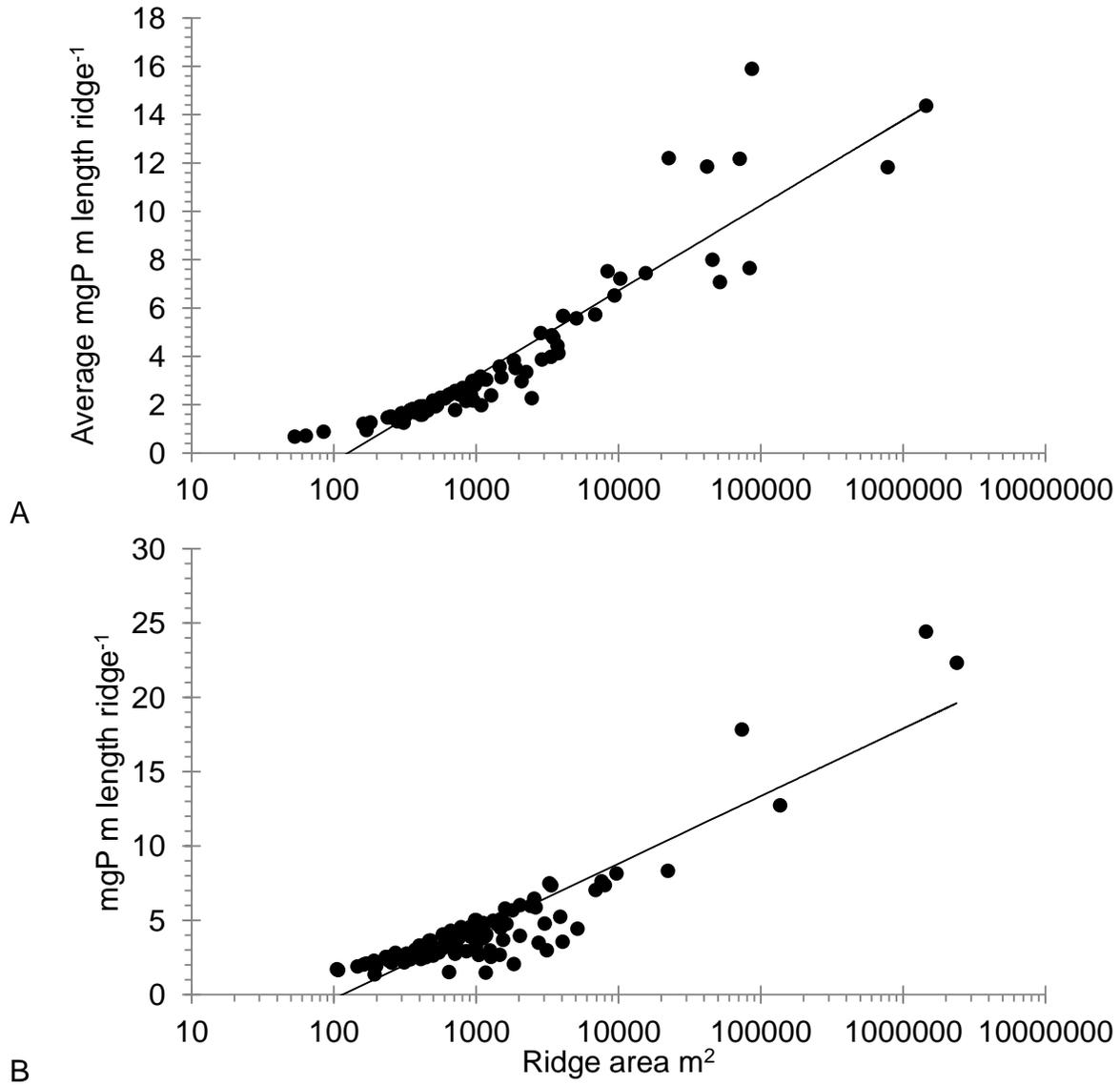


Figure 4-7. The subsidy of ET-induced convergent flow of phosphorus for the 2011 dry season into ridge edges in relation to ridge size. A) Drained (21 days) and B) Conserved (26 days).

Table 4-3. Subsidy of water and phosphorus to ridges for 2002-2011. Calculations are based on days without rainfall when hydrologic conditions are met and the sum of the ridge areas and perimeters, and thus are most appropriately considered an averaged value for the landscape.

Year	No. Days <sup>§</sup>	Avg PET <sup>⌘</sup> (cm)	Q <sub>perimeter</sub> m <sup>3</sup> m <sup>-1</sup> yr <sup>-1</sup>	Q <sub>area</sub> m <sup>3</sup> m <sup>-2</sup> yr <sup>-1</sup>	P Subsidy* mg P m <sup>-1</sup> yr <sup>-1</sup>
Drained					
2002	--	--	--	--	--
2003	32 (59)	0.43	1.95	0.095	12.75
2004	25 (46)	0.42	1.49	0.073	9.71
2005	16 (19)	0.33	0.76	0.037	4.99
2006	20 (27)	0.32	0.91	0.045	5.95
2007	20 (33)	0.27	0.77	0.038	5.03
2008	24 (41)	0.48	1.63	0.080	10.65
2009	13 (16)	0.21	0.40	0.019	2.61
2010	26 (29)	0.17	0.61	0.030	4.01
2011	8 (4)	0.17	0.20	0.010	1.29
Average	20 (30)	0.31	0.97	0.047	6.33
Conserved					
2002	32 (49)	0.59	1.39	0.115	12.32
2003	0 (0)	--	0	0	0
2004	22 (65)	0.61	0.99	0.083	8.81
2005	0 (0)	--	0	0	0
2006	25 (71)	0.59	1.52	0.126	13.51
2007	62 (127)	0.56	2.57	0.214	22.82
2008	1 (5)	0.64	0.05	0.004	0.42
2009	26 (50)	0.56	1.07	0.089	9.48
2010	0 (0)	--	0	0	0
2011	43 (79)	0.46	1.47	0.123	13.08
Average	22 (41)	0.57	0.91	0.075	8.04

<sup>§</sup>Days without rainfall (days with rainfall). The values are based on the median soil elevation from Watts and others (2010). Data not available for all of 2002 at 3AN1W1.

<sup>⌘</sup>Average of PET for the days of interest.

## CHAPTER 5 LONG-TERM IMPLICATIONS OF THE LOCAL CARBON BUDGET

### **Model Overview**

Peatlands are estimated to store a third of the world's global carbon pool (Gorham 1991). Carbon turnover in many peatlands has increased significantly due to anthropogenic nutrient increases (Debusk and Reddy 2003), reduced water tables (Gorham 1991; Oechel and others 1993), peat mining (Gorham 1991), and climate change (Carroll and Crill 1997; Gorham 1991; Maltby and Immirzi 1993). Many of these wetlands have become a source rather than a sink of atmospheric carbon (Gorham 1991; Hooijer and others 2006; Maltby and Immirzi 1993; Oechel and others 1993; Pator and others 2002). Therefore, it has become particularly important to understand the mechanisms of peat accretion as well as ecosystem thresholds and feedbacks, as these can act as constraints on restoration activities (Suding and others 2004; Tuittila 2000).

Many peatlands have a patterned microtopography where there are distinct and spatially organized higher- and lower- elevation communities. The higher-elevation areas are 'hummocks' or 'ridges', populated by denser, more productive communities than the 'hollows' or 'sloughs' (Loveless 1959; Daoust and Childers 1999; Rietkerk et al. 2004, Eppinga and others 2008). Two key questions arise in understanding this patterning: First, what causes the divergence in peat elevations between patch types, and second, what causes the scale and configuration of the patches? The former deals with point-scale processes that give rise to pattern formation. The second deals with the landscape-scale processes that give rise to pattern formation. While the two are doubtless linked, distribution metrics in peat elevations can act as indicators of

landscape stability and early indicators of landscape degradation (Watts and others 2010).

The carbon budget is the main process by which stable patterned topographic variation can occur. That is, for peatland pattern to persist requires that each element of the landscape achieve the same long-term net ecosystem carbon exchange or accretion rate. The core mechanism for maintenance of two distinct elevation modes lies in the landscape solving for two long-term stable peat accretion equilibria: one with high production and high respiration on ridges creating a stable vegetative configuration with respect to long-term average peat accretion at higher soil elevations; one with low production low respiration in sloughs which creates another at lower soil elevations (Larsen and others 2007; Cohen and others 2011; Heffernan and others in review). These configurations are bi-stable in the sense that elevations markedly different from the two equilibrium levels (i.e., deep and shallow configurations with equal peat accretion rates) are, over time, unstable as they accrete more quickly or slowly than the long-term landscape average, and thus converge over time to one or the other equilibria. Controls on carbon influx and efflux are therefore key components to patch stability in peatlands (examples include Nungesser 2003; Belyea and Baird 2006; Larsen and others 2007; Eppinga and others 2008).

A necessary next step to understanding patterning and state stability in the patterned ridge-slough Everglades lies in enumerating mechanisms behind peat accretion. A number of studies have evaluated components of the C budget, both *in situ* and in laboratory studies. Parts of the Everglades have clearly become net carbon sources to the atmosphere. For example, Everglades Agricultural Area dissolved

organic carbon (DOC) is sourced from historic peat deposits, whereas DOC is mixed modern and historic in more 'pristine' areas of the marsh system (Stern and others 2007, using  $^{14}\text{C}$ ). Chapter 3 demonstrates net annual carbon uptake throughout most of WCA 3A, excepting the northern sloughs with lower water levels. A study of net carbon exchange in the ridge-slough remnants of Everglades National Park demonstrated net annual carbon losses during a year of low rainfall (Jiminez and others 2012). Clearly linking carbon budgets to hydrology will allow us to make inferences about long-term stability of the peat landscape

Ecophysiological attributes of the main community types, ridge and slough, reinforce the hypothesis of a discontinuity in patch productivity and hence peat accretion potential. Each community is associated with distinct elevations and hydrology (water depths and hydroperiods; David 1996; Jordan 1997; Busch and others 1998; Givnish and others 2008; Zweig and Kitchens 2008; Watts and others 2010). Ridges are dominated by sawgrass, and exist at the highest elevations with the shortest hydroperiods of any of the peat marsh communities (approximately 357 days, Givnish and others 2008). Physiological limitations to inundation restrict sawgrass to the highest elevation sites (Pezeshki and others 1996; Chabbi and others 2000; Lorenzen and others 2001; Wesiner and Miao 2004;). Highest densities and biomass of sawgrass are associated with the shortest hydroperiods (Toth 1987; Busch and others 1998), although sawgrass density appears resilient to interannual (6 year) variations in hydrology (Urban and others 1993). Increased annual water depths and hydroperiod reduce the productivity of sawgrass-dominated communities, however (Childers and others 2006; Chapter 3). Sawgrass has long-lived leaves (~400 weeks) with a low

turnover rate (Davis 1989), as well as a low growth rate, low capacity for phosphorus uptake, and relatively inflexible biomass partitioning (Lorenzen and others 2001).

Sawgrass forms monocultures in part because of belowground growth habit; sawgrass produces many ramets with low internode distances resulting in high densities, particularly as compared to similar species like cattail (Miao 2004). Further, sawgrass expansion lags hydrologic drainage as expansion is primarily via rhizome; seed propagation is generally low (Ponzio and others 1995; Lorenzen and others 2000). These physiological responses to environmental conditions induce time lags for sawgrass patch expansion and contraction and ridge prevalence.

Wet prairies were relatively rare in the historic ridge-slough Everglades, have variable species assemblages, and have largely replaced sloughs in the drained portions of the landscape (Loveless 1959; David 1996; Jordan and others 1997; Daoust and Childers 1999; Childers and others 2003; Zweig and Kitchens 2008; Bernhardt and Willard 2009). Many of the species of a wet prairie require a narrow range of hydrology (David 1996, Busch 1998), and are generally found at water depths intermediate between that of ridges and sloughs (Givnish and others 2008, Watts and others 2010), and may thus represent a lagging transitional condition between states. Many wet prairie species are found in the prolific Everglades seedbank (Leeds and others 2002), and appear in sloughs any time water levels are low enough to promote germination.

Sloughs occupy a distinct elevation mode from ridges and thus are theorized to be the alternative stable peat accretion configuration to ridges. Sloughs are the deepest water communities (Loveless 1959; Jordan and others 1997; Givnish and others 2008; Watts and others 2010), where the dominant species are adapted to increased

hydroperiods (Wood and Tanner 1990; David 1996; Busch and others 1998; Zweig and Kitchens 2008). Vegetative productivity of sloughs is low compared to ridges (Daoust and Childers 1999; Chapter 3). Modern sloughs formed later than ridges in the historic Everglades, the prevalence and composition of which appear driven by regional climate variability (i.e., precipitation; Bernhardt and Willard 2009). The altered peat elevations and hydrology of the modern Everglades has led to increased species mixtures of deep-water and emergent, shallower water vegetation (i.e., wet prairie; Watts and others 2010; Zweig and Kitchens 2010). Thus, drawing the distinction between wet prairie and slough community types may only be relevant in the modern Everglades as an indicator for incipient state transitions (David 1996; Jordan 1997; Watts and others 2010).

Two Everglades-specific peat accretion models exist that attempt to draw inference of the role local carbon dynamics play in diverging peat elevations. The PeatAccrete 1.0 model (Larsen and others 2007) re-creates several aspects of the modern landscape. In PeatAccrete, net peat accretion is a function of oxygen (primarily but not entirely controlled by water depths) and phosphorus availability in ridges; sloughs modeled to perpetually accrete using a time-averaged value. The model adds sophistication using functions such as gravitational erosion (i.e., peat slumping) and drought responses (e.g., sawgrass wilting points, vadose zone water content). The model performs well in the evolution of a stable elevation difference between ridge and slough, but there are key characteristics of the soil elevation the model is not able to re-create. The model results in 2 sharply divided topographic modes without a variance around those nodes; the conditions for a 'saddle' in the soil elevation distribution between elevation modes is lacking. Further, PeatAccrete suggests that the modern

differences in ridge-slough topography are unstable (~22 cm in the best-conserved landscape). Stable ridge-slough topography is reached at elevation differences greater than 0.6 m. The robust pattern metrics (e.g., Wu and others), community structure (e.g., Zweig and Kitchens), peat accretion potential (e.g., Chapter 3), and topography (e.g., Watts and others 2010) in central WCA 3A suggests this landscape is stable, at the very least in the time-span of a management action. Further, the model is not structured to allow both communities to become net carbon losses, limiting inference that can be drawn in application to the modern Everglades. I therefore posit that the simplified carbon accounting of PeatAccrete is insufficiently responsive to explore peat accretion dynamics in the modern Everglades.

A second peat accretion model for the Everglades takes a closed-form approach to demonstrate the spontaneous divergence of elevations between patch forms (Heffernan and others in press). The model uses long-term relationships between local carbon balance, elevation, and discharge competence in (relatively) simple analytical equations that are solved for bi-stability. However, the relationships presented are for long-term means (timescales of decades to centuries), precluding the ability to test modeled landscape responses on the scale of a management action.

In this study, I construct a simple model describing net carbon accretion in response to hydrologic forcing, parameterized by existing literature values. This model presented here addresses several limitations of previous Everglades carbon models. First, it enumerates relationships between topography and community by explicitly considering both carbon uptake and losses. Second, the model incorporates state transitions in a way to consider both stochasticity and water depth controls on

community states. Third, the model is parameterized by field and laboratory observations of carbon dynamics, and thus provides a useful context in which to explore which components of Everglades carbon dynamics remain poorly constrained. The model tracks community type, hydrologic conditions, carbon balance, and transitions on annual time steps. The model allows me to test the sufficiency of point scale carbon dynamics for creating observed patterns of soil elevation (e.g., soil distribution convergence under drainage and impoundment; bimodality under moderate hydrologic conditions). If the model fails to re-create the observed patterns, I infer that spatial interactions, explicitly omitted from this model, may be necessary.

There are several goals in exploring this model. First, I wish to explore the carbon dynamics presented in Chapters 2 and 3 to evaluate longer time scales than evaluated there, particularly in terms of the theoretical model this work has been based on. In particular, I am interested in 1) whether or not the relationships suggested in this manuscript are sufficient to give rise to diverging soil elevations between ecosystem states (emergence of bimodality); 2) if the relationships described here are sufficient to maintain the characteristic microtopography found in the Everglades (maintenance of bimodality); 3) if the model is able to maintain or produce statistical patterns, such as variance around modes; and 4) if the modeled landscapes converge from a bimodal soil elevations to a single mode with hydrologic modification (via both lowered and raised water levels). Results and insights gained from this model provide an improved mechanistic understanding of the role local carbon budgets play in the formation and persistence of ridge and slough formations.

## The Model

### Initial Conditions

This model uses a two simplifying assumptions to model local peat accretion. First, this model is non-spatial; there are no neighborhood interactions. Second, annual carbon budgets are modeled as a function of median water depths, which does not take into account drivers such as the depth and length of dry down.

The baseline model selects a water stage from a normal distribution. The statistical property of the stage distribution is based on annual median stages from 1954 to 2012 for 31 WCA 3A marsh wells from DBHYDRO (<http://www.sfwmd.gov/>; based on data availability). The interannual variability (as a standard deviation) in median water depths range from 8.7 to 27.5 cm, with a weighted average standard deviation of 17.2 cm. Consequently the water stage inputs are an input for the long-term hydrologic trajectory, but with a standard deviation around the long-term value of 17 cm. Solving for local water depths uses water stage as a landscape-average water depth, such that the water elevation is the stage plus the sum of the soil elevations, divided by the number of landscape points. Local water depth is then simply the water elevation minus the local soil elevation.

The landscape commences in one of two ways: either as a flat, peat-less, entirely slough landscape (approximating pre-Everglades landscape initiation) or as a one with a bimodal distribution of soil elevations. The bimodal landscape is set so that the first mode centers at 100 cm (sloughs) and the second sets around 125 cm (ridges; representative of modern conditions across Conserved 1, 2, and ENP sites in Watts and others 2010), with a standard deviation of 6 cm within each community. Community proportions were 1:1.

## Model Solutions

The model assumes that peat accretion is a local process and thus begins by quantifying ecosystem respiration and productivity. Model notation is described in Table 5-1. The theoretical model (Figure 1-2) for peat accretion equilibria assumes monotonic increases in annual ecosystem respiration with decreasing water depths—an assumption corroborated in Chapter 2. Therefore carbon losses are modeled as

$$R_x = a_x e^{-b_x h_a} + m$$

where  $a_x$  and  $b_x$  are the terms for an exponential relationship of CO<sub>2</sub> respiration with water depths (annual median;  $h_a$ ),  $m$  is the total contribution of losses from DOC and methane, and the subscript  $x$  denotes community-specific parameterization.

Parameterization for these terms is discussed in Appendix A.

Due to differences in autecology among species and communities with respect to hydrology, ridge and slough productivity is modeled separately with an s-curve where the sum of the relationship is approximated in Figure 1-2. Observations of variability in community productivity demonstrated in both Tables 3-3 and 3-4 suggests a simplified inverse sigmoid relationship of productivity to local water depth may approximate annual relationships. Community-specific productivity ( $P_x$ ) is described as

$$P_x = A_x + \frac{K_x - A_x}{1 + e^{-B_x(-h_a + m_x)}}$$

where  $A_x$  and  $K_x$  are the minimum and maximum productivity values,  $B_x$  is the growth rate, and  $m_x$  is the shift along the annual water depth axis.

Parameterization comes from two sources: First, NEP/GPP relationships from Chapter 3 of this manuscript are used (called hereafter the *GPP* parameterization). Because these numbers were generated from one year of measurements, and thus

may not be representative of long-term productivity rates, a second parameterization was done. The NEP budget was forced to balance to approximate long-term peat accretion rates from Bernhardt and Willard (2009; hereafter referred to as the *Peat* parameterization). The resulting model forms are demonstrated in Figure 5-1.

Discussions of parameterizations are presented in Appendix A. In each case, the observations of soil elevation modes at roughly 25 cm apart (Watts and others 2010) are presumed to be evidence that the maximum peat accretion rate is equal to the difference in modes, and model maximum peat accretion is set to match. It has been argued that the historic elevation modes were farther apart, with differences between community soil elevations as high as ~90 cm (McVoy and others 2011). Although it is difficult to evaluate this claim under modern conditions, there should be no practical effect on the behavior of this model for ridges; modern water depths and hydroperiods for this community are estimated to be approximately the same as historic (>100 ybp). The effect for sloughs is dramatically different. For this model, I infer that the modern soil elevation mode coincides with the peak in peat productivity (~22 cm lower than the peak for ridges). Deeper historic sloughs would suggest that the landscape was solving for a peak peat accretion at significantly higher water depths, for which we have scant evidence, as there are no landscape points with which to evaluate the carbon balance at such depths.

The growth of peat elevation at each time step is the difference between carbon gains and losses ( $P_x - R_x$ ), converted to a height increase using average carbon content (54 % by mass) and bulk density estimates for WCA 3 (0.13 g C cm<sup>3</sup>; Bruland and others 2006). If the incremental change in peat elevation results in a loss of peat greater

than the peat profile at that point (i.e., there is no peat to lose but the net carbon balance is negative), then peat loss is equal to 0. Although the biomass inputs to peat are likely lagged in the Everglades due to the presence of standing dead vegetation, I assume that at the longer time scales of this model (simulated for 100 and 1000 years) standing dead is integrated over time.

As discussed in Chapter 3, fire may play an important role in regulating the carbon balance on ridges. The fire return interval for the marsh system is unknown, with speculated ranges quite large and the interaction between community, hydrology, and fire likely non-linear (Lockwood and others 2003). I therefore evaluate model behavior with two fire return intervals: 3 to 15 years and 10 to 30 years, representing a high and low frequency fire return. This model lacks the temporal resolution to make fine-scale decisions on the consumption of ecosystem carbon during fire events, so when fire occurs, all ridges burn with a complete consumption of all of that year's above-ground productivity (estimated at 78% of the net carbon uptake using an average above to below ground biomass of 4.6 for sawgrass; Lorenzen and others 2001). To approximate the consumption of litter and standing dead from previous years, fire events also consume 50% of the previous year's net productivity. This is admittedly an oversimplification as fire size is generally directly related to ridge patch sizes (Gunderson and Snyder 1997). These simplifying assumptions roughly account for biomass losses, but assume peat fires are very rare. These assumptions also don't account for changes in root productivity and the potential role fire recovery may play in the carbon dynamics, but do allow an investigation into trends we may observe with fire frequencies.

Temporal dynamics of patch state transitions are poorly constrained (although see Zweig and Kitchens (2009) for transitions during impoundment). The effects of changes in water level variance, mean water depth, and species composition also remains uncertain. The presence of two communities despite substantial hydrologic changes at the hydrologic end-members observations of species assemblages over time (Armentano and others 2006; Zweig and Kitchens 2008; Bernhardt and Willard 2010) suggests substantial lags in vegetative responses to hydrologic modification. Sawgrass is able to form tussocks under deeper water conditions (Snyder and Richards 2005), allowing it to persist even after the underlying substrate has broken apart. Similarly, sloughs and wet prairies have a number of sub-community types, with many species present in each. For sawgrass to invade a 'slough' under drier conditions, it must first compete with the established wet prairie species. These patch responses induce lagged responses to altered water levels. Transition occurrences between ridge and slough communities appear to be generally low, and restricted primarily to points with more marginal hydrologic conditions to each community (Zweig and Kitchens 2009). In the model, the probability of any point transitioning is defined as

$$p(\text{ridge transition}) = \text{If } h_a < w_1, p_{r.t.} = p_1;$$

$$\text{If } h_a > w_2, p_{r.t.} = p_2;$$

$$\text{If } w_1 \leq h_a \leq w_2, p_{r.t.} = p_1 + (p_2 - p_1) (h_a - w_1) / (w_2 - w_1)$$

and

$$p(\text{slough transition}) = \text{If } h_a < w_3, p_{s.t.} = p_4;$$

$$\text{If } h_a > w_4, p_{s.t.} = p_3$$

$$\text{If } w_3 \leq h_a \leq w_4, p_{s.t.} = p_4 + (p_3 - p_4) (h_a - w_3) / (w_4 - w_3)$$

where  $w_1$  and  $w_3$  are the thresholds in water depths where transition probabilities begin to rise from the minimum  $p_{1&3}$  and  $w_2$  and  $w_4$  are the water depths where the transition probability becomes the maximum  $p_{2&4}$ . Accounting for the observations of community shifts responding to multiple-years of hydrology, the actual  $h_a$  used in the simulation transitions is a 5-year averaged annual water depth (the current condition and 4 years previous). In recognition of the deep uncertainty about when and how quickly community shifts occur, the form and thresholds (i.e., where the transition probabilities change) of the transition probabilities are explored using two model forms (Table 5-2). The minimum probability is non-zero to account for stochastic community transition. Further, to maintain stochasticity in transitioning, a uniform probability distribution is generated ( $z$ ) and assigned to each landscape point for each time step. Where  $p < z$  for any point, no transition occurs.

## Model Results

### Model Parameters

The *GPP* parameterization had positive annual peat accretion rates from -8 to 40 cm on ridges and 25 to 71 cm in sloughs (Figure 5-2). The maximum peat accretion rates were 2.68 mm yr<sup>-1</sup> (ridge) and 0.908 mm yr<sup>-1</sup> (slough) The *Peat* parameterization resulted in maximum ridge peat accretion of 0.97 mm yr<sup>-1</sup> at 16 cm median annual water depths, and was positive from -2 to 39 cm annual median water depth (Figure 5-3; average of positive peat accretion values was 0.063 cm yr<sup>-1</sup>). Sloughs had the highest peat accretion of 0.24 mm yr<sup>-1</sup> at 41 cm median annual water depth and was positive from 26 to 62 cm (average of positive peat accretion values was 0.015 cm yr<sup>-1</sup>). The range of water depths for positive peat accretion as well as the maximum peat accretion was sensitive to small changes in the model parameters for both *GPP* and *Peat*

parameterizations, particularly  $K_x$ ,  $m_x$  and CO<sub>2</sub> respiratory parameters. Figures 5-2&3 demonstrate the changes to peat accretion rates when altering the parameters by 10% (see appendix B for further discussion).

The modeled landscape response to perturbations to model parameters after 100 years are presented in Appendix B. In general, parameter perturbations to both the *GPP* and *Peat* parameterizations resulted in small or negligible changes to the proportion of ridges (-9 to 10% change in proportion ridge). The sensitivity of the models with respect to soil elevations depended on whether the landscape was flat or bimodal on initiation. In general, the difference between median ridge and slough soil elevations for both models were fairly insensitive to the community growth parameter ( $b_x$ ), and more sensitive to  $K_x$ ,  $m_x$  and CO<sub>2</sub> loss parameters.

### **Peat Development**

Under a variety of water depths, a bimodal peat distribution began to differentiate from the uniformly flat conditions for the *GPP* parameterization (Figure 5-4A-B). Further, by the end of 1000 time steps, under all hydrologic conditions slough elevations were rising, most notably so under the deepest water levels (Figure 5-4C). The same was true to a lesser degree of the *Peat* parameterized simulations (Figure 5-4D-F). Under all scenarios, some proportion of the states became ridges, with the proportion relative to the water levels (i.e., predominance of ridge states with low water levels, vs. a predominance of slough states with high water levels).

### **Peat Maintenance**

Under initiating bimodal simulations, the *GPP* parameterization was able to maintain elevation differences between ridges and sloughs across a broad range of long-term mean hydrologic conditions, even though individual points may have

undergone collapse and recovery and state transitions (Figure 5-5A-C). However, the ridges converged to an elevation representative of the maximum peat accretion rate (~16 cm median annual water depths)-- something in nature that would not occur because of variability in production parameters. Although deeper interannual water depths led to a reduction in ridge proportions, some portion of the ridges maintained positive peat accretion, and thus distinct differences in state elevation modes was maintained (Figure 5-5C)

The *Peat* model parameterization was also able to maintain differences between soil elevation modes, although with less separation between modes (Figure 5-5D-F). Low water led to a general decline in soil elevations and a collapse of the differences in state modes, moderate water levels led to a general maintenance of soil elevations, and deeper water led to behavior similar to that of the *GPP* parameterization.

The water depths for the state transitions had little influence the behavior of the model. I demonstrate the effect of the water depths in the transitions in Figure 5-6 using the slough landscape with undifferentiated topography. Figures 5-6A&B demonstrate that without any water depth variance, the proportion of the landscape made of ridges traced the transition probabilities. The effect of the higher maximum transition probability for ridges ( $p_1=0.1$ ) is seen in the lagging of the proportion of ridges to the functional form in Figure 5-6A; reducing  $p_1$  to equal that of  $p_3$  results in a near-perfect tracing of the proportion ridge to the functional form. Interannual variance in water depths essentially attenuates relationships, demonstrated in Figure 5-6C and D, rendering the effect of differing transition structures on total community abundance negligible.

The magnitude of the transition probabilities ( $p$ ) also has consequences for the total number of state transitions across all points and years. In order to illustrate that proportions and ridge-slough elevation differences can be maintained even with rapid transition shifts, I kept the transitions for water depths to the original configuration, but altered the probabilities by an order of magnitude demonstrated in Figure 5-7. The base model of non-overlapping water depths was used and the manipulations are described in the figure caption. In panels 5-7A&C the ridge probabilities were manipulated (Figure 5-7B representing the original functional forms) and in panel 5-7D the slough probabilities were manipulated. Across all probability manipulations ridges and sloughs remained in roughly equal proportion and the consequences to the soil elevations was negligible after 100 time steps.

Since one of the motivating questions was the recreation of the modern degraded landscapes, I highlight in Figure 5-8 examples from a bimodal landscape subjected to modern hydrologic conditions in drained, conserved, and impounded landscapes (using the *GPP* parameterization). 'Drained' hydrology had long-term water depths of 12.8 cm (landscape average; s.d. of 22.4), 'conserved' hydrology had a mean water depth of 32 cm (s.d. of 23.1), and 'impounded' hydrology had long-term water depths of 54.2 cm (s.d. of 22.1; hydrologic parameterization came from Watts and others 2010). After 100 time steps, the slough elevation mode was maintained across all hydrologic conditions (although the Drained landscape was beginning to decline). Community proportions shift towards ridges (drained) and sloughs (impounded) with the extremes in hydrologic conditions, but remain roughly 1:1 under 'conserved' hydrologic conditions. Although the 'drained' conditions did not lead to a single landscape mode

(Figure 8-8A), observing the peat elevation trajectory through time shows the ridge elevations were collapsing towards sloughs, even as many sloughs were shifting to the ridge state. At 100 time-steps, the tendency of the ridge mode to collapse to the highest peat accretion rate was not yet observed under 'conserved' conditions, and the soil elevation distribution was maintained (Figure 8-8B). The 'impounded' hydrologic conditions best approximated modern conditions, where small proportions of points remained ridge, but an over-all spreading of the global elevation distribution and convergence of means occurred (Figure 8-8C).

There was a surprising lack of response of the landscape to the application of fire (Figure 5-9). Some ridge points demonstrated transition deflation in elevations in response to fire. Higher fire frequency resulted in a lower proportion of ridge states. When fire occurred, ridge elevations with marginal peat accretion underwent stage transitions to sloughs and rapidly deflated to the slough mode. The result was an expanded separation between soil elevation modes accompanied with the landscape generally being in an accretion trajectory. Because of the optimization of the peak productivity in the original parameterization, the long-term large separation in peat modes is not stable under any simulations that do not include fire.

### **Discussion**

Model results suggest that although point scale processes may not be sufficient to completely explain the development of divergent ridge and slough elevations, they can induce the maintenance of ridge-slough elevations. Further, responses to altered water levels can result in precipitous declines and a rapid collapse of the ridge-slough landscape. This collapse is induced solely by water levels, indicating that an interruption in local processes is sufficient to degrade a patterned landscape. Indeed, all that is

necessary to re-create modern degraded conditions is a perturbation to the local positive feedbacks; i.e., the upstream water volumes that lead to ideal water depths.

Model outputs further suggest the modes of elevations in a bimodal landscape may remain fairly invariant but individual points of both ridges and sloughs demonstrate multiple and often rapid changes in elevations over time. Although this model was unable to re-create the modern landscape for drained conditions, it did demonstrate stability of ridge-slough elevation differences and long-term carbon storage using both sets of model parameters. As the potential peat accretion in ridges is more than twice that of sloughs under these parameters, it does suggest that the interactions between water levels and carbon budgets, and ultimately stable peat accretion, responds to much longer time steps than a single year represents.

The changes to state proportions and peat elevations under modern hydrologic conditions are consistent with observations of soil elevations from Watts and others (2010). The results also support the conclusion from that pattern loss was likely due to an interruption of local scale processes. Notably, the drained simulations maintained distinct ridge-slough elevation modes, suggesting the point-model of local carbon budgets was insufficient. In this landscape, both muck fires prior to the 1980s (Schortemeyer 1980; Zaffke 1983) and peat oxidations are generally blamed for the observed loss of soil elevation bimodality. The application of severe fire in conjunction with the drainage may be necessary to more accurately simulate the modern landscape. The observations for the 'impounded' landscape are consistent with modern observations; although there has been a loss of soil elevation bimodality and a reduced

prevalence of ridges, there is no evidence that the landscape itself has collapsed through the loss of peat.

Although the *GPP* parameterization is based on a single year's observation of ecosystem carbon dynamics it is notable that the addition of fire amplified the differences in ridge-slough peat elevations. The implication is that fire has a role in maintaining peat elevations between ridges and sloughs. The note of caution is in the loss of low-accretion ridges; areas with marginal carbon budgets may be sensitive and lack resilience to fire. Since fire is currently used by natural resource management agencies throughout the region, further examination of this process on the long-term dynamics of topographic patterning is warranted.

Spatial and temporal interactions in microtopography development have implications for elucidating some of the landscape features this model was unable to re-create. This model assumed local points were acting independently of other points, rather than as an assemblage of interacting patches. This model performed particularly poorly with respect to maintaining a variance around the ridge elevation mode-- likely an artifact of the lack of variance in carbon budgets. We currently lack sufficient data to know how structured variance in the carbon dynamics may be. Although doubtless environmental conditions (rainfall, annual cloud cover, temperature) induce noise to the carbon budgets, variance may also be spatially (one point influencing a neighboring point) or temporally (generation inheritance) correlated. State transitions may also demonstrate spatial structuring. A point in the center of patch is likely buffered from the conditions that lead to state transitions because of the spatial interactions in community structure and phenology (e.g., seed fall, root propagation). Spatially explicit models with

autocorrelated neighboring responses will be necessary to ascertain whether patch configuration provides an additional control on the divergence between and prevalence of ridges and sloughs.

In addition to the carbon processes suggested here, patch elevation may adjust to flow velocities and nutrient dynamics (e.g., Ross and others 2006; Larsen and others 2007). Further, community prevalence maybe equally dictated by the lateral expansion and contraction of patches. Lateral shifts in peat and vegetation patches may provide the system with resilience to changes in hydrology and facilitate the persistence of a community not currently favored by the hydrologic regime. As the landscape hydrology (in terms of velocity, volume, and depth) is tied to vegetative patterning, small but widespread changes in community elevations under marginal conditions may feedback to reduce the strength of the hydrologic control. For example, incremental ridge contraction in response to deeper water results in a larger water storage, or conduit, capacity in sloughs, effectively reducing the water depths felt across all ridges (Heffernan and others in press).

Spatial and temporal variations in peat growth have important implications for elucidating the response to 20<sup>th</sup> century hydrologic management and the future of Everglades restoration. Laboratory and biomass studies fail to provide accurate estimates for the carbon entering the system to become peat because to date, they fail to consider the interactive roles between hydrology, microform, and vegetation. Moreover, our poor understanding of important patch-level carbon dynamics compromises estimating future responses to hydrologic management as we have only recently begun to capture peat accretion responses to to hydrology.

Although the model presented here helps elucidate some of the patterns that may be expected over larger time scales, it also elucidates unknowns to carbon responses. Important areas of research remain in the ecosystem-scale total carbon balance, particularly in terms of predicting what becomes peat (above ground vs. below ground vegetative components) and associated temporal lags from biomass to peat mass. Although recent work has elucidated the link between multi-year hydrologic conditions and shifts between ridges and sloughs under deeper water conditions (Zweig and Kitchens 2009), we still have little information on the over-all probability of state shifts, the temporal link between those shifts and hydrologic drainage, and importantly, the link between those state shifts and the local development (or decline) in microtopography.

Table 5-1. Model symbols and definitions.

Symbol	Definition	Unit
$a_x$	C efflux from CO <sub>2</sub> respiration when annual water depths = 0	g C m <sup>2</sup> yr <sup>-1</sup>
$b_x$	Decay coefficient for CO <sub>2</sub> respiration	
$m$	Contribution of methane and DOC to ecosystem respiration	g C m <sup>2</sup> yr <sup>-1</sup>
$h_e$	Annual average stage (water elevation)	cm
$h_a$	Annual average water depth at a point	cm
$R$	Annual C losses	g C m <sup>2</sup> yr <sup>-1</sup>
$P_x$	Sigmoid relationship of community productivity with water depths	g C m <sup>2</sup> yr <sup>-1</sup>
$A_x$	Parameter representing the minimum productivity of a community	g C m <sup>2</sup> yr <sup>-1</sup>
$K_x$	Parameter representing the maximum productivity of a community	g C m <sup>2</sup> yr <sup>-1</sup>
$B_x$	Community-specific growth rate	
$m_x$	Community-specific parameter representing shift along the x-axis	cm
$p_1, p_3$	Minimum transition probability	
$p_2, p_4$	Maximum transition probability	
$w_1, w_3$	Minimum $h_a$ for step function transition probability	cm
$w_2, w_4$	Maximum $h_a$ for step function transition probability	cm

Table 5-2. Parameters for the state transition functions.

	Non-overlapping transitions (base model)		Overlapping transitions		Probabilities			
	Upper water depth ( $w_1; w_3$ )	Lower water depth ( $w_2; w_4$ )	Upper water depth ( $w_1$ )	Lower water depth ( $w_2$ )	$p_1$	$p_2$	$p_3$	$p_4$
Ridge→Slough	50	60	25	45	0.1	0.001	0.01	0.001
Ridge←Slough	15	30	25	45				

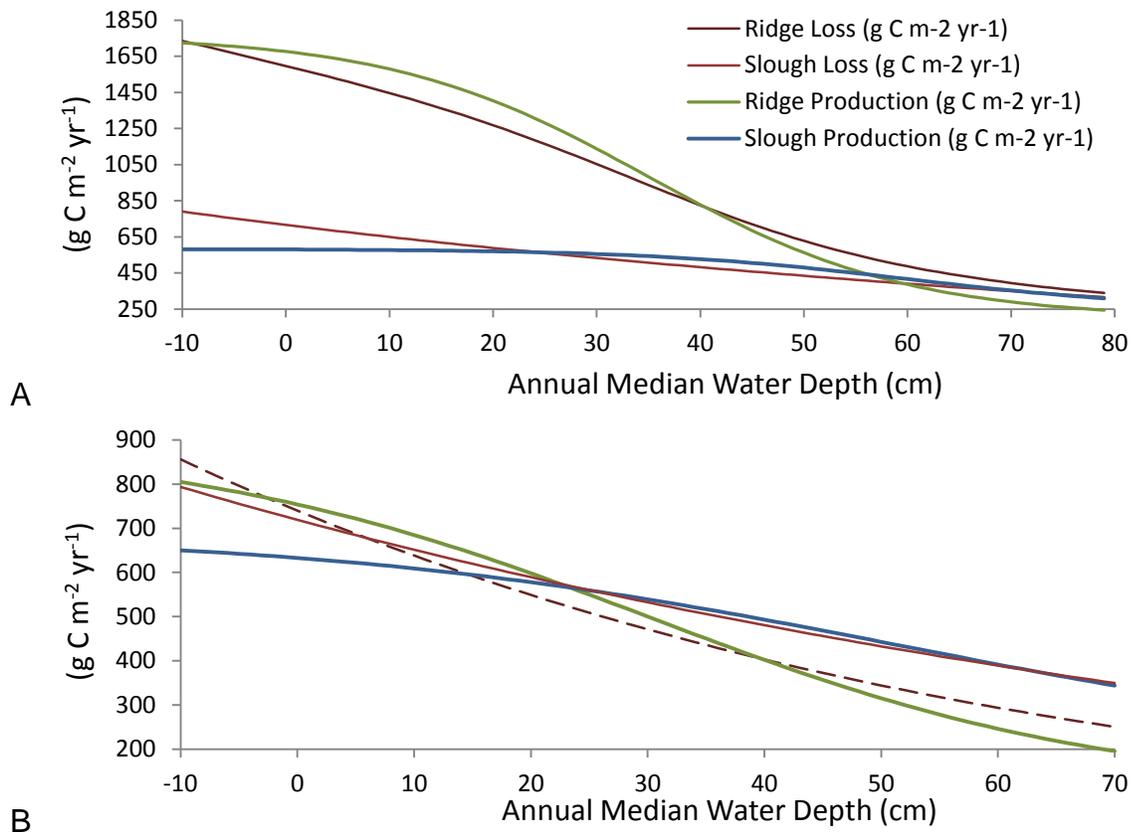


Figure 5-1. Parameterized model forms for carbon uptake and losses for ridge and slough states. A) *GPP* model parameterization; B) *Peat* model parameterization.

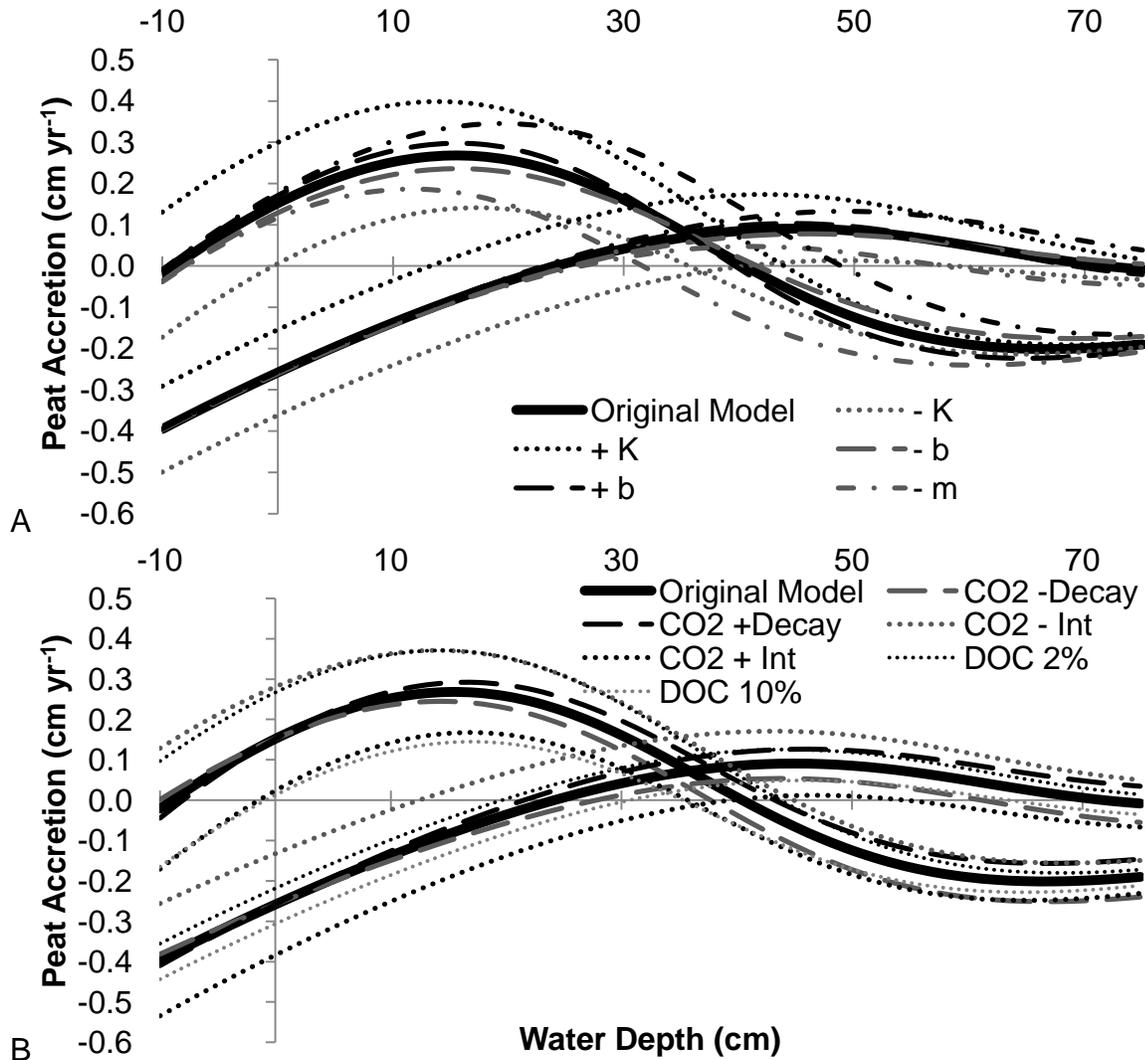


Figure 5-2. Change to peat accretion rates due to *GPP* model parameter perturbations. A) Productivity and B) carbon loss parameter perturbations. Changes to  $A_x$  and methane parameters not shown because the shifts are very small.

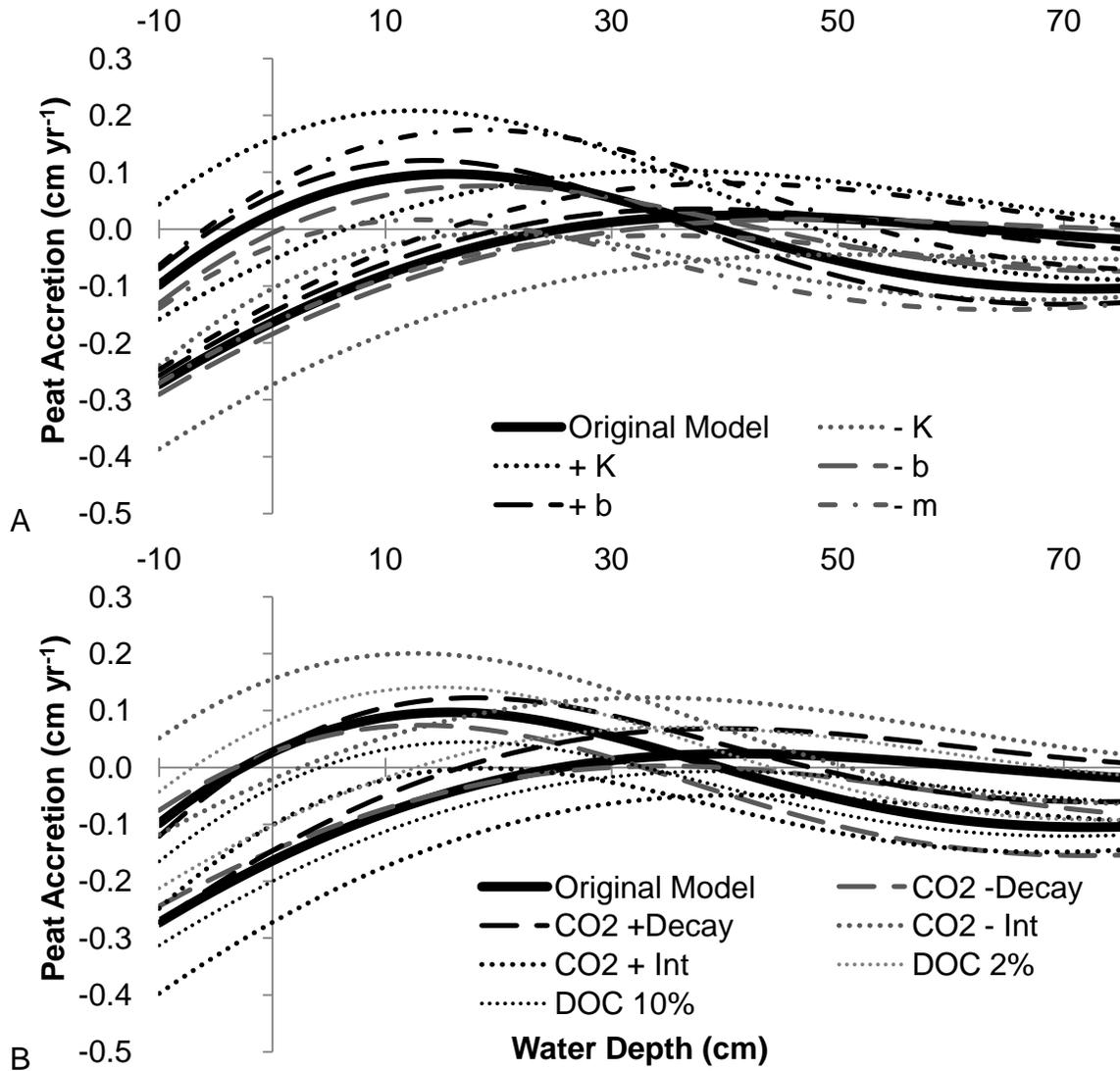


Figure 5-3. Change to peat accretion rates due to *Peat* model parameter perturbations. A) Productivity and B) carbon loss parameter perturbations. Changes to  $A_x$  and methane parameters not shown because the shifts are very small.

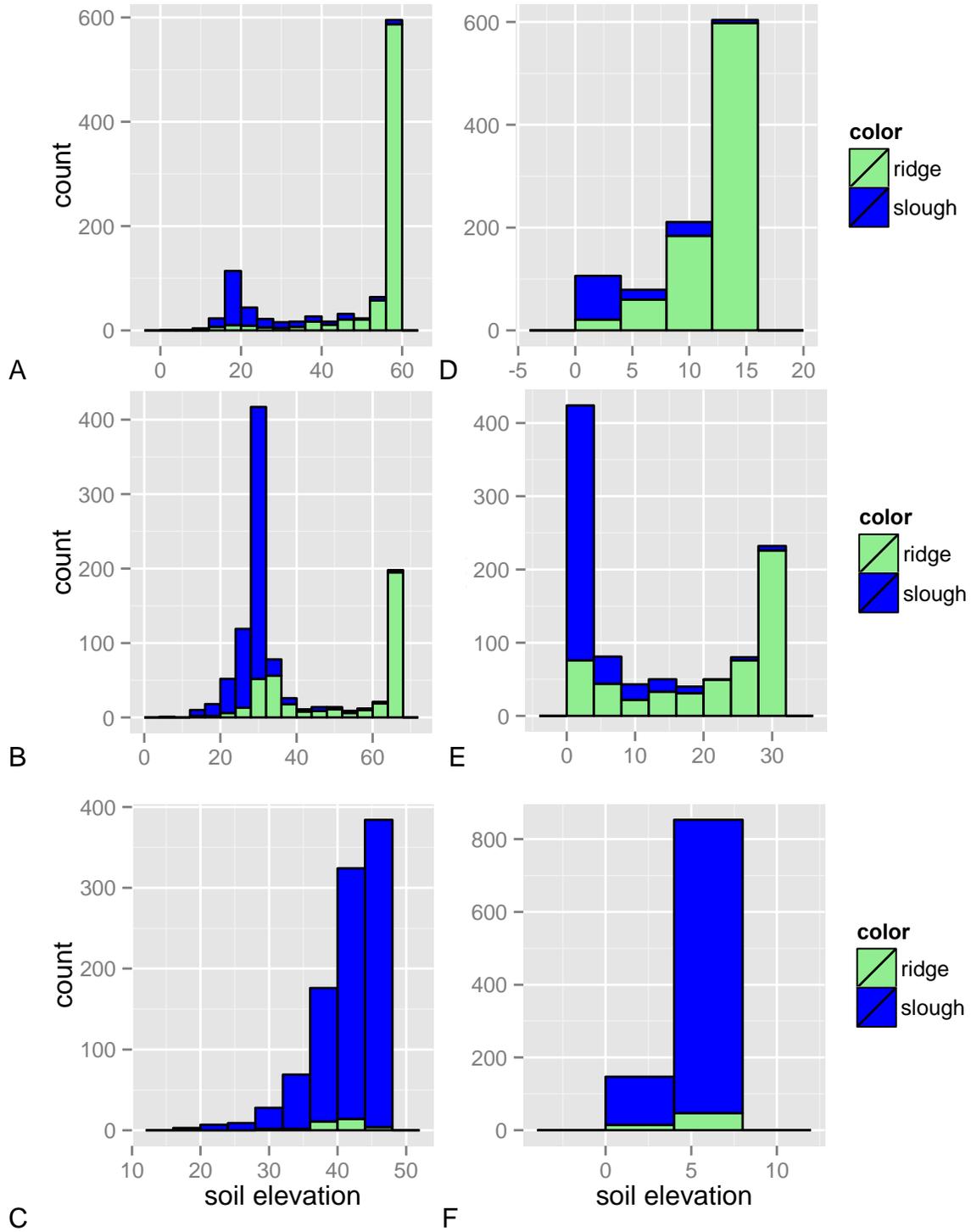


Figure 5-4. Soil elevations after 1000 years commencing from a slough, undifferentiated landscape. A-C) *GPP* model parameters and D-F) *Peat* model parameters. Hydrologic conditions are an interannual average of 10 cm (A, D), 30 cm (B, E), and 50 cm (C, F), with a standard deviation of 17 cm.

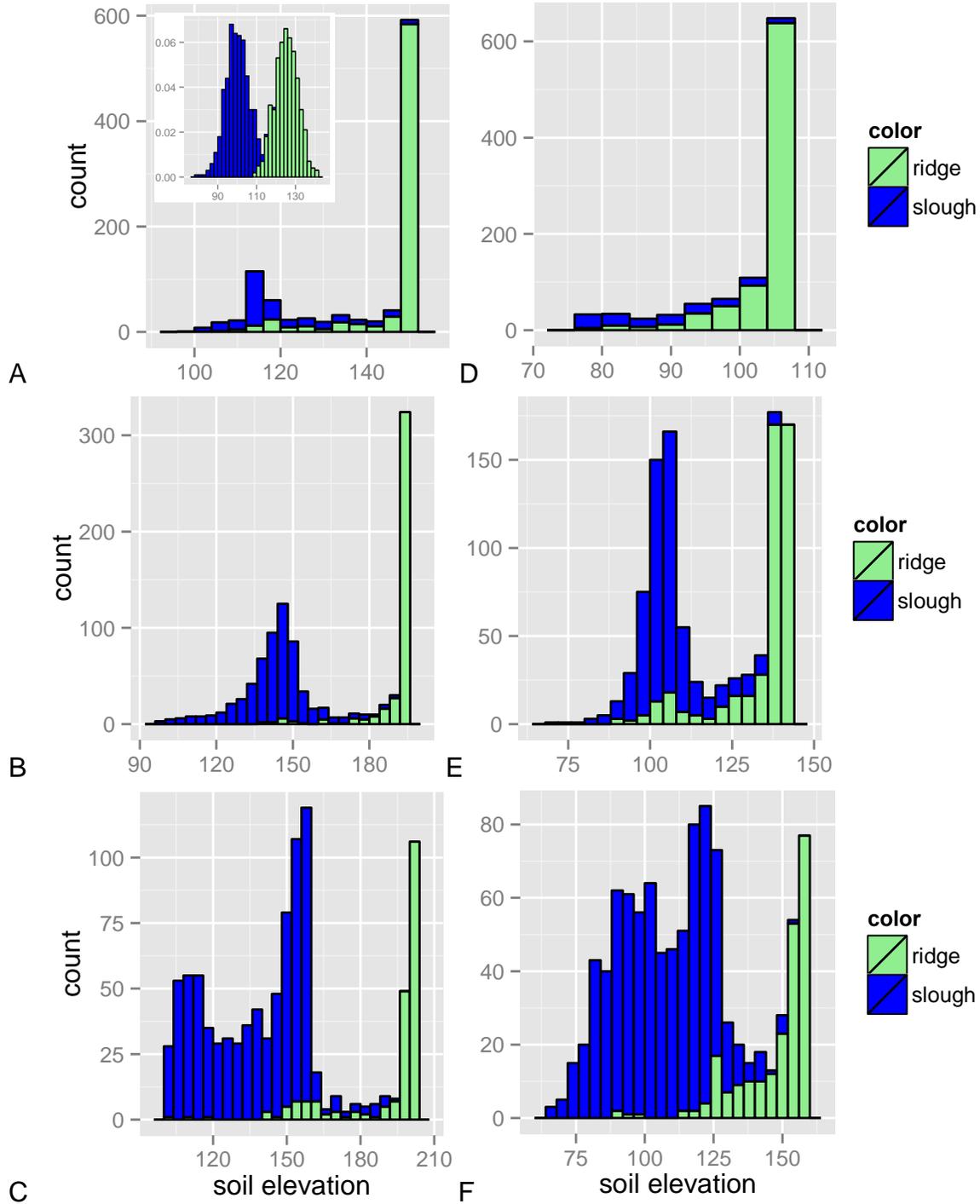


Figure 5-5. Soil elevations after 1000 years commencing from a bimodal landscape. A-C) *GPP* model parameters and D-F) *Peat* model parameters. Hydrologic conditions are an interannual average of 10 cm (A, D), 30 cm (B, E), and 50 cm (C, F), with a standard deviation of 20 cm. Inset: the starting landscape.

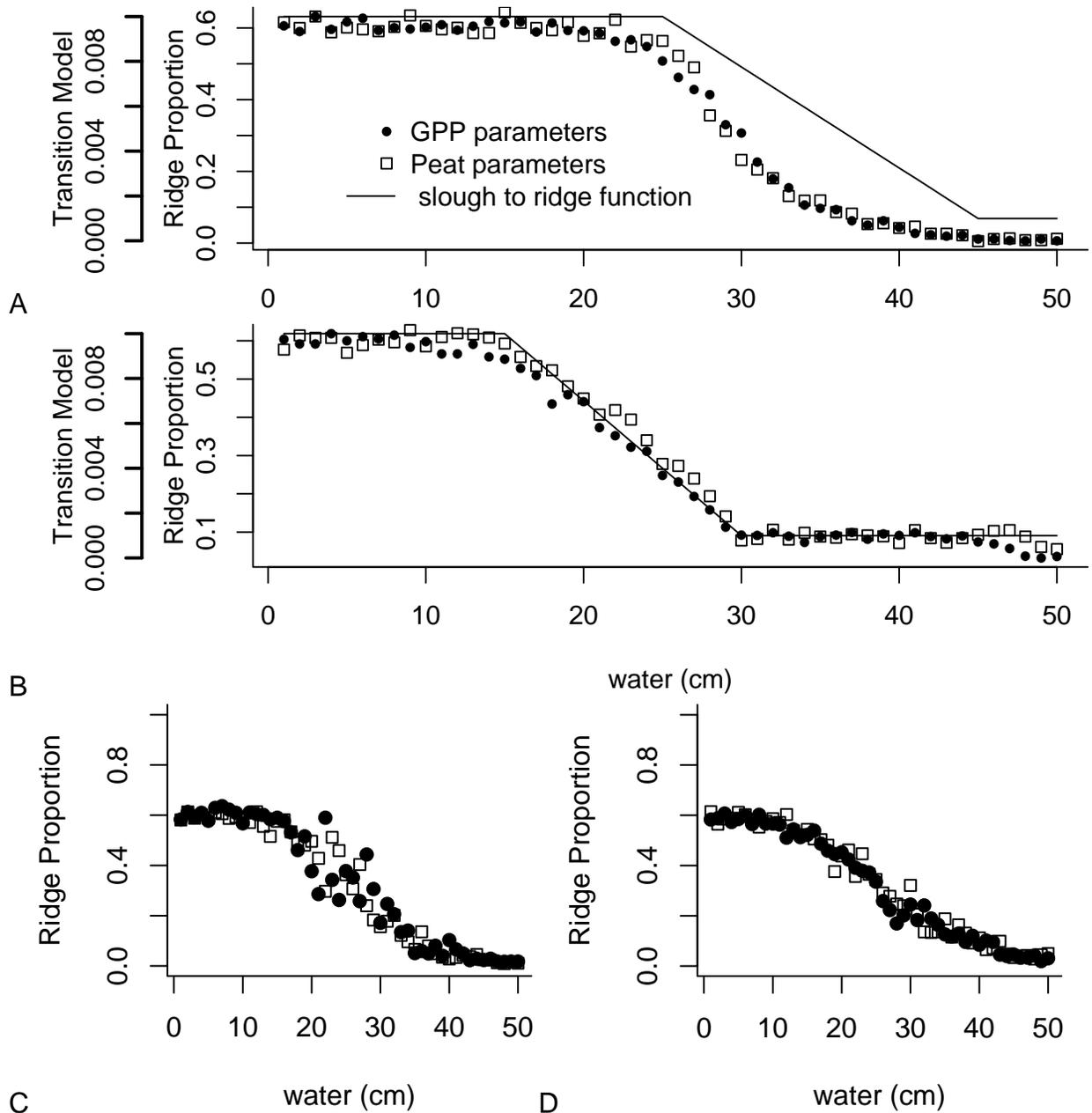


Figure 5-6. Proportion of points that become ridges after 100 times steps commencing as an undifferentiated slough landscape when transitions are manipulated. A) Overlapping and (B) non-overlapping transition ranges across a range of interannual mean water depths. Introducing variance to the water depths (s.d. of 17 cm) smooths out the relationships: C) Overlapping transition ranges; D) non-overlapping transition ranges.

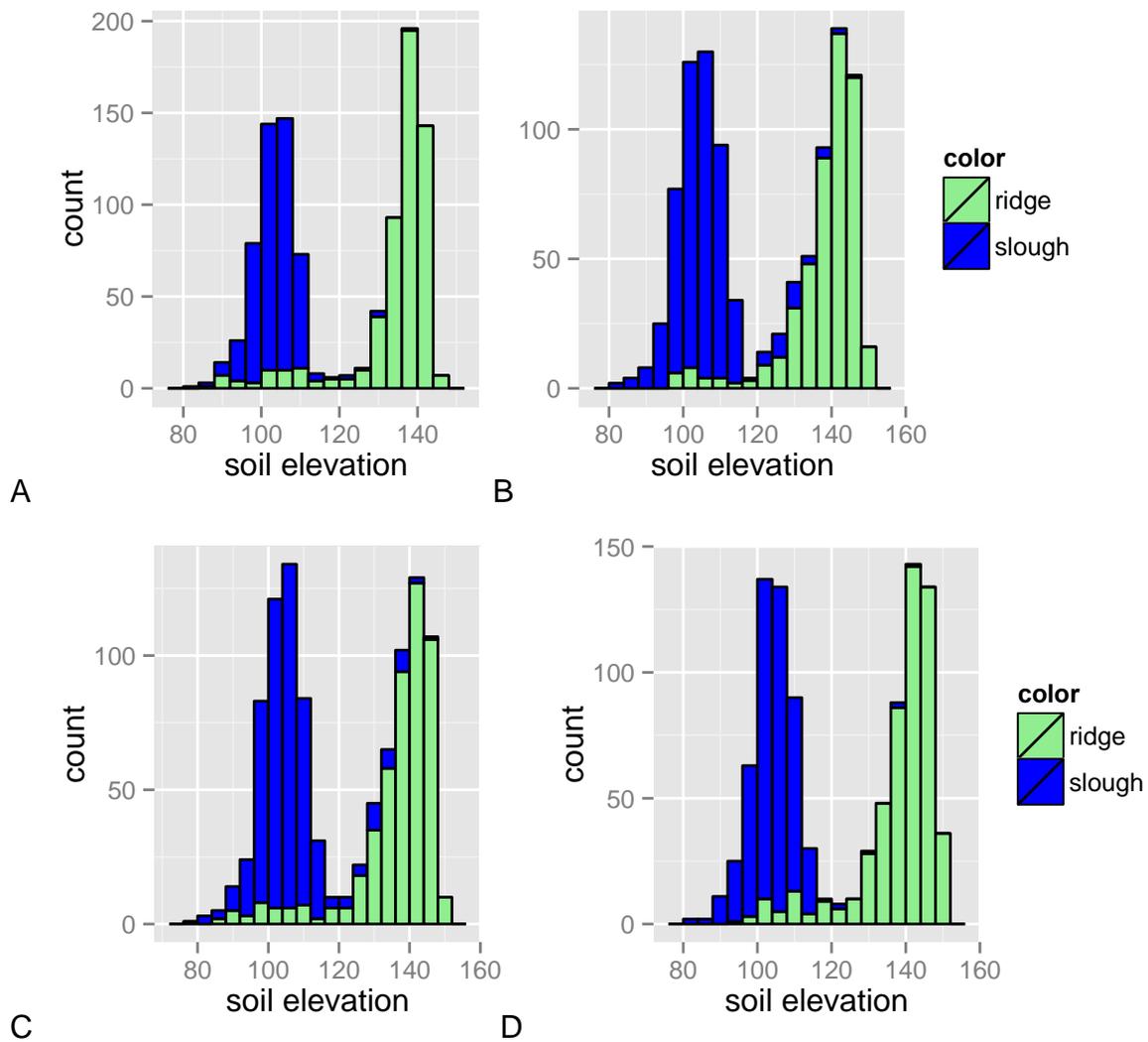


Figure 5-7. The bimodal landscape after 100 time steps with altered transition probabilities (*GPP* parameterization). Transition probabilities are A)  $p_1=0.01$  &  $p_2=0.0001$ , B)  $p_1=0.1$  &  $p_2=0.001$ , C)  $p_1=0.01$  &  $p_2=0.001$ , and D)  $p_3=0.1$  &  $p_4=0.001$ . The starting landscape is the same as in Figure 5-5.

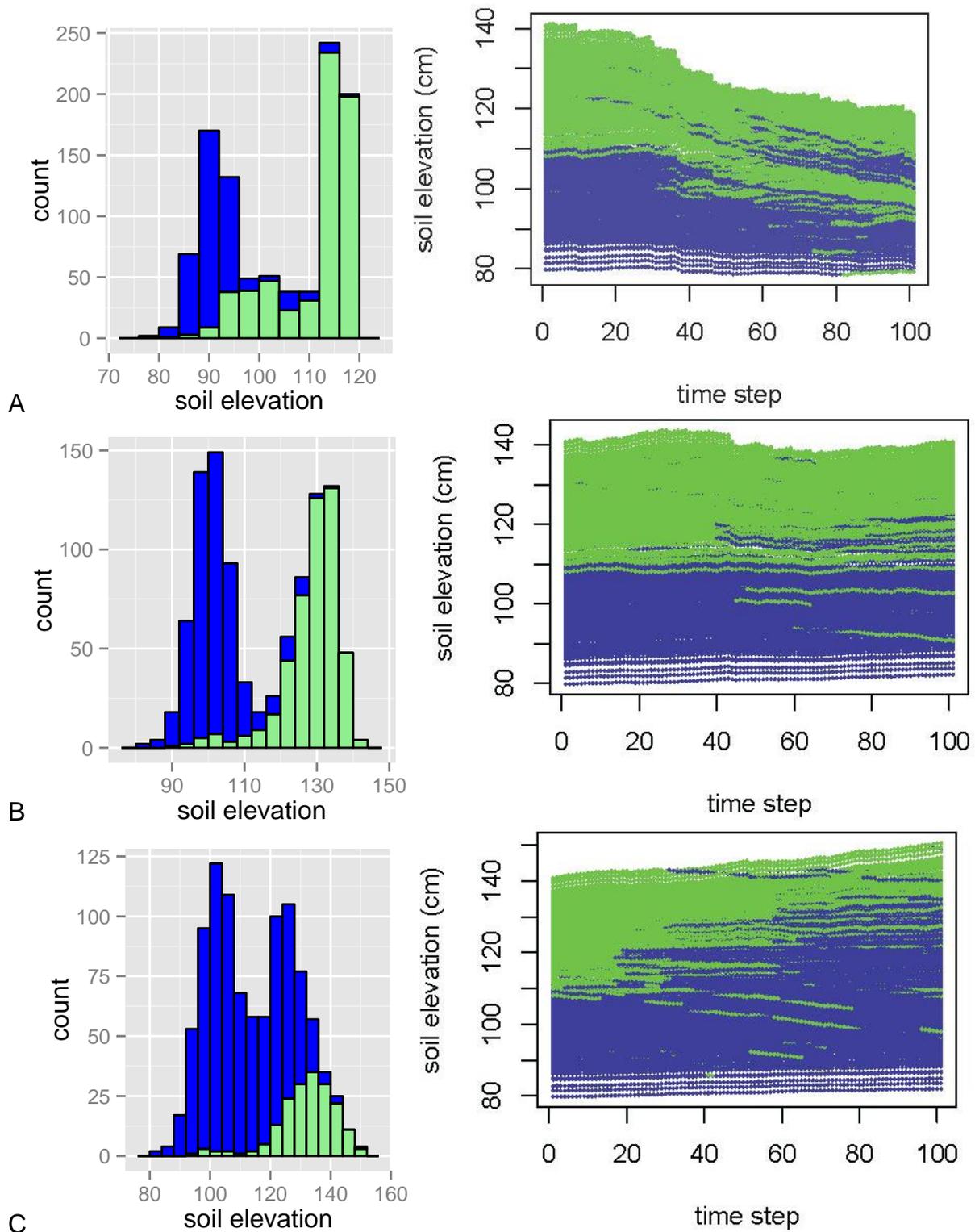


Figure 5-8. Bimodal soil elevation configurations after 100 time steps of subjections to modern hydrologic conditions. A) Drained, B) conserved, and C) impounded hydrologic conditions. Green represents ridges, blue represents sloughs. The starting landscape is the same as in Figure 5-5.

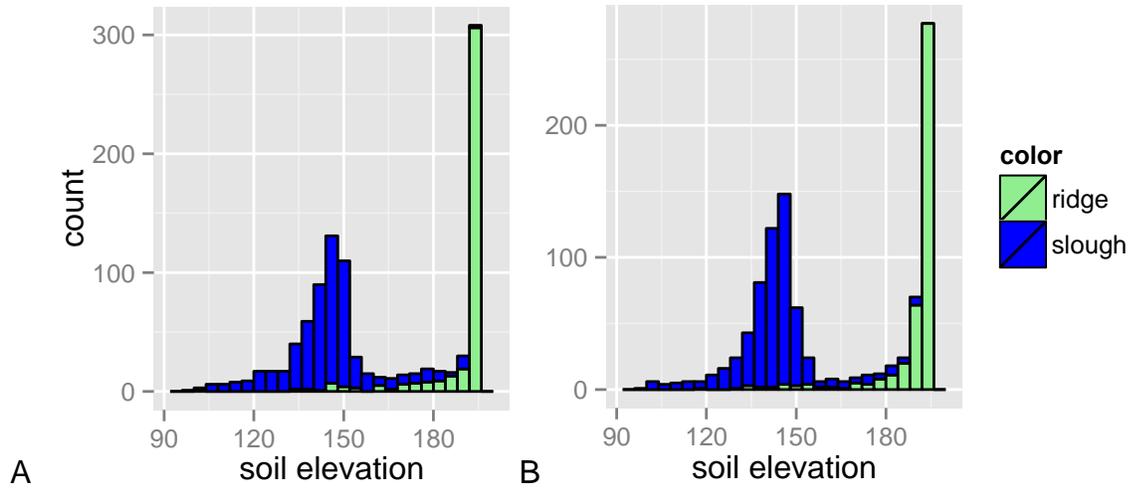


Figure 5-9. The bimodal landscape after 1000 years under differing fire return intervals in the *GPP* model parameterization. A) 3-15 year fire return intervals and B) 10-30 year fire return intervals. The starting landscape is the same as in Figure 5-5.

## CHAPTER 6 SYNTHESIS

The Everglades is a series of hydrologically interconnected ecosystems. The Everglades landscape has to adjust to short-term seasonal variability, pronounced inter-annual variability, and long term climate variation in response to global phenomena (Bernhardt and Willard 2009; Obeysekera and others 2011). Uncertainty in these ecological conditions induces ecological resilience, manifested by the extended temporal scales of ridges and sloughs and the presence of many of the pre-hydrologic modification features of the landscape.

Self-organized patchiness may indicate proximity to environmental thresholds (Rietkerk and others 2004), and it is generally thought that the same mechanism that induces alternative stable states also plays a role in the self-organized patterning. In the Everglades, self-organized patterning has been variously hypothesized to be due to nutrient concentration (e.g., Ross and others), preferential deposition (Larsen and others), or landscape discharge competence (Cohen and others). While not mutually exclusive, each of these hypotheses suggests a locally positive feedback in peat accretion that is mediated by a landscape control that is scale dependent. Shifts from patterned to unpatterned conditions has been observed across the Everglades in response to nutrient additions and altered hydrology (Wu and others; Watts and others 2010). The aim of this dissertation was to explore the strengths of the local feedbacks as they relate to the third dimension of patterning in the Everglades- microtopography, and to explore the linkage between those patch dynamics and the greater landscape hydrology.

My research approach was a combination of empirical study and simulation. The four studies presented here are united in their examination to the mechanism behind observed patterns in vertical relief across the Everglades. In Chapters 2, 3, and 4, I extrapolated measured fluxes to larger temporal and spatial scales in order to explore the implications of the findings to observations of landscape pattern. In Chapter 5 I go a step further, and explore the implications of the model proposed in Chapter 1, in combination of the findings in Chapters 2 and 3, at significantly longer times steps. At this point it becomes appropriate to revisit the questions raised in Chapter 1.

1. Does respiration demonstrate a monotonic and inverse relationship to water depths, as described in Figure 1-2?

In Chapter 2, I conclude that water depths represent the strongest predictor of local water column respiration in a relationship that is indeed is both monotonic and inverse. Ultimately there is some control on the rate of CO<sub>2</sub> efflux that is community based, and is likely attributable to the differences in aquatic productivity and community phenology between ridges and sloughs. Further, there is a non-linearity to the relationship, wherein increased water depths do not have a proportionate increase in flux rates. Extrapolations to extant hydrologic conditions in the landscape blocks across multiple years demonstrate the role drought and drainage have in dramatically increasing the source of CO<sub>2</sub> to the atmosphere.

2. Do observations of ecosystem productivity corroborate the predictions from the s-curve relationship described in Figure 1-2?

In Chapter 3 I explore ecosystem CO<sub>2</sub> carbon budgets and their responses to local water depths and community type. The results agreed qualitatively with the prediction that there is a discontinuity in the net ecosystem productivity between ridges and sloughs. The trend in productivity with water depths was sufficiently obfuscated that

the research question cannot be answered with a simple yes, however. When comparing annual extrapolations of the net ecosystem productivity to ecosystem respiration, no equivalence in the potential peat accretion rate was observed. Ridges were persistently net autotrophic across a wide range of hydrologic conditions, with peat accretion rates as much as three times higher than those of sloughs. Further, there was the somewhat surprising finding of a large potential for peat accretion in ridges in the drained landscape block, where shallower peat depths and a loss of microtopography suggested previously this landscape would be in a net peat loss condition. I concluded that *either* the year of carbon exchange study was an unusual year, where hydrologic conditions allowed an unusually large carbon uptake *or* the landscape deflation was due to more severe drainage prior to the 1980s and increased water delivery has resulted in a shift towards peat accretion rather than loss.

3. Can productivity-induced differences in evapotranspiration reinforce patch differentiation in the ridge-slough?

Although there are many pattern forming processes exhibited in nature, nutrients have been demonstrated to play a pivotal role in maintaining patch differences in some patterned peatlands. Indeed, the interactive effects of pattern forming processes have implications for the type and dimension of the pattern formation (Eppinga and others 2009). The hypothesis of resource concentration in ridges induced by the convergent flow of pore water propelled by higher evapotranspiration on ridges gains credence by demonstration of a water subsidy to ridges. In Chapter 4 I provide such a demonstration by observing that there is a critical period of time when the diurnal water table in inundated sloughs is nearly exactly matching the diurnal water table of exposed ridges. In other words, the water table is in lock step, so that the amplified response of the

water table to evapotranspiration in the soil profile in ridges is matched closely in sloughs. The water table reaching this critical time period-- ridge soil surfaces are exposed but sloughs remain inundated—is pivotal, as this is the only time when we can presume that some portion of the demand of water on ridges is not answered locally; when there is standing water, the porous nature of peat means water would be supplied vertically, and when both communities are dry there is no proof of a horizontal subsidy. The size of the demand is patch size dependent, but results in a large potential movement of water from sloughs to ridges. Patch differentiation would therefore be reinforced by a nutrient flow into ridges, particularly at ridge edges, where increased nutrient availability would spur greater sawgrass growth. Further, this mechanism can only occur when there are elevation differences between ridges and slough.

4. What are the long-term implications of considering patches from the point-scale of Figure 1-2?

In Chapter 5 I explore the longer time- scale implications of the model presented in Chapter 1. Parameterization of the model using information from the literature and Chapters 2 and 3 allowed me to demonstrate that 1) much of our understanding of Everglades carbon accretion remains poorly constrained and 2) modern carbon budgets result in a strong forcing of much of the landscape in favor of ridges, but is balanced at longer time scales. Parameterizing the model so that accretion dynamics conforms to long-term peat accretion rates (described by Bernhardt and Willard) demonstrates that very small peat accretion rates end up being very sensitive to internannual variability. The results of the comparison of the two parameterizations suggest that a higher peat accretion potential in ridges may be necessary in the long term to provide resilience in the landscape to interannual variability.

However, much additional work remains to be done to understand the role hydrology has in maintaining the patterns observed in the Everglades. Much of our current knowledge comes from laboratory analyses, which may not replicate actual environmental conditions, or from studies at sufficiently small time scales that seasonal and annual variability is not captured. Chapter 3 admittedly represents one such study, but is also the first study into whole-ecosystem carbon dynamics that encompasses the ridge-slough Everglades along a hydrologic gradient.

The idea that carbon retention in peatlands depends on hydrology (and vice versa) is hardly new. This dissertation does, however, explore that balance as it relates to a system with substantial seasonal and interannual variability in water table. Further, this dissertation suggests that alternative stable states in this setting are the results of an averaging of conditions over much longer time periods than the common ecological study. Management implications also arise out of this study. For one, there is apparently a wide range of hydrologic conditions for peat accretion in the Everglades, barring extreme or catastrophic events. Thus the prognosis for long-term carbon storage in the central portions of the Everglades remains positive. Model results starting from an undifferentiated landscape suggests the spontaneous divergence in peat elevations in regions that have lost topographic variation will likely take significantly longer than the time scale of a management action, however. And although the spatial configuration of patches is a tantalizing avenue for understanding state stability, the research represented here suggests that the dynamics leading to vertical patterns are equally fruitful avenues.

## APPENDIX A MODEL PARAMETERIZATION

Order-of-magnitude realistic parameter values were taken directly from previous carbon studies, both from the literature and from the studies in this manuscript.

### **Carbon Losses**

#### **Methane**

As discussed in Chapter 2, no predictive relationship for CH<sub>4</sub> evolution has been established in the Everglades. In order to approximate reasonable values, I used data from Debusk and Reddy (2003) laboratory study evaluating CH<sub>4</sub> and CO<sub>2</sub> fluxes in response to altered water levels. Cores C4 & C5 are considered to be from outside of the phosphorus enrichment-front in WCA2, so only data from these cores are included. A linear relationship with CO<sub>2</sub> is used, such that CH<sub>4</sub> flux increases with increased CO<sub>2</sub> in relation to lowered water levels (Figure A-1A), and assumes that this relationship remains true across seasons. This was preferred over the measured relationship with water depth, as that regression caused a negative methane value for water depths over 6.75cm. Extrapolating the relationship in Figure A-1A alongside the CO<sub>2</sub> extrapolations from 2009-2011 in Figure A-1B forms the relationship of annual methane efflux equaling  $21.18 * (\text{annual water depth}) - 0.2$ . While actual fluxes may be more stochastic or controlled by variables not yet identified, this does allow the model to account for some methane carbon loss, with increases in CH<sub>4</sub> efflux with increased water depths.

#### **Dissolved Organic Carbon**

DOC is produced by leaching of plant material, detritus, and peat as well as produced by microbial breakdown of plant matter. Qualls and Richardson (2003) of DOC production in the central portion of the Everglades. They calculate a DOC

production by sawgrass of 5.6% of NAPP (estimated from Table 2 in Qualls and Richardson 2003). Although slough material may produce more DOC, absent a similar relationship I default to using this value as a DOC loss term for all communities. I may therefore be underestimating the loss of carbon through this pathway.

### **Carbon Dioxide**

In Chapter 2 I develop a relationship between soil/water column and local water depths. By using the extrapolations for the three years of study across the hydrologic gradient and among communities, I can estimate annual soil respiration as a function of annual hydrology (Figure A-1B).

### **GPP Parameters**

When using the GPP values generated by Chapter 3 for this model, I am not accounting for the respiratory loss due to autotrophic respiration in the respiration component of the model. In Chapter 3 I compare modeled ecosystem CO<sub>2</sub> efflux to that of modeled soli/water column CO<sub>2</sub> efflux and note that autotrophic CO<sub>2</sub> losses (the difference between net ecosystem and soil respiration) were between 0.3 and 0.56 times GPP in ridges (across all models). To include autotrophic respiration here, I added a respiratory loss ( $R_{\text{auto}}$ ) of 0.48 (averaged ratio) times GPP to approximate the contribution by autotrophy in ridges. In comparison, sloughs ecosystem respiration and  $R_{\text{aq}}$  were nearly equal, likely due the integration of the water column in my  $R_{\text{aq}}$  methods. I used the base model for respiration of sloughs, assuming that the annual  $R_{\text{aq}}$  estimate includes the autotrophic component.

### **Peat Parameters**

The second parameter set forces the system to accumulate peat equal to estimates from Bernhardt and Willard (2009), which I do by adjusting the NEP

relationship and allowing the respiration model to remain the same. Therefore, the base model is used.

### **Productivity**

Lacking any data on the growth rate and x-axis shift parameters ( $B_i$  and  $M_i$ ), I drew inference from observations of community abundance with long-term annual water depths from Watts and others (2010). My reasoning is thus: Reduced community abundance is likely do to reaching thresholds in community tolerance to environmental conditions, which is consistent with the hypothesis that self-organized patterned systems exist in a narrow range of environmental conditions, between thresholds for conversion of the landscape to a homogenous condition of one or the other of the two states. The observation of reduced ridge abundance between 30 and 55 cm annual median water levels suggests that within this range ridges are no longer producing enough peat to overcome anoxic stress. Similarly, increased wet prairie abundance is observed at 20 cm, but rarely at 30 cm or deeper.  $B_i$  and  $M_i$  are set to approximate observed relationships with community prevalence and productivity (Table A-1), but are admittedly poorly constrained.

The remaining parameters are evaluated as two sets: *GPP* (set 1) uses values from Chapter 3 to estimate growth  $K_i$ , with a minimum value  $A_i$  to allow some small but negligible amount of deep-water productivity. Parameter set 2 (*Peat*) forces the landscape carbon balance to approximate the long-term peat accretion values described in Bernhardt and Willard (2009).

### ***GPP* Parameters**

The maximum *GPP*,  $K_i$ , was estimated using the global model developed in Chapter 3 (Table A-1).  $A_R$  was simply set to 200 and 250 as arbitrary values to keep

productivity from being equal to 0, but allowing it to go very low. The result is a NEP balance that goes positive again at a balance outside of the hydrologic conditions of the Everglades. NEP is positive (uptake) for all ridge water depths between -8 and 40 cm and positive for all slough water depths between 25 and 71 cm. Maximum peat accretion for ridges is  $0.27 \text{ cm yr}^{-1}$  (~15-16 cm water depth) and for sloughs is  $0.09 \text{ cm yr}^{-1}$  (~45 cm water depth).

### ***Peat Parameters***

As noted in Chapter 3, the estimated accretion rates therein are higher compared to the long-term peat accretion rates described in Bernhardt and Willard (2010; Table A-2). Zweig and Kitchens (2008) describe modern communities that are substantially different from older accounts of community assemblages, evidenced by increases in deep water species in the impounded regions. Bernhardt and others (2004) describe sawgrass ridges that are increasingly dense and productive since the 1900's, as inferred from pollen samples. These accounts suggest that carbon balances prior to anthropogenic modification to hydrologic cycles may have been substantially different from the modern conditions. Reflecting this possibility, a *Peat* parameter set was developed to approximate the much lower long-term peat accretion rates described by Bernhardt and Willard (2010). As the base model was used for respiration, productivity parameters are more appropriately viewed as net primary production values. The resulting model has positive peat accretion rates for median water conditions between  $-1$  and  $39 \text{ cm yr}^{-1}$  on ridges and  $26$  to  $62 \text{ cm yr}^{-1}$  in sloughs. The accretion rate for the model in Table A-2 is the average accretion rate across all positive values.

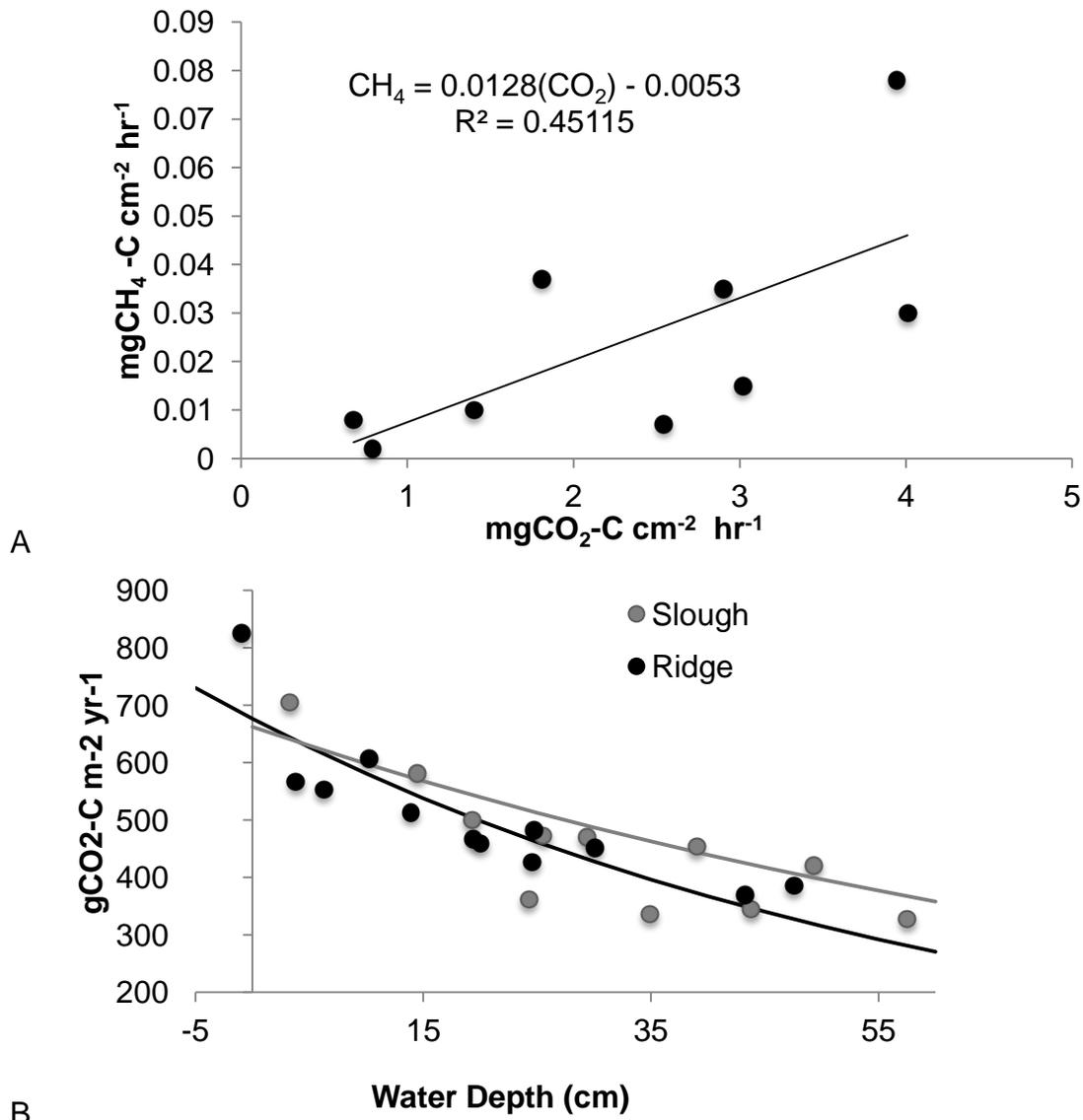


Figure A-1. Parameterization of respiration values. A)  $\text{CH}_4$  and B)  $\text{CO}_2$ .  $\text{CH}_4$  relationships are from cores C4 & C5 in Debusk and Reddy (2003).  $\text{CO}_2$  model is based on results from Chapter 2, parameters are in Table A-1.

Table A-1. Default model parameters. All carbon parameters are in  $\text{gC m}^{-2} \text{yr}^{-1}$ , water parameters are median water depths in cm.

	Set 1 ( <i>GPP</i> )	Set 2 ( <i>Peat</i> )
Ridge		
A	200	100
K	1766	900
B	0.08	0.05
M	35	30
R <sub>auto</sub>	0.48	--
Slough		
A	250	175
K	583	690
B	0.08	0.04
M	60	52
Losses (both <i>GPP</i> and <i>Peat</i> parameterization)		
Ridge CO <sub>2</sub>		
a (intercept)		676.5
b (decay rate)		-0.015
Slough CO <sub>2</sub>		
a (intercept)		662.6
b (decay rate)		-0.010
DOC		0.056
CH <sub>4</sub> intercept		21
CH <sub>4</sub> slope		-0.2

Table A-2. Ridge and slough accretion rates described by Bernardt and Willard (2009), and the average accretion rate for all positive rates for the *Peat* parameterization.

Peat accretion (cm yr <sup>-1</sup> )	Pre-MWP (>1500 BP)	MWP-LIA (1000-1500BP)	LIA (400-100 BP)	<i>Peat</i> average accretion
Ridge	0.018	0.025	0.06	0.063
Slough	0.011	0.013	0.01	0.015

## APPENDIX B SENSITIVITY ANALYSIS OF CARBON PARAMETERS

Parameters were individually set to to +/- 10% of the original parameter value, except in the cases of x-axis shift parameter ( $m_x$ ; in cm) for the s-curve and the DOC as a % of productivity. In these cases, the x-axis shift was +/- 5cm for  $m_x$  and reduced to 2% (0.02) or increased to 10% (0.1) from the base of 0.056 for the DOC parameter. Rather than adjust each of the intercept and slope terms for methane loss, the curve itself was shifted upwards and downwards by 10% by adjusting only the CH<sub>4</sub> intercept. The resultant effect of model perturbations to the difference between (median) ridge and slough elevations and proportion of ridges of an average of 50 model runs for 100 time steps for 1000 points is provided in Figures B-1 (*GPP* parameterization) and B-2 (*Peat* parameterization). Two initial landscape configurations are shown. First, the landscape is set to emerge from an initially undifferentiated with no sawgrass (landscape initiation; Figure B-1A & 1B, B-2A & 2B). Secondly, the landscape commences as bimodal in peat elevations, with a separation between modes of 25 cm with a standard deviation of each of 6cm and equal proportions 1:1 ridge and slough. In both cases the interannual water levels are set at  $30 \pm 17$  cm. Parameter adjustments to peat accretion rates are shown in Figures B-3 (undifferentiated landscape) and B-4 (bimodal landscape).

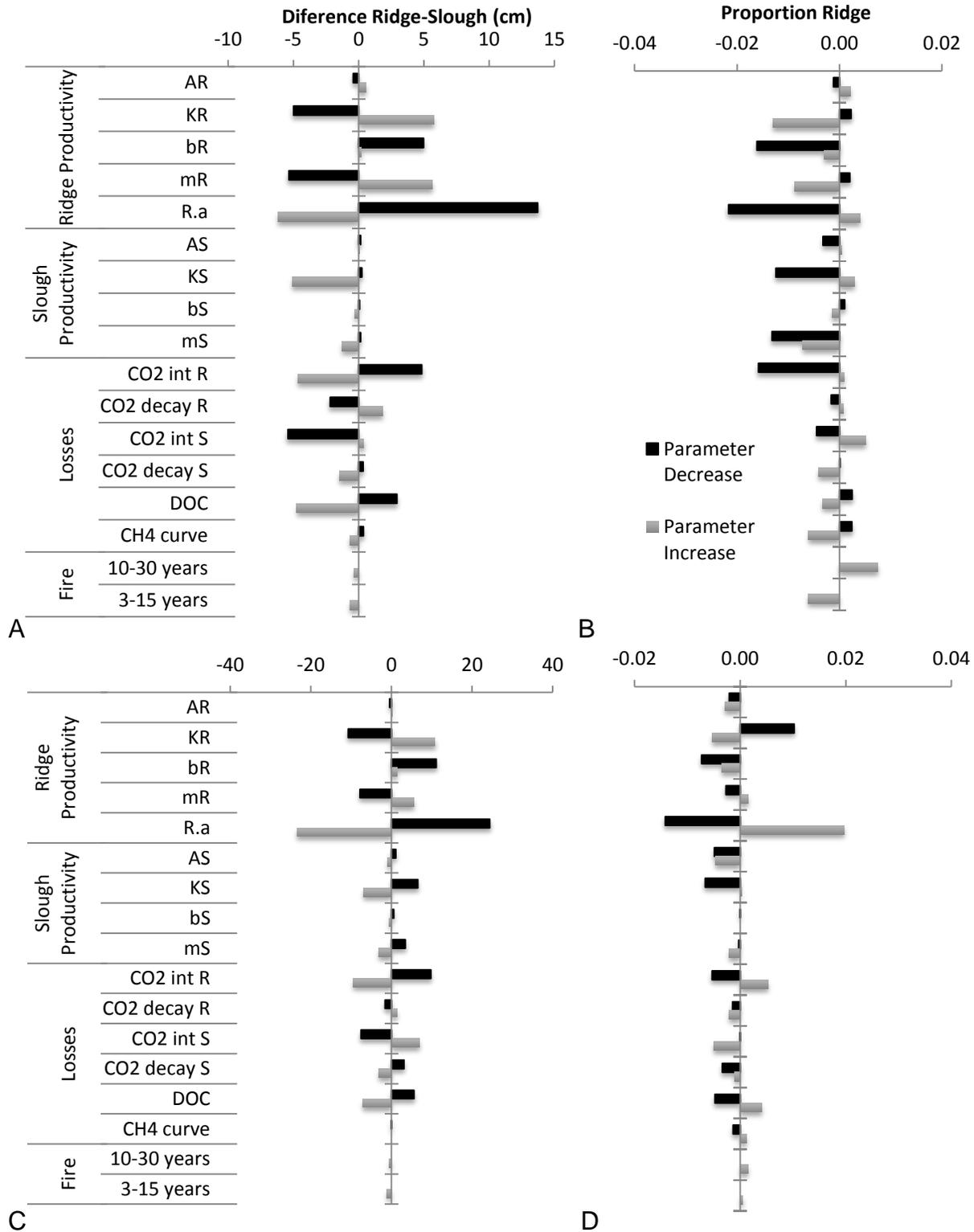


Figure B-1. Sensitivity of landscape conditions to perturbations to the *GPP* model parameters relative to baseline conditions. A) and B) initiate from a flat landscape, C) and D) from a bimodal one.

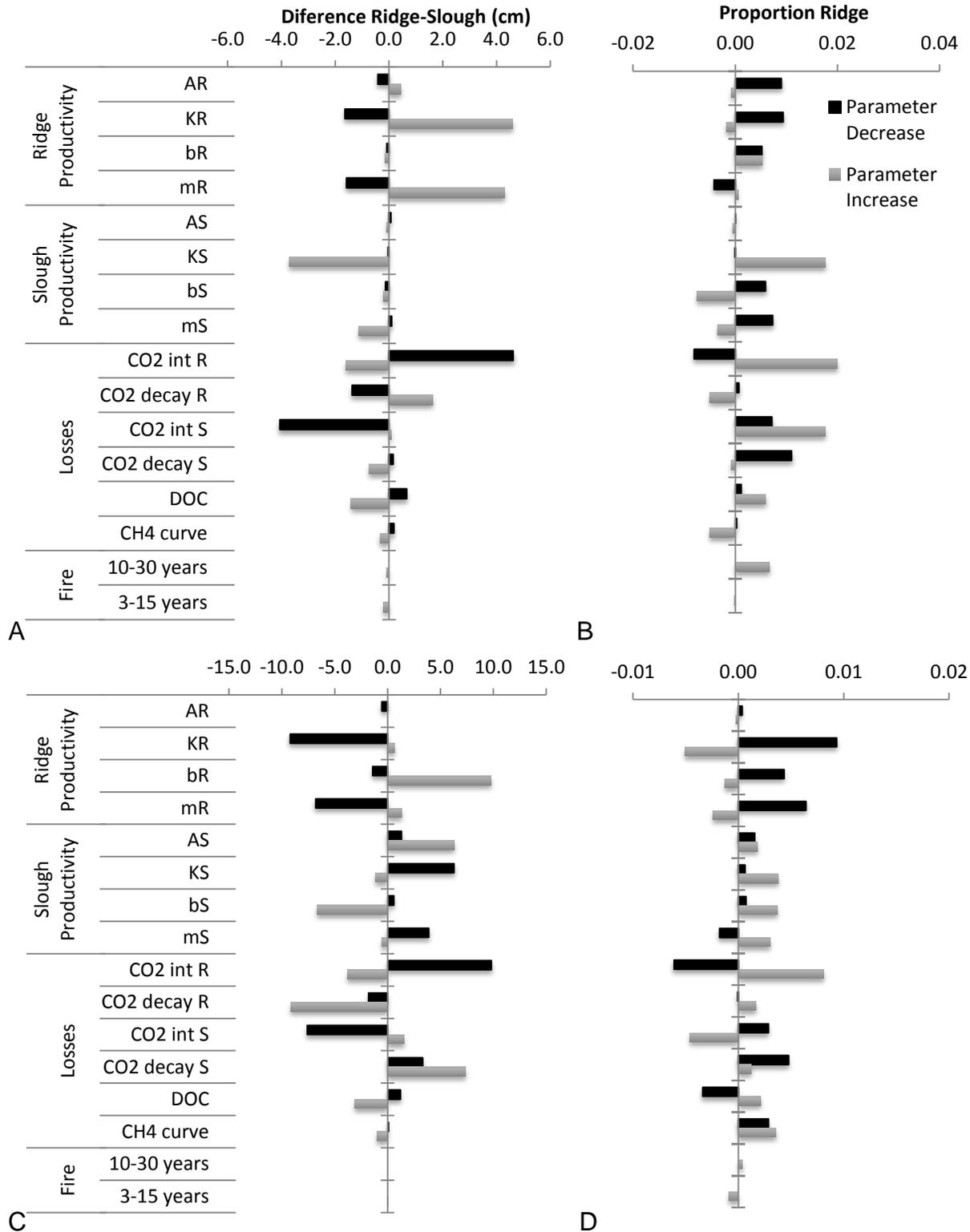


Figure B-2. Sensitivity of landscape conditions to perturbations to the *Peat* model parameters relative to baseline conditions. A) and B) initiate from a flat landscape, C and D) from a bimodal one.

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## BIOGRAPHICAL SKETCH

Danielle Watts developed a passion for natural systems while growing up as a 'Keys Rat' in the southern portion of the Florida Keys. As an undergraduate at the University of Florida, Watts majored in wildlife ecology and conservation while learning that not all plants should be petted and the unobserved parts of an ecosystem are sometimes the most interesting. Watts accomplished her dream of visiting Africa and living abroad by serving as a Peace Corps Volunteer in Guinea, West Africa. While sitting on top of a plateau during the sub-Saharan Harmattan season, Watts realized she had a passion for the low, wet areas of the world. Chasing after a desire to study these systems, she completed a M.S. degree in interdisciplinary ecology at the University of Florida investigating landscape pattern dynamics in the Everglades. Those studies led to the research accomplished in this dissertation.