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Linking Hydroperiod with Water Use and Nutrient Accumulation in Wetland Tree Islands

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LINKING HYDROPERIOD WITH WATER USE AND NUTRIENT
ACCUMULATION IN WETLAND TREE ISLANDS

By

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Nutrient Accumulation in Wetland Tree Islands

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Many large terrestrial ecosystems have patterned landscapes as a result of a positive
feedback system between vegetation communities and environmental factors. One
example is tree island habitats in the Florida Everglades. Although they only occupy a
small portion of the Everglades landscape, tree islands are important features as the focus
of nutrient accumulation and wildlife biodiversity in the Everglades ecosystem. The
hardwood hammock community on the elevated head of tree island habitats can
accumulate high phosphorus concentration in the otherwise P-limited Everglades
ecosystem. In this dissertation, I examined two hypotheses derived from the
chemohydrodynamic nutrient accumulation model, which suggests that high transpiration
of tree island hammock plants is the driving force for nutrient accumulation in tree island
soil. According to this model, I hypothesized that tree islands with lower dry season
transpiration should have less phosphorus accumulated than the tree islands with higher
dry season transpiration. By examining the water use and nutrient status from 18 tree
islands in both slough (perennially wet) and prairie (seasonally wet) locations, I was able
to compare water availability and nutrient accumulation in slough and prairie tree islands
with different marsh hydroperiods. Chapter 1 uses elemental and stable isotope analysis
to look at water stress and nutrient concentration in tree island plants. I showed that the
prairie tree island plants suffer from drought stress during the dry season, when the

marshes in the prairies dry out. Prairie tree islands also have lower soil and plant P concentration than the slough tree islands. Moreover, I showed that foliar N isotope ratio serves as a stable proxy for community level P availability for tree island plants, and prairie tree island plants have less P available than slough tree island plants. In Chapter 2, I showed that the satellite imagery derived normalized difference water index (NDWI) provides a robust indicator of community level canopy water content of these tree islands. NDWI, used as a proxy for water status, was positively related to foliar N isotope ratio, which suggests that water availability is linked to nutrient availability in the tree island hardwood hammock plant communities. These findings are consistent to the chemohydrodynamic nutrient accumulation model. In Chapter 3, I used sap flow sensors on individual trees to provide a real-time measurement of plant transpiration. I showed that tree island plant transpiration is affected by multiple factors including weather fluctuations, marsh water depth regulated by local water management, and canopy structure of different tree islands. Overall, my dissertation establishes a link between tree island plant water use and nutrient accumulation. It could be potentially important for future restoration plan of tree islands and Everglades hydrological management.

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Introduction

Background of study

<u>Wetland Ecosystems</u>

Wetlands ecosystems are transitional lands between terrestrial and aquatic systems. They are found all over the world from tropical to boreal regions, and exist in a wide variety of forms including bogs, marshes, mangroves, flooded forest swamps, etc (Mitsch and Gosselink, 2000). Wetland ecosystems have distinguishing features including periodically flooded shallow surface water, saturated soil, and the predominance of hydrophytes (Cowardin et al., 1979). Wetlands have high primary productivity compared to land or aquatic ecosystems (Brinson et al., 1981). Wetland ecosystems provide unique habitats for many plant and wildlife species, including many endangered bird, fish, and reptile species. Moreover, many wetlands are nutrient sinks and can improve water quality (Dorioz and Ferhi, 1994). Being the interface between terrestrial and aquatic systems, wetlands can regulate ground water level and prevent extreme flood or drought situations (Carter, 1994).

Wetlands are facing increasing threats and becoming endangered ecosystems. In the United States, more than 50% of wetlands have been lost during the past century (Noss et al., 1995). Changes in the hydrological regime are the most important factor affecting wetlands. Small changes in hydrology can have a major impact in other wetland attributes, such as the degree of soil anoxia, nutrient availability, salinity, and pH level (Mitsch and Gosselink, 2000). Hydrological fluctuations also regulate plant communities and production of wetland ecosystems (Euliss and Mushet, 1996). Any change of hydrology

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could lead to shifts in the vegetation composition and degradation of the ecosystem. For example, the construction of drainage canals in the Florida Everglades has changed the hydrology such that half the original ecosystem habitats have been lost (Davis et al., 1994). Another factor affecting coastal wetlands is sea level rise which can convert a large portion of tidal wetland habitats into open water in the near future (Nicholls et al., 1999). In addition, salt water intrusion is causing plant communities to shift in the coastal wetlands (Baldwin and Mendelssohn, 1998). Maintenance of wetland hydrology has always been the top priority for wetland conservation and restoration. In this study, I focused on tree island habitats, which are one example in which hydrology can affect wetland landscape structures and nutrient cycling.

Tree Islands

Many terrestrial ecosystems have patterned landscapes, with a heterogeneous vegetation composition and nutrient concentrations that are non-randomly distributed (Rietkerk et al., 2002; Rietkerk et al., 2004). These non-random patterns could be formed by self-organizing processes with positive feedback loops (van der Valk and Warner, 2009). The feedback mechanism usually involves vegetation affecting redistribution of materials and therefore leading to alteration of the environmental conditions such as local and regional hydrology, which in turn influences vegetation functioning (Rietkerk et al., 2004; Larsen et al., 2007; Eppinga et al., 2009; Larsen and Harvey, 2011).

One example of these self-organizing patterned landscapes are wetlands with tree islands. Tree islands are typical components of many large, flat wetlands in the world. Wetzel (2002a) defines tree islands as patches of woody vegetation within a freshwater wetland matrix dominated by non-woody species. Tree islands are relatively young

habitats in the wetlands, and are developed as a result of landscape processes and feedback between hydrological and climatic factors after wetland formation (Foster et al., 1983; Glaser, 1987; Wetzel, 2002b; Gumbricht et al., 2004).

<u>Tree Islands in the Everglades</u>

The south Florida Everglades is the largest wetland ecosystem in the United States. The annual precipitation of the Everglades ecosystem ranges from 1,270 to 1,620 mm, approximately 70-90% of which falls during the wet season, from June to November (McNab and Avers, 1994; Renken et al., 2006). The average annual temperature is from 22 to 25 °C, and the frost-free growing season lasts for 330 to 365 days (McNab and Avers, 1994). The region has a gentle elevation gradient of less than 4.5 cm per kilometer with a 48 km-wide sheet flow of surface water concentrated in the Shark River Slough (Fling et al., 2004). The Everglades is a complex wetland ecosystem composed of a variety of terrestrial and marine habitats, including upland pinelands and hammocks, freshwater marshes, tree islands, mangroves, and coral reefs (Lodge, 2004).

Tree islands in the Everglades appear as elevated tree patches surrounded by fresh water marshes. There are two main types of tree islands in the Everglades: small, rounded floating tree islands called pop-up tree islands, and large, elongated stationary tree islands (Sklar, 2002).

The latter, teardrop-shaped stationary tree islands are one of the unique features of the Everglades. These islands have an elevated head and an elongated tail in the direction of surface water flow (Fig. 1.1). The head of these tree islands remains unflooded all year round and is populated by flood intolerant hardwood hammock tree communities. The tail, also known as bayhead swamp, is flooded during the wet season and supports flood

tolerant trees and shrubs such as *Salix caroliniana*, *Persea borbonia*, *Morella cerifera* and *Annona glabra*. Although tree islands occupy only a small portion of the vast Everglades landscape, they support the highest biodiversity in the Everglades, having two to three times the species diversity of their surrounding marshes (Willard, 2003). As the only habitats that remain above water during the wet season west of the Miami Rock Ridge, tree islands provide essential habitats for wildlife including reptiles, birds and mammals and upland plant species that do not tolerate flooding.

Everglades tree islands are formed by a slow sedimentation process during the past thousands of years (Orem et al., 2002). The sedimentation process allows the tree islands to grow in size, height, and nutrient concentration (Orem, 2002). The head of the tree islands can have six to a hundred times the nutrient (especially phosphorus) concentration of the surrounding marshes (Wetzel, 2005). Sediments, as well as nutrients, also are deposited towards the back of the islands by surface water flow which form the elongated bayhead tails (Orem, 2002). Everglades tree islands can derive nutrients from several sources. Unlike the surrounding marshes, which use precipitation as the primary nutrient source, tree islands have a wider range of nutrient input including precipitation, surface water surrounding the tree island, groundwater upwelling, plant litter and bird guano deposition, and bedrock mineralization by tree exudates (Wetzel, 2005). Another critical factor determining tree island structure and vegetation is hydrology. A survey done in the northern Everglades (WCA 3) has shown that the hydrological gradient has a significant impact on tree island vegetation species diversity and species richness (Wetzel, 2008). Hydrology also can affect other disturbances such as fire. For example, Wetzel (2002b) found that frequently dry islands have more herbaceous species after fire disturbance than

frequently flooded islands. With altered hydrology and increasing agricultural activities in the past century, tree islands have become one of the most critical endangered habitats in the Everglades. Tree island loss has been documented in the northern Everglades (WCA 2 and WCA 3) (Hofmockel, 1999). Previous studies suggest that water level changes seem to be the major reason of loss of tree islands (Schortemeyer, 1980; Zaffke, 1983). Conservation and restoration of tree islands is one key component for maintaining the Everglades.

<u>Tree Island Nutrients and Hydrology</u>

Despite the significance of tree islands in the Everglades ecosystem, our knowledge about them is very limited. In the Everglades, tree islands have extremely high soil phosphorus concentration compared to the fresh water marshes. However, the P concentration is not homogenous among different tree islands. Preliminary studies indicate that tree islands located in perennially flooded marshes have higher total soil P concentration than tree islands in marshes that are only flooded during the wet season (Shamblin, 2007). As I discussed before, tree islands have a variety of P input sources which could contribute to the inhomogeneous P distribution. P concentration in tree islands is believed to have reached a steady state, with input of P including guano, transpirational pumping, dust, aerosols, water vapor condensation and atmospheric deposition, and output of P including soil leaching, and erosion and loss of litter and debris during flood events (D'Odorico et al., 2011). D'Odorico et al. (2011) also suggests that most of these P input sources are plant-related, therefore there is a positive feedback mechanism between P availability and tree biomass in different tree islands.

Although the different P input sources are not exclusive of each other, researchers are interested to find out the major P source determines the P distribution in different tree islands. There are two major hypotheses on how tree islands generate and maintain their high P levels: the bird guano deposition and the transpiration hypothesis. Givnish et al. (2008) constructed a theoretical model of tree island function under the assumption that bird guano deposition is the major P input for the tree islands. However, no direct evidence was provided to support this hypothesis. Although there is evidence showing that bird guano is a possible nutrient source for tree islands (Frederick, 1994), bird surveys done in the Everglades revealed no clear preference pattern of bird activities (Gawlik, 1998), which would be difficult to explain the heterogeneous P pattern in different tree islands. Another study conducted by Oliver and Legovic (1988) in the Okefenokee marshland in Georgia, showed that wading bird nesting activities can increase P input in the ecosystem by four to eight times. However, bird guano alone could not explain the 100 times higher P concentration in the Everglades tree island habitats. The other hypothesis is the chemohydrodynamic nutrient accumulation model which suggests that tree islands accumulate and maintain their high P level by harvesting nutrients from groundwater associated with surrounding marsh water (Wetzel et al., 2005; Ross et al., 2006). This model hypothesizes that high transpiration rates of tree island hardwood hammock plant communities cause them to take up water and nutrients from the surrounding groundwater, especially during the dry season when rain water is limited. Previous observations indicate that during the wet season, when there is plenty of precipitation, upland trees use rainfall entrapped in the emergent soil layer as their primary water source while lowland trees use marsh water surrounding the tree islands

(Saha et al., 2010b). During the dry season, however, both upland and lowland trees use groundwater associated with the surrounding marsh because there is very little soil water from precipitation available for upland plants (Saha et al., 2010b). These findings support the transpiration-driven chemohydrodynamic nutrient accumulation model, and suggest that tree island nutrient accumulation happens during the dry season.

In my dissertation research, I examined two different aspects of the transpiration driven chemohydrodynamic nutrient accumulation hypothesis: tree island plant water availability and transpiration rates, and tree island plant nutrient availability and concentration. I examined 18 tree islands from the Everglades National Park located in landscapes with different marsh water depth and hydroperiods (Fig. 1.2), in order to establish a link between tree island water status and nutrient status. I used three powerful techniques to establish this link: stable isotopes as proxy for nutrient status and water deficits, satellite remote sensing to assess canopy water and nutrient content, and sap flow probes that measure transpiration rates.

Techniques used in the study

Stable isotopes

A chemical element is said to occur in different isotopic forms if atoms differ in the number of neutrons but have the same number of protons and electrons. Therefore isotopes have the same chemical properties but only differ in mass. There are two different types of isotopes, stable isotopes and radioactive isotopes. For example, carbon has three isotopes, ^{12}C, ^{13}C, and ^{14}C, with 6, 7 and 8 neutrons respectively. ^{14}C is radioactive, as it is unstable with a half-life of $5,730 \pm 40$ years, while ^{12}C and ^{13}C are both stable isotopes and do not decay over time. For most elements, the lightest isotope is

usually the most common isotope, and the heavier isotopes are rare isotopes. For example, ^{12}C constitutes 98.9% of total carbon in the world, while ^{13}C only is about 1.1% (Fritz and Fontes, 1980). The composition of heavy and light isotopes differs among different substances. The isotopic composition of an element can be measured using a mass spectrometer. The isotopic composition, δ, is expressed as a ratio of the heavier isotope to the lighter isotope, with reference to an internationally defined standard as:

δ (‰) =[(R_{sample}/R_{std}) -1]*1000.

The mass differences between isotopes can result in partial separation of the light isotopes from the heavy isotopes during chemical reactions and during physical processes such as diffusion and vaporization. This process is called isotope fractionation. The extent of isotope fractionation can be expressed by a fractionation factor, alpha (α). This factor is the ratio of the concentrations of the two isotopes in one substance divided by the ratio in the other substance. In ecological studies, one can use stable isotopes as a tracer for water and mineral nutrients flow through ecosystems, and use isotope fractionation to examine physiological processes (Fritz and Fontes, 1980; Peterson and Fry, 1987). The most commonly used stable isotopes used in ecological research are Carbon, Nitrogen, Sulfur, Hydrogen and Oxygen. In this study, I used ^{13}C and ^{15}N of plant leaf tissue to examine plant water deficits and nutrient status.

The foliar $\delta^{13}C$ pattern can be used to examine plant water deficits during photosynthetic processes (Farquhar et al., 1982; Farquhar and Richards, 1984; Farquhar et al., 1988). Isotopic fractionation happens during CO_2 diffusion and enzymatic reactions during photosynthetic CO_2 assimilation (Farquhar et al., 1982; Farquhar and Richards,

1984; Farquhar et al., 1988). Foliar $\delta^{13}C$ in C_3 plants can be calculated using the following formula:

$\delta^{13}C_{plant} = \delta^{13}C_{atm}$ - a - (b - a)p_i/p_a

in which $\delta^{13}C_{atm}$ is the $\delta^{13}C$ value of atmospheric CO_2, a is the fractionation factor during diffusion of CO_2 through the stomatal pore (a = 4.4‰), b is the fractionation factor during photosynthetic CO_2 assimilation in the Calvin cycle (b = 27‰), p_i is the pressure of CO_2 inside the leaf, and p_a is the partial pressure of CO_2 in the atmosphere. In C3 plants, the principal carboxylation enzyme, Ribulose Bis-Phosphate Carboxylase (RuBisCo), discriminates against the heavier isotope ^{13}C during CO_2 assimilation. Stomatal closure, such as that caused by water stress, limits CO_2 supply for photosynthesis and thus lowers the leaf internal CO_2 concentration and the RuBisCo discrimination against ^{13}C (Farquhar et al., 1982). According to this equation, foliar $\delta^{13}C$ is higher with greater stomata limitation which is often caused by plant water deficit (Farquhar et al., 1982; Farquhar and Richards, 1984; Hubick et al., 1986; Farquhar et al., 1988). In my dissertation, I compared carbon isotope ratios of tree island plants in wet season and dry season to assess plant dry season water deficits in different landscapes.

The stable isotope of nitrogen, foliar $\delta^{15}N$, is used as an indicator of phosphorus availability. Nitrogen isotope fractionation happens during plant N uptake. Plants discriminate against ^{15}N during N uptake. However, the degree of fractionation is related to N demand relative to the supply in the rhizosphere (Handley and Raven, 1992). When the demand for N is high and the supply is limited, this discrimination is diminished or non-existent (Mariotti et al., 1981). It has been shown in many studies that in P limited environments, P fertilization can increase N demand and therefore lower the

discrimination against ^{15}N during plant N uptake and result in an increase in foliar δ^{15}N (Nadelhoffer et al., 1996; McKee et al., 2002; Clarkson et al., 2005). In the Florida Everglades, where P is generally limiting, foliar δ^{15}N of plants has been shown to be an indicator of ecosystem P availability (Inglett and Reddy, 2006; Inglett et al., 2007). In my dissertation research, I used foliar nitrogen isotope ratios to compare phosphorus availability among different tree islands.

Satellite remote sensing analysis

Satellite sensors measure the reflectance values of surfaces at different bandwidths. In ecological studies, reflectance values of multiple spectral bands can be used to calculate a single value to assess vegetative characteristics, this value is said to be a vegetation index. In this study, I examined two vegetation indices to assess plant canopy water and nutrient status. The normalized difference vegetation index (NDVI) uses the reflectance value of red and near infrared (NIR) bands (Rouse, 1974), and is calculated as:

$NDVI = (ref_{NIR} - ref_{RED}) / (ref_{NIR} + ref_{RED})$.

At the canopy scale, NDVI provides an indirect measurement of absorbed photosynthetically active radiation and canopy stomatal conductance (Verma et al., 1993) and has been widely used in vegetation monitoring for plant canopy characteristics such as chlorophyll content and leaf area index (LAI)(Tucker, 1979). The normalized difference water index (NDWI) uses the near infrared band and shortwave infrared (SWIR) band (Gao, 1996), and is calculated as:

$NDWI = (ref_{NIR} - ref_{SWIR}) / (ref_{NIR} + ref_{SWIR})$.

NDWI provides an indirect measurement of canopy water content and is widely used for drought monitoring (Jackson et al., 2004; Chen et al., 2005; Gu et al., 2007). In this study,

I used NDVI and NDWI to assess canopy water and nutrient content of tree island plant communities.

Granier sap flux velocity measurement

I used Granier sap flow sensors (Dynamax, United States) to measure the transpiration rates of hardwood trees. Each sensor has two thermocouple needles which are inserted into the sapwood, the upper one containing an electric heater. The needles measure the temperature difference (dT) between the upper heated needle and the lower unheated needle. The temperature difference is lowest when transpiration is most intensive during the day as water flow in the xylems cools the upper needle. Temperature difference is converted to sap flux velocity by the equation:

$$F = 119((T_{diff,max}-T_{diff})/T_{diff})^{1.23} \, ,$$

in which F is the sap flux velocity ($\mu m/s$), $T_{diff,max}$ is the maximum temperature difference of the day, which is usually during the night when there is no transpiration, and T_{diff} is the temperature difference at the time velocity is calculated (Granier, 1987; Saugier et al., 1997). The sap flux velocity measures the volume of water taken up by a plant per unit sap wood area (Granier, 1987). In this study I assumed that sap flux velocity is proportional to transpiration, and used it as a proxy for transpiration (Small and McConnell, 2008).
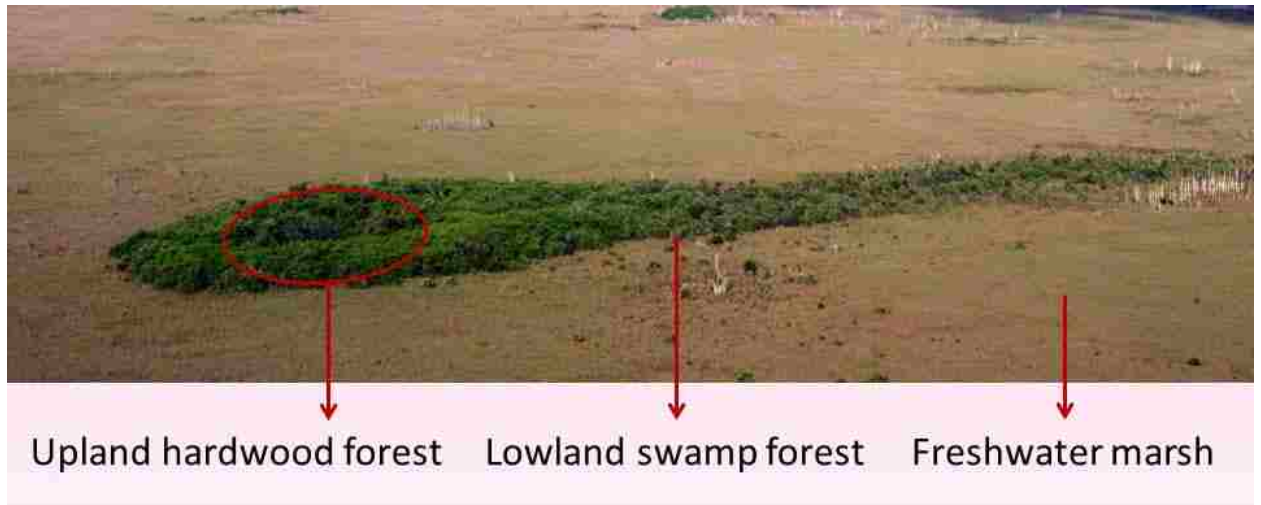
Figure 1.1 A tree island in the Everglades National Park.
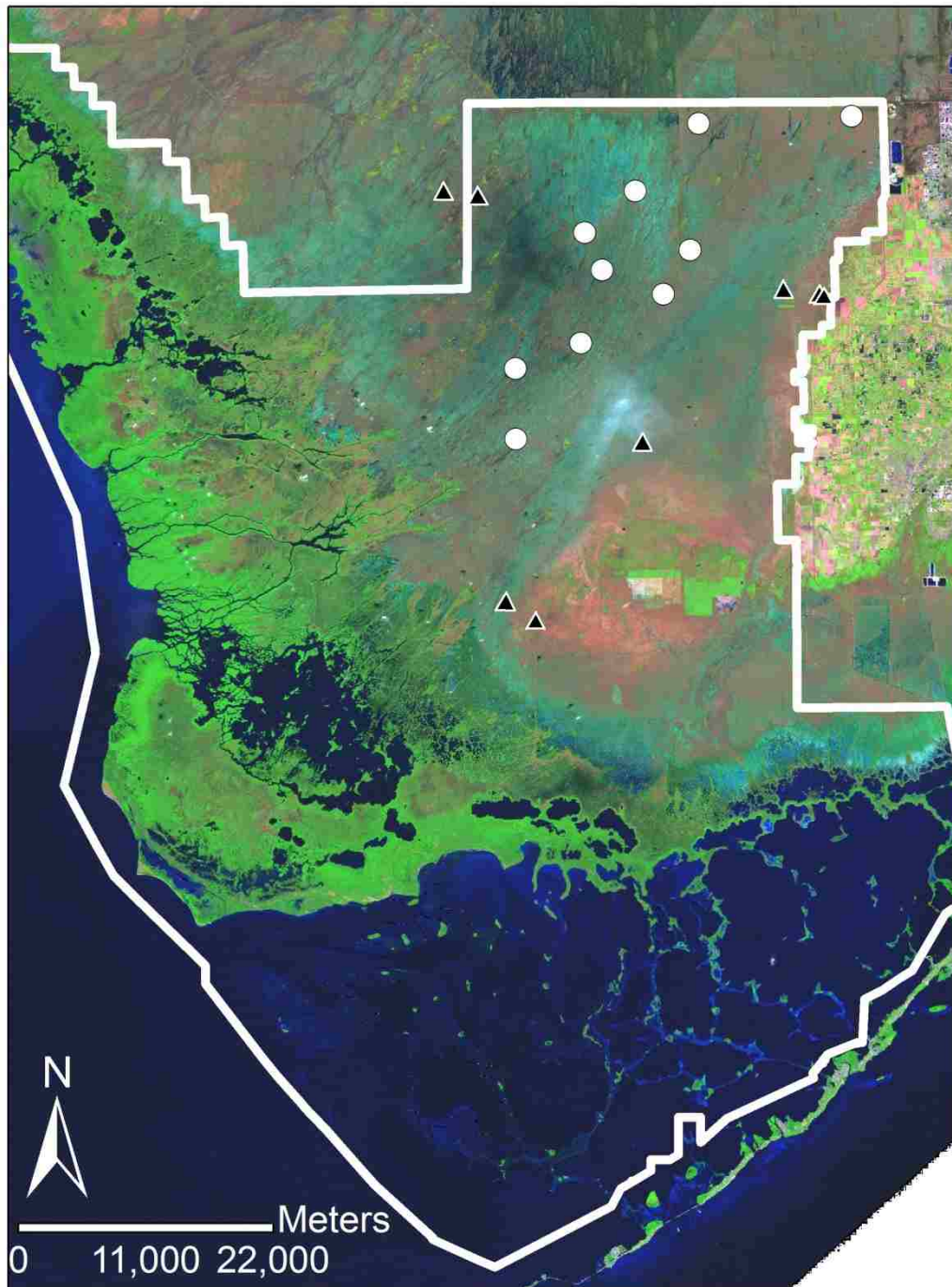
Figure. 1.2 Map of Everglades National Park. White bold line represents national park boundary. Study sites marked in ○ and ▲ to represent tree islands located in different landscapes. Landsat image was taken on 4/18/2004 and bands shown are band 5, 4 and 3. Image obtained from Florida Coastal Everglades Long Term Ecological Research data network (FCE. LTER, http://fce.lternet.edu/data/GIS/).

Chapter 2

Isotopic and elemental analysis of water use and nutrient status in tree island upland
hammock plant communities in the Everglades National Park, USA[1]

Summary

The tree island hammock communities in the Florida Everglades provide one possible

examples of self-organizing feedbacks between environment and vegetation. However,

little is understood about why these elevated tree island communities have higher nutrient

concentration than the surrounding freshwater marshes. Here I used stable isotopes and

elemental analysis to compare dry season water limitation and soil and foliar nutrient

status in upland hammock communities of 18 different tree islands located in the Shark

River Slough and adjacent prairie landscapes. By examining shifts in foliar $\delta^{13}C$ values, I

observed that prairie tree islands, having a shorter hydroperiod, suffer greater water

deficits during the dry season than slough tree islands. I also found that prairie tree

islands have lower soil total phosphorus concentration and higher foliar N/P ratio than

slough tree islands. Foliar $\delta^{15}N$ values, which often increase with greater P availability,

also were found to be lower in prairie tree islands than in slough tree islands. Both the

elemental N and P and foliar $\delta^{15}N$ results indicate that the upland hammock plant

communities in slough tree islands have higher amounts of P available than those in

prairie tree islands. My findings are consistent with the transpiration-driven nutrient

harvesting chemohydrodynamic model. The water limited prairie tree islands

hypothetically transpire less and harvest less P from the surrounding marshes than slough

tree islands during the dry season. These findings suggest that hydroperiod is important to

nutrient accumulation in tree island habitats.

Background

Similar to most terrestrial mosaic landscapes such as savannas, many large wetland ecosystems have patterned landscapes, with a heterogeneous vegetation composition and nutrient concentration that are non-randomly distributed (Rietkerk et al., 2002; Rietkerk et al., 2004). These non-random patterns are proposed to be self-organized by positive feedback loops (van der Valk and Warner, 2009; Larsen and Harvey, 2011). The feedback mechanism usually involves vegetation affecting redistribution of materials and therefore leading to alteration of the environmental conditions such as local and regional hydrology, which in turn impacts on vegetation functioning (Rietkerk et al., 2004; Eppinga et al., 2009). One example of these self-organizing patterned landscapes are wetlands with tree islands. Wetzel (2002b) defines tree islands as patches of woody vegetation within a freshwater wetland matrix dominated by non-woody species. Tree islands are relatively young habitats in the wetlands, and are developed as a result of landscape processes and feedback between hydrological and climatic factors after wetland formation (Foster et al., 1983; Glaser, 1987; Wetzel, 2002b; Gumbricht et al., 2004). Tree islands may be initiated at a range of nucleation sites: on slightly elevated bedrock, floating peat mass, submerged tree branches, or aggregation of floating aquatic plants (Huffman and Lonard, 1983; Glaser, 1987; Olmsted, 1993). In wetlands that accumulate peat, tree islands are often in the form of elevated peat mounds resulting from organic matter accumulation on top of a preexisting base. These tree islands are able to grow in size and nutrient concentration by accumulating litter or root material deposited by woody plants. They generally have a higher nutrient concentration and higher species richness than the surrounding wetland matrix (Slack et al., 1980; Wetzel, 2002b).

In this study, I focused on tree islands of the south Florida Everglades. They are the focus of a wide range of nutrient inputs from potential sources such as precipitation, surface water surrounding the tree island, groundwater, plant litter and bird guano deposition, capture of aerosols, and bedrock mineralization by tree exudates (Wetzel et al., 2005). Therefore tree islands generally have relatively high phosphorus concentration compared to the fresh water marshes. There are two major hypotheses on how tree islands generate and maintain their high P levels. Givnish et al. (2008) suggest that guano deposition is the major P input for the tree islands. The other hypothesis is the chemohydrodynamic model (Wetzel et al., 2005; Ross et al., 2006), which suggests that tree islands accumulate and maintain their high P level by harvesting nutrients from surrounding water and groundwater. This hypothesis suggests that the high transpiration rates of tree island hammock communities cause them to take up water and nutrients from the surrounding marsh and the groundwater, especially during the dry season, and that nutrients gradually accumulate through this process (Wetzel et al., 2005). These two hypotheses are not mutually exclusive to each other, but this study will be focusing on ramifications of the chemohydrodynamic hypothesis. This hypothesis has been supported by previous studies that have shown that tree island plants can use marsh water during the dry season (Ross et al., 2006; Saha et al., 2010a). One of the predictions of the chemohydrodynamic model is that since nutrient harvesting is transpiration-driven, tree islands with low dry season transpiration will have lower nutrient accumulation rates than tree islands with high dry season transpiration.

In this study I tested two hypotheses related to the chemohydrodynamic model of transpiration-driven nutrient harvesting. First, I hypothesized that tree islands located in

areas where the surrounding marshes dry out during the dry season will experience

greater stomatal limitation to photosynthesis and transpiration than those located in areas

which are flooded continuously throughout the year. I used shifts of foliar carbon isotope

ratios from wet season to dry season to assess dry season stomatal limitation, as drought

stress will cause an increase in foliar carbon isotope ratio due to stomatal limitation of

photosynthesis (Farquhar et al., 1988). According to the chemohydrodynamic model, tree

islands located in areas with longer hydroperiods will harvest relatively more nutrients

from the surrounding marshes. I, therefore, tested as a second hypothesis that tree islands

surrounded by continuously flooded marsh will exhibit higher total soil P and more P

available to plants compared to those located in areas with shorter hydroperiods. I

assessed this by measuring total soil P, foliar nitrogen isotope ratios, foliar P

concentration and foliar N/P ratios, where total soil P, foliar nitrogen isotope ratio and

foliar P concentration are related to P availability (Inglett and Reddy, 2006; Ross et al.,

2006; Inglett et al., 2007; Eppinga et al., 2008) and foliar N/P ratio are indicator of N or P

limitation (Koerselman and Meuleman, 1996).

Methods

<u>Study area</u>

    The Everglades ecosystem has an annual rainfall averaging 1300 mm, approximately

70-90% of which falls during the wet season, from June to November (Renken et al.,

2006). The region has a gentle elevation gradient of less than 4.5 cm per km with a 48

km-wide sheetflow of surface water concentrated in the Shark River Slough (Fling et al.,

2004). As a coastal wetland ecosystem, the Everglades consists of a variety of terrestrial,

aquatic, estuarine, and marine habitats including upland pinelands and hammocks,

sawgrass marshes, tree islands, mangroves, and coral reefs (Lodge, 2004). Covering about 70% of the Everglades area, the freshwater marsh consists of two distinct types of landscape: the mixed ridge-slough matrix and the marl prairies (Bernhardt and Willard, 2009). The ridge-slough habitat is characterized by deep organic soils, flooding throughout the year, and maximum water depths of ~ 1 m. The marl prairies are characterized by marl soils, shallow water (< 0.5 m) and short (< 180 day) hydroperiods. The Shark River Slough, with water flowing southwestwards into the Gulf of Mexico, serves as the primary flow path in the Everglades ecosystem. The fresh water ridge and slough in the Shark River Slough are dominated by sawgrass (*Cladium jamaicensis*) in the ridges and spikerush grass (*Eleocharis cellulose*) and water lilies (*Nymphaea odorata*) in the slough, while those of the adjacent prairies are commonly dominated by muhly grass (*Muhlenbergia filipes*), which is adapted to a shorter hydroperiod than sawgrass (Fig. 1). Both sloughs and prairies feature scattered, elevated tree islands.

Tree islands are common features in both ridge-and-slough and marl prairie landscapes. In both cases, the best developed islands are characterized by an elevated, mesic head with flood-intolerant hardwood hammock tree communities, and an encircling swamp forest comprised of flood tolerant trees and shrubs (Sklar and van der Valk, 2002; Wetzel, 2002a). In the ridge-and-slough environment, the surrounding swamp forest forms an elongated tail, while the tails of marl prairie tree islands are often inconspicuous or absent. The heads of such bi-phased tree islands typically remain unflooded in both landscapes, even during the wet season. Decomposition rates in the moist, well-drained environments of the tree island heads in both landscapes are apparently quite rapid, based on litter turnover rates of 0.6 – 1.2 times per year (Ross

unpublished data). However, soil characteristics vary markedly in the two settings. Soils

in the highest portions of marl prairie tree islands are shallow (<30 cm), primarily organic

(mean of 51.1% organic matter, determined by loss on ignition, in the surface 10 cm at 6

sites), with relatively low mineral content, circumneutral pH. (Ross et al. in press). These

Histosols are commonly mapped as Dania or Matecumbe mucks (USDA-NRCS, 1996),

and resemble the Folists that develop directly on limestone bedrock in the Florida Keys

(Ross et al., 2003).   In contrast, most ridge-and-slough tree island soils studied so far

feature organic (mean of 21.2% organic matter for 62 sites) surface layers above mineral

subsoils, with alkaline reaction (Ross et al. in press). Coultas et al. (2008) recently

described two profiles from large islands in northeastern Shark Slough.   Organic matter

decreased downward, and the soils were therefore classified as Mollisols. Most notably,

a petrocalcic layer of ~ 20 cm thickness was present mid-profile, beginning ~60 cm

below the surface.   The mechanism of development of the petrocalcic layer is uncertain,

but has been hypothesized to involve the precipitation of calcite from calcium-rich

capillary waters originating in the shallow water table (Coultas et al., 2008; Graf et al.,

2008).

Eighteen tree islands were selected along the Shark River Slough and in the adjacent

marl prairies. GPS coordinates were recorded for each tree island during field sampling.

Ten of the 18 tree islands were located in the Shark River Slough (henceforth called

slough tree islands) and 8 of them were located in the adjacent prairies east and west of

the slough (henceforth called prairie tree islands). The selection of specific tree islands

within each habitat was based on accessibility and permission by the National Park

Service (Fig. 2.1).

Species and sampling

The hardwood hammock community on the head of each tree island is dominated by about 5 to 10 evergreen or deciduous subtropical tree species. Species common to both slough and prairie tree islands include *Myrsine floridana*, *Bursera simaruba*, *Coccoloba diversifolia*, *Eugenia axillaris*, and *Sideroxylon foetidissimum*. *Celtis laevigata* and *Chrysophyllum oliviforme* are typically restricted to the slough islands, while *Ardisia escallonioides*, *Lysiloma latisiliqua*, *Nectandra coriacea*, *Quercus virginiana*, and *Sideroxylon salicifolium* are more common on the prairie islands. All of these species are intolerant of prolonged flooding (Saha et al., 2010a). The deciduous species (*Bursera simaruba* and *Celtis laevigata*) lose their leaves during the January to May dry season, with a leafless period of about one month. There were only a few species common to both slough and prairie tree islands, and species overlap was slight among the prairie tree islands I sampled. For each tree island, species were ranked with Importance Values based on relative density and basal area (Shamblin et al., 2008), and the 4 species with highest Importance Values in each tree island were selected for isotopic and nutrient analysis (1-3 in cases where the island had low woody plant diversity and 5 when Importance Values of the fourth and fifth most abundant species were indistinguishable) (Table 2.1).

Foliar samples were collected during the wet season (September) and dry season (May) between 2006 and 2008 (Table 2.1). Samples collected from all tree islands during the wet season were used for elemental (N and P) and isotopic (C and N) foliar analysis. The youngest fully expanded four to five leaves per tree were sampled from ten individual trees of the four most abundant species in each tree island. Out of the 18 tree

islands studied, a subset of seven tree islands (four slough tree islands and three prairie tree islands) were selected to be sampled during both wet season and dry season for a seasonal comparison (Table 2.1). I compared seasonal shifts between wet season 2006 and dry season 2007 for three tree islands (two slough and one prairie), and between wet season 2007 and dry season 2008 in four tree islands (one slough and three prairie). A paired T-test was used to compare the precipitation of each month from July 2006 to June 2007 and from July 2007 to June 2008, and showed no difference between these two years. In these tree islands, leaf samples were collected during the dry season in the same manner and from the same species as wet season samples. Leaf samples were collected from five individual trees of each species for isotopic C and N analysis. A subset of six tree islands (three slough and three prairie) were also selected for collecting sawgrass samples near the tree island for N isotope analysis to ensure there is no inherent difference in N isotope ratios of the surrounding marsh water of slough and prairie tree islands. Five replicates of newly grown sawgrass blade samples were collected during the wet season from about 10 to 15 meters off the north end (upstream) of each tree islands in order to minimize the influence from tree island runoff.

Foliar C and N analysis

Leaf samples were dried in an oven at $50^{o}C$ for at least two days. Dried leaf samples were then ground and loaded (5mg) into individual tin cups. The samples were then analyzed by an automated elemental analyzer (Euro-EA-Elemental Analyzer, Eurovector, Milan, Italy) connected to a continuous flow isotope ratio mass spectrometer (Isoprime, Elementar, Hanau, Germany) for leaf N concentration and C and N isotopic composition. Leaf N concentration is measured as a weight percentage of total foliar N relative to total

leaf dry mass, and C and N isotopic compositions are reported as $\delta^{13}C$ and $\delta^{15}N$ values

respectively. $\delta^{13}C$ and $\delta^{15}N$ values are expressed as:

$\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{std}) -1]*1000$

where R_{sample} and R_{std} represent the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotopic concentration ratios in the

sample and in the standard respectively. The internal lab standards were calibrated for C

isotope to the Vienna PeeDee belemnite formation of South Carolina, and for N isotope

to air. The precision of the N concentration analysis was ±1 ppm (±1σ) and the precision

of the C and N isotopic analysis was ±0.1‰ (±1σ). The analyses were done at the

Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami.

Foliar P analysis

Approximately 0.3g of ground leaf samples were weighed out in porcelain crucibles

and oxidized in a furnace at $600^{o}C$ for 6 hours. The ashes were then digested in 5ml of

4% sulfuric acid, filtered through glass fiber filter paper (Whatman, UK), and diluted

with double distilled water to 25ml solution. The filtered sample was analyzed by an

Alkem 3000 Phosphorus analyzer (Alpkem, OI Analytical, Texas, USA) using the

USEPA method 365.1 (USEPA, 1984) by the molybdate blue colorimetric approach

(Fiske and Subbarow, 1925). As in N concentration, the P concentration is measured as a

weight percentage of total foliar P relative to total leaf dry mass with an analytical

precision of ±0.1ppm (±1σ).

Total soil P analysis

Soil was collected from 15 tree islands, nine in slough and six in prairie, by driving a

5.25 cm diameter acrylic core into the soil to a depth of 10 cm, or to the underlying

bedrock surface at a few points where soils were shallower than 10 cm. Cores from three

locations near the center of the tree island were bulked to obtain a representative substrate. The samples were subsequently stored in plastic bags in the refrigerator until analysis. TP was determined by a modification of sample preparation methods described by Solórzano and Sharp (1980). Samples were oxidized by dry combustion and all phosphorus-containing compounds were hydrolyzed to SRP using $MgSO_4/H_2SO_4$ and HCl, followed by colorimetric analysis according to the standard method for orthophosphate P (EPA method 365.1).

<u>Data Analysis</u>

Foliar $\delta^{13}C$ value: Since foliar $\delta^{13}C$ values showed non-homogeneity, I used non-parametric statistical tests. A series of Wilcoxon signed-rank tests were performed to test for the significance of seasonal foliar $\delta^{13}C$ shift on each individual tree island. The significance level of the Wilcoxon signed-rank tests was adjusted by a Bonferroni correction (Sokal and Rohlf, 1995).

Foliar N/P ratio and absolute foliar P concentration: A Mann-Whitney U test was performed to examine the differences of foliar N/P ratios between slough and prairie tree islands at the community level (i.e. pooling all species together). In addition, a series of Mann-Whitney U tests were performed on each of the common species found in both slough and prairie tree islands to examine the N/P differences between both island types. The significance level of the Mann-Whitney U tests was adjusted by a Bonferroni correction (Sokal and Rohlf, 1995). The same statistical tests were performed to examine the differences of absolute foliar P concentration between slough and prairie tree islands at the community level and at the species level for the five common species.

Foliar δ^{15}N value: A two-way ANOVA was performed to examine the effects of season and tree island type (slough vs. prairie) on foliar δ^{15}N values from the seven tree islands that were sampled in both wet season and dry season. This analysis was done at the community level and species was not considered as a separate factor. Another two-way ANOVA was performed to examine and compare the effects of species and tree island types (slough vs. prairie) on foliar δ^{15}N values of species found in both slough and prairie tree islands. Only the wet season samples were used in the latter analysis. In addition, a nested one-way ANOVA was performed to examine the main effect of tree island types (slough vs. prairie) and the nested effect of individual tree islands on foliar δ^{15}N values of sawgrass growing near different tree islands. Before each ANOVA, Q-Q plots for normal distribution were performed to confirm normality and Fligner-Killeen tests were performed to confirm homogeneity of variances. Finally, average foliar δ^{15}N values of the upland hammock in the wet season and those of the nearby sawgrass where samples were taken were mapped as geographical points onto a land cover map of the ENP area obtained from the Florida Gap Project using software ArcGIS (ESRI, USA).

Many of the above data analyses were done at the community level without considering different species as a separate factor for two reasons. First, these tree islands are isolated habitats, and species composition is quite different among all the tree islands selected. There were only five species common to both slough and prairie tree islands due to their differential hydrological characteristics. These facts make it difficult to test the effect of species in most analyses comparing slough and prairie tree islands. Second, the species selected in these sampling and analyses were the most dominant species on each tree island. As most tree island hammocks are only occupied by five to ten hardwood

species (Shamblin et al., 2008), it is safe for me to assume that the four most dominant species are representative of the hardwood hammock community, and that community level comparisons are reliable indicators of most species behavior.

Results

Foliar $\delta^{13}C$ value

The Wilcoxon signed-rank test showed no significant difference in foliar $\delta^{13}C$ between wet and dry season for the three slough tree islands, while three out of four prairie tree islands showed significant increase in foliar $\delta^{13}C$ from wet season to dry season (Fig. 2.2).

Soil P concentration

Soil P concentration showed a sharp contrast between slough and prairie tree islands. Total soil P concentration for slough tree islands had much higher values averaging 52987 ± 17142 μg/gdw (± σ, n = 9) than those for prairie tree islands averaging 2123 ± 2419 μg/gdw (± σ, n = 6) (Fig. 2.3).

Foliar N/P ratio and foliar P concentration

Significant differences in foliar N/P ratios and foliar P concentration were found between slough and prairie tree islands at the community level by the Mann-Whitney U test, where slough tree islands had lower foliar N/P ratios (Fig. 2.4) and higher absolute P concentration than prairie tree islands (Fig. 2.4). This pattern was confirmed at the species level, where 4 out of the five species common to slough and prairie tree islands showed significantly lower foliar N/P and higher absolute P concentration in slough tree islands than in prairie tree islands (Fig. 2.4).

Foliar $\delta^{15}N$ value

The average foliar $\delta^{15}N$ of each tree island showed a distinct geographical pattern: slough tree islands had foliar $\delta^{15}N$ values averaging $+6.06 \pm 1.89$‰ ($\pm \sigma$, n = 10), which were higher than those for prairie tree islands averaging -1.58 ± 1.53‰ ($\pm \sigma$, n = 8) (Fig. 2.1). The foliar $\delta^{15}N$ differences between slough and prairie tree islands were confirmed by the two-way ANOVA (Table. 2.2a, Table. 2.2b). However, no significant seasonal effects on foliar $\delta^{15}N$ were found among the seven tree islands sampled during dry and wet seasons (Table. 2.2a, Fig. 2.5). Analysis of species common to both types of tree islands showed that species effects, although significant (P<0.001, F = 22.70, df = 4), were less distinct in comparison to differences attributed to tree island types (P<0.001, F = 1228.28, df = 1) (Table. 2.2b, Fig. 2.6). Foliar $\delta^{15}N$ values of sawgrass collected near the islands, although significantly different among individual tree islands, were significantly lower near slough tree islands than near prairie tree islands (P < 0.001, F = 17.55, df = 1) (Fig. 2.1, Table. 2.2c), with foliar $\delta^{15}N$ values of sawgrass near slough tree islands averaging -0.1 ± 0.5 ($\pm \sigma$, n = 15) and those near prairie tree islands averaging $+1.7 \pm 0.4$ ($\pm \sigma$, n = 15).

Discussion

These results support both my hypotheses related to the chemohydrodynamic feedback model. Hammock trees in prairie tree islands show a greater stomatal limitation during the dry season than those in slough tree islands based on C isotope ratios, which supports the hypothesis that prairie tree island plants suffer from water deficits during the dry season. Also, the N, P, and isotopic analyses show that slough tree islands have

higher soil P concentration as well as less P limitation to the hardwood hammock plants compared to prairie tree islands.

Previous studies have shown that foliar $\delta^{13}C$ is related to plant water use efficiency (Farquhar et al., 1988). In C_3 plants, the principal carboxylation enzyme Ribulose Bis-Phosphate Carboxylase (RuBisCo) discriminates against the heavier isotope ^{13}C during CO_2 assimilation. Stomatal closure, such as that caused by water stress, limits CO_2 supply for photosynthesis and thus lowers the leaf internal CO_2 concentration and the RuBisCo discrimination against ^{13}C (Farquhar et al., 1982). It has been shown by several investigations that plants under water stress increase their foliar $\delta^{13}C$ relative to those without water stress (Farquhar et al., 1982; Farquhar and Richards, 1984; Hubick et al., 1986; Farquhar et al., 1988). I show here a significant increase in foliar $\delta^{13}C$ values from wet to dry season in the prairie tree islands (Fig. 2.2), which indicates that prairie tree island plants have stomatal limitation of their carbon uptake during the dry season. This stomatal limitation also would lower transpiration during the dry season in prairie tree islands. On the other hand, plants in slough tree islands have the same foliar $\delta^{13}C$ values during both wet and dry season (Fig. 2.2). We, therefore, conclude that prairie tree islands suffer greater dry season water deficits than slough tree islands. These results are consistent with the differences in the average water levels and hydroperiod of the marshes surrounding the slough and prairie tree islands. In a previous study using stable isotope ratios as a tracer of water uptake in tree islands, Saha et al. (2010a) showed that Everglades tree island plants use soil trapped-rain water during the wet season and marsh water during the dry season. My foliar $\delta^{13}C$ results suggest that slough tree islands avoid

water stress by accessing marsh water supply during the dry season, while prairie tree island plants experience water stress as the surrounding marshes dry out.

My results, along with those of Saha et al. (2010a) are consistent with a temporal component to the chemohydrodynamic model. In this scheme, tree island hammock plants take up water and nutrients from the surrounding marshes during the dry season when there is little or no rain water available. Because the heads of tree islands are rarely flooded, the nutrients taken up by hammock trees remain in the tree island soil and accumulate over time. As suggested by the chemohydrodynamic model, high transpiration and the consequential movement of marsh water is the driving force of nutrient (including P) accumulation in tree islands (Wetzel et al., 2005). According to Saha et al. (2010a), this would occur mainly during the dry season, which is therefore designated as the nutrient harvesting phase. My results suggest that during the dry season, unlike slough tree islands, prairie tree island plants are under water limitation due to the lack of available water in the surrounding marshes. These islands are expected to have a lower dry season transpiration rate. Therefore I hypothesize that they should also have a lower nutrient accumulation rate than those of slough tree islands. Conversely, slough tree island plants can maintain high water and nutrient uptake rates using surrounding marsh water during the dry season. I thus expect that slough tree islands will have higher P accumulation rates than prairie tree islands and this will be reflected in their P nutrient status.

My results of total soil P concentration and foliar N/P ratio are consistent with the above scenario of tree island P accumulation. Total soil P concentrations in slough tree islands are 10 to 100 times of those in prairie tree islands (Fig. 2.3). Most P in tree island

soils are found in unavailable forms (Sklar and van der Valk, 2002), and may not reflect

P accumulation through transpiration, but rather the mineral substrate of the tree islands.

However, Ross et al (2006) has shown that in similar vegetation types, total soil P

concentration is reflective of the general pattern of soluble active P that is available for

plants uptake. This is evidenced by leaf concentrations, which show that slough tree

islands have significantly lower N/P ratio than prairie tree islands (Fig. 2.4). Foliar N/P

ratio is known to be inversely correlated with P availability (Han et al., 2005), and has

been proposed as an indicator of the relative availability and limitation of N and P

elements to plants (Gusewell, 2004). Foliar N/P ratios of plants worldwide range from 3

to 89 for different ecosystems, and are in part related to climate and geographical

locations (Reich and Oleksyn, 2004; Wright et al., 2005). However, Gusewell et al. (2004)

found that in most terrestrial ecosystems, biomass N/P ratios <10 or >20 often indicate N

or P limitation to plant growth respectively. Foliar N/P ratios of plants in European

freshwater wetlands range from 7 to 30, with ratios higher than 16 indicating P limitation

and lower than 13.5 indicating N limitation at the community level (Gusewell and

Koerselman, 2002). Foliar N/P ratios in prairie tree islands have a mean value of 21.1 ±

12.6 ($\pm \sigma$), ranging from 17.4 to 38.0 depending on the species; while foliar N/P ratios in

slough tree islands have a mean value of 10.1 ± 5.4 ($\pm \sigma$), ranging from 5.9 to 14.6

depending on the species (Fig. 2.4). According to these results, plants in prairie tree

islands are P limited. On the other hand, the average foliar N/P ratios in slough tree

islands generally show a stoichiometry indicative of an adequate supply of P relative to N.

The comparison of foliar δ^{15}N in slough and prairie tree islands is also consistent with

greater P limitation in prairie tree islands. Foliar δ^{15}N is determined by both the isotopic

composition of the N source and the isotopic fractionation during N assimilation

(Delwiche and Steyn, 1970; Handley and Raven, 1992; Robinson, 2001). If marsh water

is the ultimate nutrient source for the tree island soils, foliar $\delta^{15}N$ values of sawgrass near

the tree islands should be indicative of the isotopic composition of the N sources of the

hammock plants. However, I found that the $\delta^{15}N$ values of sawgrass showed an opposite

pattern than the foliar $\delta^{15}N$ of the hammock plant communities, with sawgrass foliar $\delta^{15}N$

values in the slough significantly lower than those in the prairie (Fig. 2.1). Therefore,

different N sources from the marsh water cannot be the reason for the observed foliar

$\delta^{15}N$ pattern for tree island plants. Source effects also include N uptake preference of

each individual species (Evans et al., 1996; Waser et al., 1998; Houlton et al., 2007), and

N fixing effects (Nair, 1993; Nguluu et al., 2002). All the species studied here are tropical

hammock species intolerant of flooding and not known to be N-fixers (Jones et al., 2006);

thus I make the assumption that N uptake preference is not a significant factor among

these species. The fractionation effect, therefore, should be related primarily to N demand

relative to the supply in the rhizosphere (Handley and Raven, 1992). Plants will naturally

discriminate against ^{15}N during nitrogen uptake. However, when the demand of N is high

and the supply is limited, this discrimination is diminished or non-existent (Mariotti et al.,

1981). In P-limited environments, increased N demand due to P fertilization lowers the

discrimination against ^{15}N during plant N uptake and thus increases foliar $\delta^{15}N$

(Nadelhoffer et al., 1996; McKee et al., 2002; Clarkson et al., 2005). In the generally P

limited Everglades, foliar $\delta^{15}N$ of plants has been shown to be an indicator of ecosystem

P availability (Inglett and Reddy, 2006; Inglett et al., 2007). In addition to foliar N/P

ratios, absolute foliar P concentration is also an indicator of P availability both at the

community level and within individual plant species (Eppinga et al., 2008; Eppinga et al., 2009). Higher foliar P concentration found in slough tree islands compared to prairie tree islands suggests slough tree island plants have higher P available at the community level as well as at species level for 4 out of 5 of the common species between slough and prairie tree islands.

The overall pattern of foliar $\delta^{15}N$ is consistent with those of soil P, foliar N/P ratio and foliar P concentration, with slough tree islands having higher foliar $\delta^{15}N$ values than prairie tree islands (Fig. 2.1, 2.5, 2.6). Average foliar $\delta^{15}N$ values of tree islands vary geographically, where the tree islands within the Shark River Slough tend to have higher foliar $\delta^{15}N$ than tree islands located in the prairies (Fig. 2.1). This general pattern is not affected by seasonal changes (Fig. 2.5), and although foliar $\delta^{15}N$ values differ between species, the differences between slough and prairie tree islands are clear for species that are common to both slough and prairie tree islands (Fig. 2.6). All 4 analyses (total soil P, foliar N/P ratio, foliar P concentration and foliar $\delta^{15}N$ value) support my hypothesis that slough tree islands have higher P than prairie tree islands, which is consistent with the chemohydrodynamic model. Moreover, although this study does not disprove the bird guano hypothesis suggested by Givnish et al. (2008), bird surveys done in the Everglades revealed no clear preference pattern of bird activities to hydroperiod and water level (Gawlik and Rocque, 1998), which makes it difficult to explain the heterogeneous P pattern observed in tree islands located in slough and prairie landscapes. Whether or not the substrate differences between prairie and slough tree islands is responsible for the contrasting nutrient status observed here needs to be further studied. Studies need to

focus particularly on whether these substrate differences might also be caused by the hydrological contrast between prairie and slough tree islands.

Because this study is correlational, and manipulative experiments to prove a nutrient accumulation process which might have taken thousands of years are impossible, I cannot conclude that the chemohydrodynamic model has been proved. In addition to bird guano nutrient deposition, there are other possible sources of nutrient such as groundwater or the original parent material of the tree island. These alternate sources are still in question and need future research. My study, however, shows consistency between the transpiration regime, nutrient status, and the predictions of the chemohydrodynamic model.

In this study I used foliar $\delta^{13}C$ shifts as a diagnostic for plant WUE and foliar $\delta^{15}N$ values as a diagnostic for plant P availability at the community level. Foliar $\delta^{13}C$ diagnostic uses the shift of $\delta^{13}C$ from wet season to dry season to integrate the variation of WUE from wet to dry season. Although it is only a proxy, the foliar $\delta^{13}C$ diagnostic is easier to determine than continuously measuring transpiration or water uptake for an entire year and could be applied when the capacity for continuous measurement is not available. The foliar $\delta^{15}N$ values as a P availability diagnostic are constant through the entire year and had no seasonal variations, which makes it a more reliable measurement for P availability than any one time soil nutrient measurements because of the frequent fluctuations of soil pore water (Trent, 2009). As compared to the foliar N/P ratio, the process of foliar $\delta^{15}N$ analysis requires much less of a labor investment. In habitats like Everglades tree islands, where it is difficult to perform continuous or frequent plant and

soil analysis due to the difficulties of access, the foliar $\delta^{13}C$ and foliar $\delta^{15}N$ diagnostics can be reliable and practical tools.

Conclusions

The findings from this study add knowledge to the nutrient accumulation process of tree island habitats. I showed that the hydrological characteristics of the areas surrounding the tree islands (i.e. marsh dry season water level) is connected to the dry season stomatal limitation of tree island hammock community and to differential P accumulation rates of tree islands. My findings are consistent with the chemohydrodynamic hypothesis. Tree islands located in the prairies have water limitation during the dry season and therefore have a lower capacity of transpiration-driven nutrient accumulation compared to the slough tree islands. This hydrologically induced difference in P accumulation is a long term effect and has a large impact on the P availability of these tree islands.

Table 2.1: Type of island, geographical locations, list of sampled species, and time of sampling of each selected tree island. Bold tree island names indicate tree islands that were sampled during both wet season and dry season. Species name abbreviations stand for: *Ardisia escallonioides* (AE), *Lysiloma latisiliqua* (LL), *Myrsine floridana* (MF), *Nectandra coriacea* (NC), *Quercus virginiana* (QV), *Sideroxylon salicifolium* (SS), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), *Sideroxylon foetidissimum* (SF), *Celtis laevigata* (CL) and *Chrysophyllum oliviforme* (CO). Bold species abbreviations indicate species that were sampled in both slough and prairie tree islands.

Tree island	Type	Latitude	Longitude	Sampled Species	Time of Sampling
Satin Leaf	Slough	25.6115	-80.6883	CL, **EA**, **CD**, CO, **BS**	Sep 06, May 07
Chekika	Slough	25.7452	-80.6572	CL, **EA**, **MF**, **SF**	Sep 06, May 07
Vulture	Slough	25.5735	-80.7592	**BS**, CL, **EA**, **SF**	Sep 07, May 08
Irongrape	Slough	25.6152	-80.5842	**BS**, CL, **EA**, **SF**	Sep 07
Gumbo Limbo	Slough	25.6306	-80.741	**BS**, CL, **EA**, **SF**	Sep 07
Black	Slough	25.646	-80.6648	**BS**, CL, **EA**, **SF**	Sep 07
Panther	Slough	25.4982	-80.8154	**BS**, CL, **EA**	Sep 07
Manatee	Slough	25.6925	-80.712	**BS**, CL, **EA**, **SF**	Sep 07
SS37	Slough	25.3565	-80.7987	**BS**, **CD**, CL, **EA**, **SF**	Sep 07
SS81	Slough	25.6599	-80.7558	CL	Sep 07
Grossman	Prairie	25.4956	-80.7058	AE, **BS**, **CD**, NC	Sep 06, May 07
A4900	Prairie	25.6887	-80.8477	**BS**, **CD**, LL, **SF**	Sep 07, May 08
E4200	Prairie	25.5534	-80.816	**CD**, QV, SS	Sep 07, May 08
NP205	Prairie	25.6923	-80.8774	**BS**, **CD**, EA, **SF**	Sep 07, May 08
Ficus Pond	Prairie	25.3708	-80.824	**CD**, **EA**,SS	Sep 07
Mosquito	Prairie	25.7503	-80.525	**BS**, **MF**, QV, SS	Sep 07
Edge A	Prairie	25.61	-80.5498	**MF**, SS	Sep 07
Edge B	Prairie	25.6108	-80.5524	**MF**, SS	Sep 07

Table 2.2: Results of univariate two-way ANOVA examining: seasonal and tree island type effects on seasonal and tree island type effects on foliar $\delta^{15}N$ of 7 tree islands (a), species and tree island type effects on foliar $\delta^{15}N$ of the common species (b), and nested univariate one-way ANOVA examining effects of individual tree islands nested in different tree island types on foliar $\delta^{13}C$ of sawgrass growing near 6 tree islands (c).

a: Dependent Variable: $\delta^{15}N$

Source	d.f.	F	P
season	1	2.962	0.086
type	1	1471.02	1.04E-137
season * type	1	1.538	0.216

b: Dependent Variable: $\delta^{15}N$

Source	df	F	Sig.
Type	1	1338.28	2.03E-106
Species	4	22.702	3.58E-16
Type * Species	4	8.887	9.38E-07

c: Dependent Variable: $\delta^{15}N$

Source	df	F	Sig.
Type	1	17.546	3.27E-04
Island (Type)	4	9.763	7.80E-05
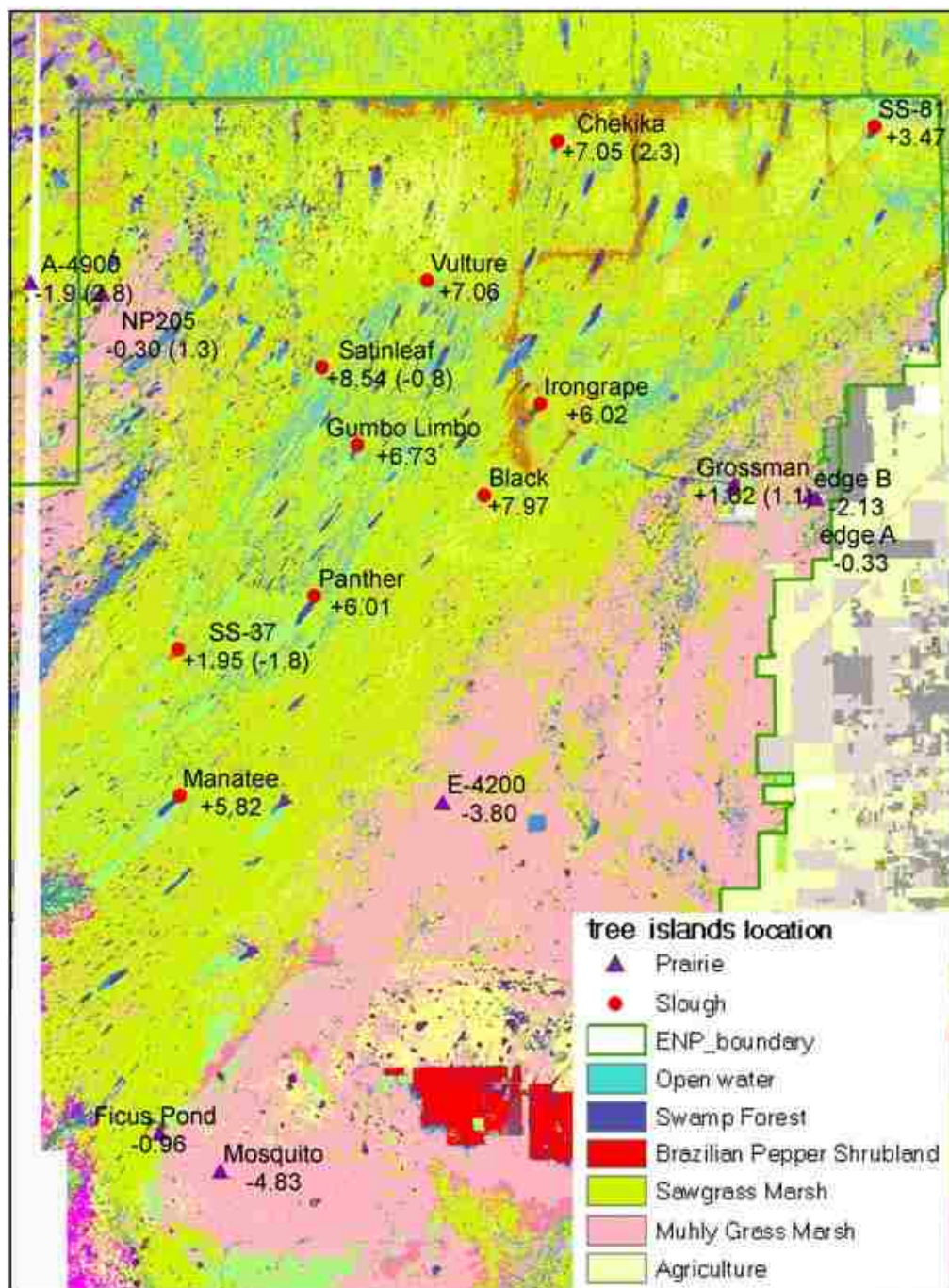
Figure 2.1: Geographic map of slough (●) and prairie (▲) tree islands sampled along the Shark River area. The values following each tree island indicate the average foliar $\delta^{15}N$ values (‰) of the upland hammock community, and the values in the parenthesis indicate the average foliar $\delta^{15}N$ values (‰) of sawgrass sampled near the particular tree island. Background map of land cover by vegetation class obtained from the FL Gap Project final report. Slough tree islands are surrounded by sawgrass (*Cladium jamaicensis*) mixed marsh, and prairie tree islands are surrounded by muhly (*Muhlenbergia filipes*) mixed marsh.
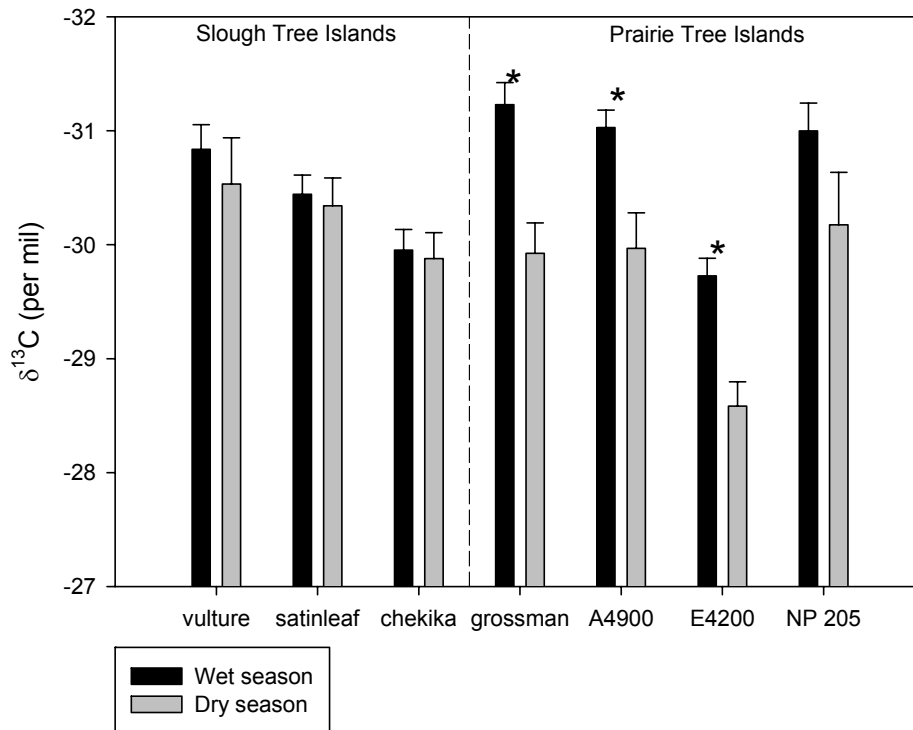
Figure 2.2: Average foliar $\delta^{13}C$ (‰) of wet (black) and dry (grey) seasons for three slough tree islands and four prairie tree islands. Error bars represent Standard Error of the Mean (SEM). Stars (*) indicate significant differences between wet and dry season at α=0.007 (experimental wise error rate after Bonferroni correction).
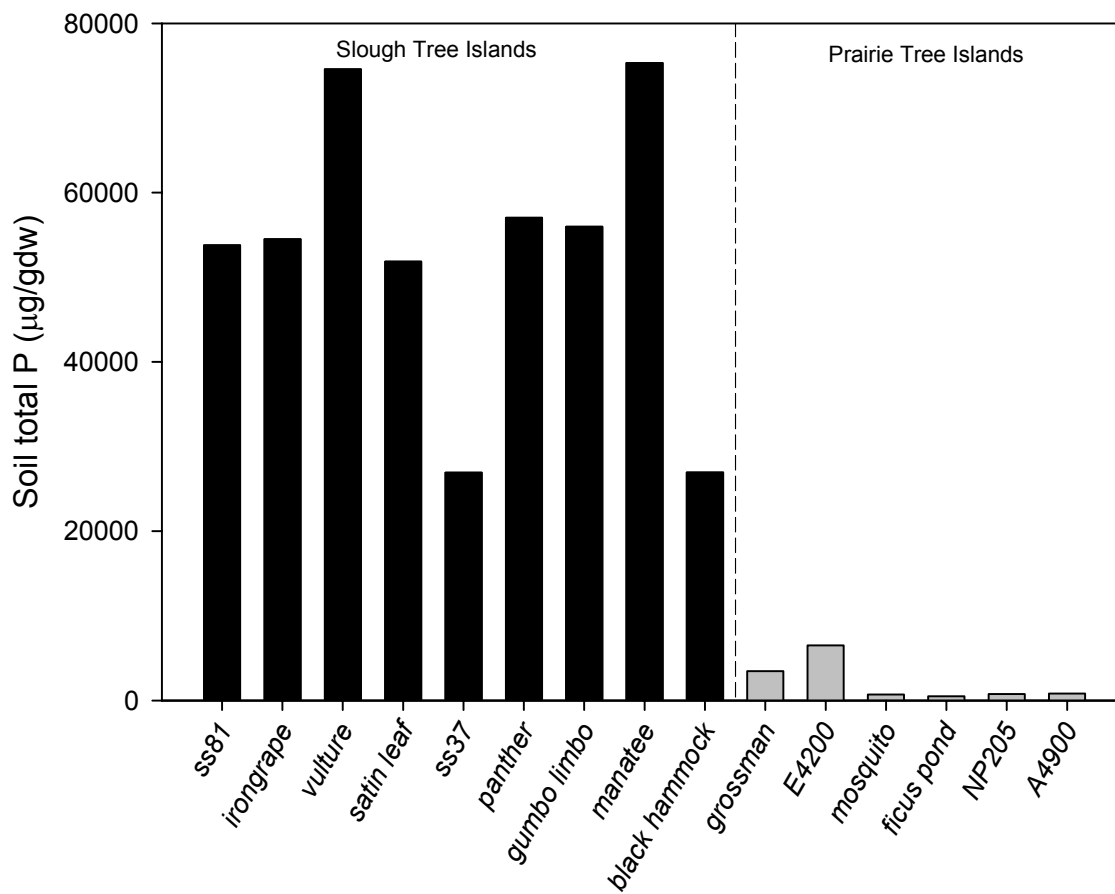
Figure 2.3: Soil total P concentration (μg/gdw) in the surface 10 cm of slough (black) and prairie (grey) tree islands.
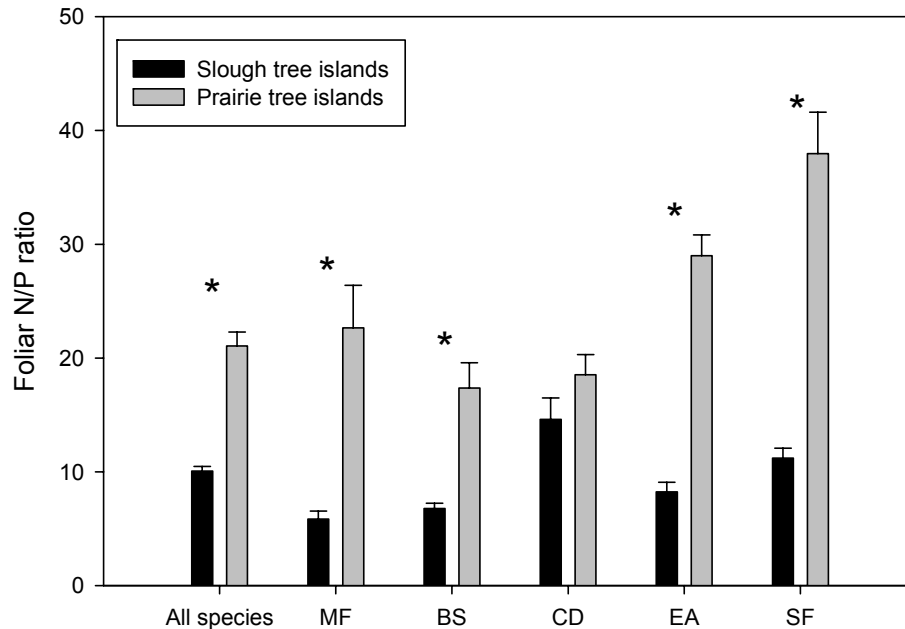
Figure 2.4: Average foliar N/P ratios of all species and the common species within each tree island type. Error bars represent Standard Error of the Mean (SEM). Stars (*) indicate significant differences of P concentration between slough and prairie tree islands at $\alpha = 0.05$ for the community level analysis and $\alpha = 0.01$ (experimental wise error rate after Bonferroni correction) for the species level analysis. Common species between slough (black) and prairie (grey) tree islands include *Myrsine floridana* (MF), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), and *Sideroxylon foetidissimum* (SF).
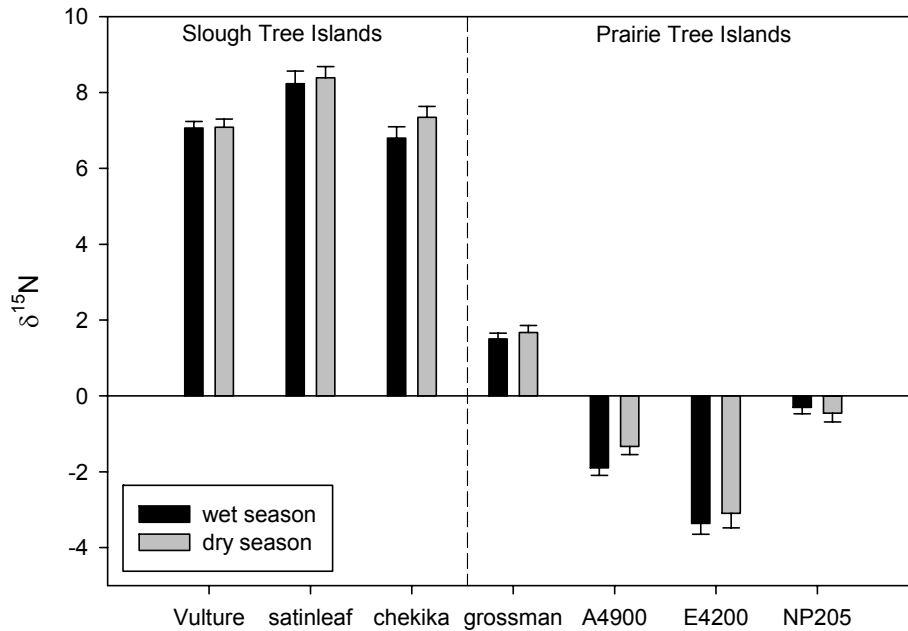
Figure 2.5: Average foliar $\delta^{15}N$ (‰) in wet (black) and dry (grey) seasons for three slough tree islands and four prairie tree islands. Error bars represent standard error of the mean (SEM). n= 20 – 40 per tree island. No significant differences were found between wet and dry seasons.
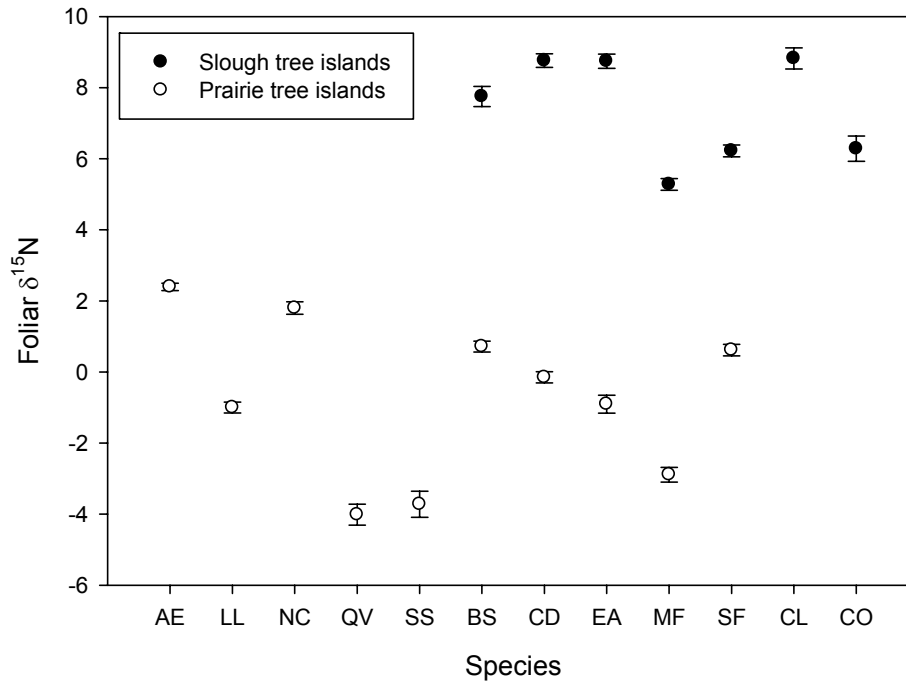
Figure 2.6: Foliar δ^{15}N (‰) of different species within each island type. Data represent species averages throughout the year and across all slough (●) and prairie (○) tree islands. Error bars represent standard error of the mean (SEM). Species include *Ardisia escallonioides* (AE), *Lysiloma latisiliqua* (LL), *Myrsine floridana* (MF), *Nectandra coriacea* (NC), *Quercus virginiana* (QV), *Sideroxylon salicifolium* (SS), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), *Sideroxylon foetidissimum* (SF), *Celtis laevigata* (CL) and *Chrysophyllum oliviforme* (CO).

Chapter 3

Foliar nutrient and water content in subtropical tree islands: A new chemohydrodynamic link between satellite vegetation indices and foliar δ^{15}N values[2]

Summary

I examined the relationships between two satellite-derived vegetation indices and foliar δ^{15}N values obtained from dominant canopy species in a set of tree islands located in the Everglades National Park in South Florida, USA. These tree islands constitute important nutrient hotspots in an otherwise P-limited wetland environment. Foliar δ^{15}N values obtained from a previous study of 17 tree islands in both slough (perennially wet) and prairie (seasonally wet) locations served as a proxy of P availability at the stand level. I utilized five cloud-free SPOT 4 multispectral images (20m spatial resolution) from different times of the seasonal cycle to derive two atmospherically corrected vegetation indices: the normalized difference vegetation index (NDVI) and the normalized difference water index (NDWI), averaged for each tree island. NDWI, which incorporates a shortwave infrared (SWIR) band that provides information on leaf water content, showed consistently higher linear fits with island foliar δ^{15}N values than did NDVI. In addition, NDWI showed greater variation throughout the seasonal cycle than did NDVI, and was significantly correlated with average water stage, which suggests that the SWIR band captures important information on seasonally variable water status. Tree islands in slough locations showed higher NDWI than prairie islands during the dry season, which is consistent with higher levels of transpiration and nutrient harvesting and accumulation for perennially wet locations. Overall, the results suggest that water availability is closely related to P availability in subtropical tree islands, and that NDWI may provide a robust indicator of community-level water and nutrient status.

Background

Tree islands are unique and important features in many large wetland ecosystems. Tree

islands are patches of woody vegetation within a freshwater wetland matrix dominated by

non-woody species (Wetzel, 2002b). These habitats are developed after wetland

formation as a result of landscape processes and feedback between hydrological and

climatic factors (Foster et al., 1983; Glaser, 1987; Wetzel, 2002b; Gumbricht et al., 2004).

As the only elevated woody habitats in a non-woody wetland matrix, tree islands can

affect local hydrology and redistribution of materials and are often the focus of nutrient

concentration and species richness in wetland ecosystems (Slack et al., 1980; Wetzel,

2002b).

In this study, I focused on tree islands of the South Florida Everglades. The Everglades

ecosystem is the largest subtropical wetland ecosystem in the United States. Tree islands

in the Everglades exist as upland plant communities scattered in a matrix of fresh water

marshes that spread over the Everglades' vast slough and marl prairie landscape.

Although they occupy only a small portion of the landscape, tree island habitats

constitute biodiversity and nutrient hotspots in the Everglades ecosystem (Slack et al.,

1980; Wetzel, 2002b). Everglades tree islands provide essential habitats for wildlife and

plant species that do not tolerate flooding, and they have two-to-three times the species

richness of surrounding marshes (Willard, 2003).

Tree islands are also the focus of nutrient accumulation in the otherwise oligotrophic

Everglades ecosystem, with soil phosphorus (P) concentrations up to 100 times higher

than in surrounding fresh water marshes (Wetzel et al., 2005). However, the P

distribution is not homogenous among different tree islands. Tree islands have a wide

range of nutrient sources such as precipitation, surface water surrounding the tree island, groundwater, plant litter and bird guano deposition, and bedrock mineralization by tree exudates (Wetzel et al., 2005). Givnish et al. (2008) suggest that bird guano deposition is the major P input for the tree islands while others propose the chemohydrodynamic nutrient accumulation model, which suggests that transpiration drives nutrient accumulation through groundwater harvesting (Wetzel et al., 2005; Ross et al., 2006). This model hypothesizes that high transpiration rates of tree island hardwood hammock plant communities cause them to take up water and nutrients from the surrounding groundwater, especially during the dry season when rain water is limited. Nutrients accumulate through this process in the tree island soil as the heads of the tree islands are never flooded. This model has been supported by previous studies showing that tree island plants can switch their water source from rain water to marsh associated groundwater during the dry season (Ross et al., 2006; Saha et al., 2009).

In a previous study, I compared the geographical patterns of community level P and water availability of different tree islands. The results supported the chemohydrodynamic nutrient accumulation model by showing that tree islands with higher dry season water deficits and water use efficiency accumulate less P than tree islands with plenty of water available during the dry season (Wang et al., 2010). In that study, I used foliar nitrogen stable isotope ratio (expressed as foliar $\delta^{15}N$) as proxy for P availability, and showed that foliar $\delta^{15}N$ is a superior index for long-term, community level measurements of P availability than soil or foliar P concentrations that often show a larger variation with time and sampling locations (Wang et al., 2010).

Work by Saha et al. (2009) and Wang et al. (2010) established a link between water

deficits and nutrient availability in tree island habitats. In order to extend these findings

in both space and time, I examined satellite-derived vegetation indices over a three-year

span to determine how photosynthetic activity and stomatal conductance relate to

measurements of foliar $\delta^{15}N$ values. Among the many vegetation indices available, I

selected the normalized difference vegetation index (NDVI) and the normalized

difference water index (NDWI) for my analysis because they are well studied and have

well-established links between plant physiological processes and states. At the canopy

scale, NDVI provides an indirect measurement of absorbed photosynthetically active

radiation and canopy stomatal conductance (Verma et al., 1993) and has been widely

used in vegetation monitoring for plant canopy characteristics such as chlorophyll content

and leaf area index (LAI)(Tucker, 1979). In the Florida Everglades, NDVI has been

shown to be a good indicator of P availability in sawgrass and cattail-dominated

freshwater marshes (Rivero et al., 2009). The NDWI, which incorporates the shortwave

infrared (SWIR) band (Gao, 1996), provides an indirect measurement of canopy water

content and has been used for drought monitoring (Jackson et al., 2004; Chen et al., 2005;

Gu et al., 2007).

NDVI and NDWI show different responses to leaf water content, atmospheric effects and

soil background reflectance. NDVI is most closely related to chlorophyll concentration

and photosynthetic activity, which may relate to canopy water content (Tucker, 1980).

However, Ceccato et al. (2001) noted that although it has been used to assess canopy

water stress, NDVI has been found to be insensitive to leaf water content in some cases.

Using laboratory measurements and model simulations the authors also showed that both

the shortwave infrared (SWIR) and the near infrared (NIR) wavelength ranges provide

direct information on the equivalent water thickness (EWT), which corresponds to a

hypothetical thickness of a single layer of water averaged over the whole leaf area.

Further, Gao (1996), who introduced the NDWI, showed that this index may be sensitive

to soil background effects, that most soils possess negative NDWI values and that NDWI

may be reduced by approximately 0.05 in a pixel with 50 percent canopy cover. He also

demonstrated these effects do not differ greatly for wet and dry soils and it is possible to

infer EWTs over areas with complete vegetation cover, such as the tree islands analyzed

in my study. Gao's work (1996) also demonstrated that at large NDVI values (>0.63),

this index typically saturates while NDWI values remain sensitive to liquid water in

green vegetation. Finally, both indices may be sensitive to shadowing to some extent;

however, several authors (Asner and Warner, 2003; Galvao et al., 2009) have shown that

red reflectance (and hence NDVI) is weakly affected by shadow fraction. SWIR

reflectance may also be affected by shadowing (Deering et al., 1999), although

systematic evaluation of these effects on NDWI appears lacking.

According to the chemohydrodynamic nutrient accumulation model, water status and

nutrient status are closely related to each other in tree island habitats (Wetzel et al., 2005;

Ross et al., 2006; Saha et al., 2010a; Wang et al., 2010). Therefore, I hypothesize that the

two vegetation indices can be used as indicators of water deficits and P status, as it is

reflected by foliar $\delta^{15}N$ values, in Everglades tree islands. However, given sources of

variation in these vegetation indices described above, I expect that NDWI may provide a

more robust index for my analysis of average foliar $\delta^{15}N$ values than NDVI.

Methods

<u>Study site</u>

The study was done in the Everglades National Park, which is part of the South Florida

Everglades ecosystem (Fig. 3.1). The Everglades ecosystem has an annual rainfall

averaging 1300 mm, approximately 70-90% of which falls during the wet season, from

June to November (Renken et al., 2006). The region has a gentle elevation gradient of

less than 4.5 cm per kilometer with a 48 km-wide sheet flow of surface water

concentrated in the Shark River Slough (Fling et al., 2004). The Everglades is a complex

wetland ecosystem composed of a variety of terrestrial and marine habitats, including

upland pinelands and hammocks, freshwater marshes, tree islands, mangroves, and coral

reefs (Lodge, 2004). The freshwater marsh habitat covers about 70% of the Everglades

area, and consists of two distinct types of landscape: the mixed ridge-slough matrix

(hereafter referred to as slough) and the marl prairies (hereafter referred to as prairie)

(Bernhardt and Willard, 2009). The sloughs are flooded throughout the year, with

maximum water depths of ~ 1 m; while the prairies are characterized by shallow water (<

0.5 m) and short (< 180 day) hydroperiods. The Shark River Slough is the largest slough

in the Everglades National Park, with water flowing southwestwards into the Gulf of

Mexico.

Tree islands are common features in both slough and prairie landscapes. The Everglades

tree islands have a unique tear-dropped shape, which is composed of a never-flooded

upland head dominated by subtropical hardwood hammock plant communities, and a

lowland tail dominated by partially flood-tolerant swamp forest (Sklar and van der Valk,

2002; Wetzel, 2002a). In this study, I selected 17 tree islands from the Shark River

Slough and its adjacent marl prairies in the Everglades National Park (Fig. 3.1). As the

largest slough in the Everglades National Park, the Shark River Slough serves as the

primary flow path that carries surface water sheet flow southwestwards into the Gulf of

Mexico (Fig. 3.1). The marshes in the Shark River Slough are flooded throughout the

year, while the marshes in the adjacent prairies dry out during the dry season (from

January to May). Ten of the selected tree islands are located in the Shark River Slough,

and the other seven are located in the eastern and western prairies adjacent to the slough.

The selected tree islands are well preserved and do not suffer from degradation or flood.

Ross and Sah (2011) measured the elevation of 10 out 17 selected tree islands and

showed that the head of these islands remain above mean water stage by 0.74 ± 0.11 ($\pm\sigma$,

n=10) meters.

Ground measurements

These 17 tree islands were selected following a previous study for ground measurements

of foliar $\delta^{15}N$ values as proxy for P availability of each island at the community level, as

well as soil total P concentration (Wang et al., 2010). The $\delta^{15}N$ values were measured for

mature leaf samples from the four most dominant upland hardwood tree species of each

tree island, such as *Bursera simaruba, Celtis laevigata, Coccoloba diversifolia, Eugenia

axillaris, Sideroxylon foetidissimum*. Leaf samples were collected during 4 sampling

periods in the wet season (September) and dry season (May) of 2007 and 2008. I

collected 4 to 5 mature leaves from 10 individual trees of each sampled species from each

selected tree island, making a total of 40 samples per tree island for each sampling period.

Ground leaf samples were then processed with a continuous flow isotope ratio mass

spectrometer (Isoprime, Elementar, Hanau, Germany) to measure $\delta^{15}N$. I found no

significant fluctuation of foliar $\delta^{15}N$ values among different sampling periods (Wang et al., 2010). An average $\delta^{15}N$ value was then calculated for each tree island to represent the mean foliar $\delta^{15}N$ for the two-year time span of ground sampling. In addition, I obtained daily water stage data taken by 18 Everglades water monitoring stations in or near Shark River Slough between 2007 and 2009 from the Everglades Depth Estimation Network (EDEN, http://sofia.usgs.gov/eden/). Monthly average water stage above sea level was calculated for the months that SPOT 4 images were acquired.

Satellite image processing

I utilized five cloud-free SPOT 4 multispectral images (20m spatial resolution) representing the mid wet season (28-Oct-2008), the end of the wet season (16-Nov-2007), the beginning of the dry season (29-Jan-2007), the mid dry season (5-Feb-2009) and the end of the dry season (23-Apr-2009) during a three-year-span that partly overlaps the ground sampling periods (Fig. 3.2a). Because of the extreme difficulty of acquiring cloud-free images over the Everglades, these five images were the best available to represent seasonal phenology. I also obtained a set of color infrared orthophotos (1m spatial resolution) taken in 1999 from the South Florida Information Access (SOFIA, http://sofia.usgs.gov/). The 1999 orthophotos were chosen instead of the 2004 orthophotos because they have higher image quality and are more suitable to facilitate georeferencing and classification of the SPOT 4 images. All SPOT 4 images were georeferenced based on the 1999 orthophotos. Using the high-resolution orthophotos, I visually identified the upland hammock communities within the selected tree islands and manually digitized their extents as study areas (Fig. 3.2b, Fig. 3.2c). These areas are dominated by broadleaf subtropical tree species that I sampled for foliar $\delta^{15}N$ values, and

range in size from approximately 80 to 200 meters in diameter. Manually classified

polygons were used to sample and extract mean values of NDVI and NDWI from the

upland parts of tree islands where field sampling was done. Mixed pixels along the edges

of digitized polygons were excluded if 50% or more of that pixel fell outside the target

area. The size of the digitized polygons range from 6 to 15 pixels (Table. 3.1).

To allow comparison of vegetation index values across time, radiometric calibration and

atmospheric correction were performed on the five SPOT 4 images. Calibration

coefficients were based on in-flight calibration data supplied with each image. View and

solar zenith and azimuth angles were also obtained from SPOT 4 image metadata.

Atmospheric correction was done using the Atcor2 radiative transfer method, which

accounts for path radiance, adjacency effects, and reflected radiation from the land

surface for multispectral satellite wavebands ranging from 0.4-2.5μm (Richter, 1996). As

the terrain in the Everglades is essentially flat, I considered corrections for topographic

effects unnecessary. Because my images may have contained substantial aerosol and

water vapor heterogeneity from nearby maritime and urban influences, I simplified the

analysis by assuming a standard atmosphere (mid-latitude, rural conditions) for the five

SPOT 4 scenes. Standard atmospheres in Atcor2 are based on climatologies for aerosols,

water vapor and absorbing gasses and are obtained from look-up-tables of radiative

transfer calculations made with MODTRAN-4 code (Richter, 2005). Visibility was set to

be 50km for all 5 SPOT 4 images during atmosphere corrections.

<u>Statistical analysis</u>

Mean NDVI and NDWI values were computed for each of the 17 tree islands. Images

from some dates only cover 15 (29-Jan-2007) or 16 (28-Oct-2008 and 05-Feb-2009) of

the tree islands because of limited extent of the satellite image. NDVI and NDWI values computed from each SPOT 4 image were correlated to the previously obtained foliar δ^{15}N values (Wang et al., 2010). I also used a linear mixed model to analyze the relationship between foliar δ^{15}N and NDVI and NDWI respectively, with image date considered a fixed effect.

A one-way ANOVA was used to compare the average NDVI and NDWI values between the five different image dates respectively, followed by a Tukey's post-hoc test to determine the significant differences among dates. Since the vegetation index values showed non-homogeneity between slough and prairie islands, I used Mann-Whitney U test to compare NDVI and NDWI values between prairie and slough tree islands within each SPOT 4 image. The significance level of the Mann-Whitney U tests among the five different images was adjusted by a Bonferroni correction to $P \leq 0.05/5 = 0.01$ (Sokal and Rohlf, 1995). A one-way ANOVA was also used to compare the average water stage among months during which SPOT 4 images were taken, followed by a Tukey's post-hoc test to determine the significance of differences between each month. A Pearson's correlation analysis was performed between monthly average water stage and average NDVI and NDWI, respectively.

Results

Figs. 3.3a and 3.3b show the results of the atmospheric correction of the NDVI and NDWI values. As expected, given the impacts of aerosols on SPOT 4 band 2, the atmospheric effect on NDVI (Fig. 3.3a) was substantially greater than on NDWI (Fig. 3.3b) with differences before and after correction ranging from approximately 0.37-0.60 NDVI units for the February and October images, respectively. In contrast, the difference

between atmospherically corrected and uncorrected NDWI was typically about 0.13-0.16

NDWI units. Although the SPOT 4 images originated from different years, Figs. 3.3a and

3.3b display the vegetation index sequence by month and thus show how the atmospheric

correction produced vegetation index series more consistent with known foliar phenology

than uncorrected values. Vegetation index values are expected to decrease from the

middle of the wet season (October, November) to the dry season (January to April) as

water for plant growth and photosynthesis becomes limited.

Despite producing the expected phenological pattern, atmospheric correction did not

result in stronger relationships between foliar δ^{15}N values and corrected vegetation index

values. In five cases (November NDWI, January NDVI and NDWI, February NDVI and

April NDVI) the relationship between foliar δ^{15}N and the corrected vegetation index

values resulted in very slight increases in Pearson's correlation coefficients versus

uncorrected values; whereas in the other five cases, atmospheric correction resulted in

slightly reduced correlations between the two variables (Table. 3.2). Below, I present and

analyze these relationships as they apply only to the atmospherically corrected vegetation

index values.

Average NDVI and foliar δ^{15}N values showed significant correlations only from SPOT 4

images taken on 29-Jan-2007 and 5-Feb-2009 (Fig. 3.4c and 3.4d). On the other hand,

NDWI values from all five SPOT 4 images showed significant correlations with foliar

δ^{15}N values taken from the tree island hammocks (Fig. 3.4). The linear mixed model

showed that NDVI values are affected by both foliar δ^{15}N values ($P<0.05$) and image date

($P<0.0001$), but not by the interaction between these two factors ($P>0.05$, Table. 3.3a).

Similarly, the linear mixed model for NDWI also showed significant effects of foliar

δ^{15}N values (P<0.0001) and image date (P<0.0001), but no significant effect of the interaction (P>0.05, Table. 3.3b).

Significant differences were found for both NDVI and NDWI between images taken on different dates. Tukey's post-hoc test showed that the SPOT 4 image taken on 28-Oct-2008 has the highest NDVI and NDWI values, followed by 16-Nov-2007. No difference was found among the three dry season images for both NDVI and NDWI (Fig. 3.5a and 3.5b). I found significantly lower NDWI in prairie tree islands than in slough tree islands from images taken on 5-Feb-2009 and 23-Apr-2009, but not on the other dates (Fig. 3.3b). No difference was observed between slough and prairie tree islands for the NDVI index (Fig. 3.3a). Monthly average water stage was also plotted in monthly sequence regardless of the year (Fig. 3.5c). Average water stage was found to be significantly different among the five dates, with 28-Oct-2008 being the highest and 23-Apr-2009 being the lowest (Fig. 3.5c). Moreover, I found a significant positive correlation between average water stage and average NDWI values (P<0.05), but no significant correlation between average water stage and average NDVI values (Fig. 3.6).

Discussion

Foliar δ^{15}N values were used as a proxy for P availability at the community level. It has been shown that in the generally P-limited Everglades ecosystem, foliar δ^{15}N of plants is an indicator of ecosystem P availability (Inglett and Reddy, 2006; Inglett et al., 2007; Wang et al., 2010). I chose to use island foliar δ^{15}N as the proxy, because, unlike any direct measurement of plant available P, foliar δ^{15}N value is a stable parameter through time that does not fluctuate with year and season (Wang et al., 2010). Therefore, I could compare it with vegetation indices derived from satellite images taken between 2007 and

2009. The linear mixed models showed that both image dates and island δ^{15}N have

significant effects on NDVI and NDWI values (Table. 3.3), indicating that tree island

NDVI and NDWI are sensitive to the long term proxy of island nutrient status and to

annual hydrology status (dry and wet seasons). However, the NDWI value showed

consistently higher image-by-image linear fits with island δ^{15}N than did NDVI, with all

five correlations being significant (Fig. 3.4). This is consistent with my hypothesis and

general understanding of NDWI, which is highly sensitive to canopy EWT provided

canopy cover is sufficiently high (>80 percent) (Gao 1996). On the other hand,

significant correlations between NDVI and island δ^{15}N values were obtained for only two

dry-season images, (29-Jan-2007 and 5-Feb-2009, Fig. 3.4c and 3.4d). I found no

significant interaction between image date and island foliar δ^{15}N value on NDVI and

NDWI (Table. 3.3), suggesting that the correlation between δ^{15}N and the vegetation

indices is independent of the date. Because NDWI is considered an indicator of canopy

water content and the community level foliar δ^{15}N value as a proxy for P availability, the

positive relationship between NDWI and island δ^{15}N supports the chemohydrodynamic

hypothesis that plant water availability is positively associated with tree island nutrient

status.

Wang et al. (2010) showed that prairie tree islands, surrounded by dry marshes during the

dry season, experience greater water deficits than slough tree islands and, therefore, show

reduced transpiration and nutrient accumulation during the dry season relative to slough

tree islands. These observations are consistent with the chemohydrodynamic nutrient

accumulation model. Here, I found that both NDVI and NDWI values showed significant

decreases through the monthly sequence from October to April as expected (Fig.3.5a and

3.5b). However, NDWI showed greater variation throughout the seasonal cycle than did NDVI (Fig. 3.5b), and this seasonal variation showed similar decreasing pattern from wet season to dry season as monthly water stage above sea level (Fig. 3.5c). The significant positive correlation between average NDWI and average water stage confirmed that the seasonal variation of NDWI follows the variation of water availability (Fig. 3.6). This result suggests that the NDWI index is more sensitive in capturing seasonal variation in nutrient and hydrologic status than the NDVI index. I also found no significant difference in NDVI between slough and prairie tree islands (Fig. 3.3a); while two out of three dry season images (5-Feb-2009 and 23-Apr-2009) showed significantly lower NDWI in prairie tree islands than in slough tree islands (Fig. 3.3b), indicating that prairie tree islands have lower canopy water content than slough tree islands during the dry season. Moreover, the only dry season image that did not show significant differences in NDWI between slough and prairie tree islands was taken at the beginning of the dry season (29-Jan-2007), when the marsh water level was still high and not different from the two wet season dates (Fig. 3.5c). Again, this result is consistent with evidence presented by Wang et al (2010), supporting the chemohydrodynamic nutrient accumulation model. This result suggests that NDWI, especially the SWIR band, is highly sensitive to canopy-level water status. Overall, my results show that both NDVI and NDWI indices can be used to monitor the geographical and seasonal variation in nutrient and water status for Everglades tree island habitats, but NDWI provides a stronger predictor of water status across different seasons and years. Nonetheless, unexplained variation in relationships between NDWI and foliar $\delta^{15}N$ may be attributed to soil background, canopy shadowing and unaccounted for atmospheric effects. The NDWI-foliar $\delta^{15}N$ relationships showed

somewhat stronger relationships during the dry season when the semi-deciduous trees lost a portion of their leaf canopies, which suggests that soil background effects did not affect my results. However, further investigation of these influences on NDWI may be warranted in my study area. Moreover, the pattern revealed by NDWI and island foliar δ^{15}N values agrees with the chemohydrodynamic nutrient accumulation model, suggesting that prairie tree islands, which have lower dry season water availability than slough tree islands, accumulate less P than slough tree islands.

This study is novel in applying remote sensing techniques specifically on tree island habitats. Previous remote sensing studies in the Everglades ecosystem mostly focused on the freshwater marshes (Rivero et al., 2009). Although Givinish et al. (2008) included tree island habitats in their NDVI survey, NDVI was only used to show the distribution of biomass in the Everglades landscape. This study is one of the first to utilize satellite-derived vegetation indices in combination with stable isotope analysis of leaf tissues. Strong relationships between foliar δ^{15}N and NDWI, in particular, suggest that NDWI can be used to monitor canopy-level P accumulation over large areas in wetland and other communities, when the link between foliar δ^{15}N and P status is supported by ground studies. Although my analysis is limited to a specific wetland habitat type (tree islands), the linearity of the relationship between canopy-level nutrient status and NDWI suggests that many operational, satellite sensor systems can be used to map and monitor available P, which is a critical, limiting nutrient in many terrestrial and wetland ecosystems. Further work is required to extend and test this hypothesis in other terrestrial and wetland ecosystems that are characterized by spatial and temporal heterogeneity of nutrient flux and availability.

Table 3.1: Number of pixels (n) within the digitized polygon of the target area used to derive vegetation indices for each tree island. Mixed pixels were not included if 50% or more of that pixel fell outside the target area.

Slough islands	n	Prairie islands	n
Chekika	8	Grossman	12
Gumbolimbo	12	Edge	7
Vulture	10	E4200	6
Satinleaf	8	Ficus	6
Irongrape	10	Mosquito	15
Black	6	NP205	14
SS37	6	A4900	7
Manatee	12		
Panther	14		
SS81	6		

Table 3.2: Pearson's correlation coefficient (r) values from correlation analysis between average foliar $\delta^{15}N$ values and average uncorrected and atmospherically corrected NDVI (a) and NDWI (b) values of each SPOT 4 satellite image.

Source	28-Oct-08	16-Nov-07	29-Jan-07	5-Feb-09	23-Apr-09
a. NDVI					
Uncorrected	0.52	0.51	0.75	0.61	0.31
Corrected	0.48	0.42	0.78	0.68	0.39
b. NDWI					
Uncorrected	0.57	0.71	0.80	0.83	0.60
Corrected	0.54	0.72	0.81	0.80	0.60

Table 3.3: Results of linear mixed model ANOVAs examining effects of island average foliar δ^{15}N value and date of satellite images on NDVI (a) and NDWI (b).

Source	d.f.	F	Sig.
a. Dependent variable: NDVI			
Foliar δ^{15}N	1	8.307	0.0114
Image date	4	37.596	<.0001
δ^{15}N*date	4	0.992	0.4196
b. Dependent variable: NDWI			
Foliar δ^{15}N	1	29.2587	0.0001
Image date	4	46.2453	<.0001
δ^{15}N*date	4	1.5363	0.2042
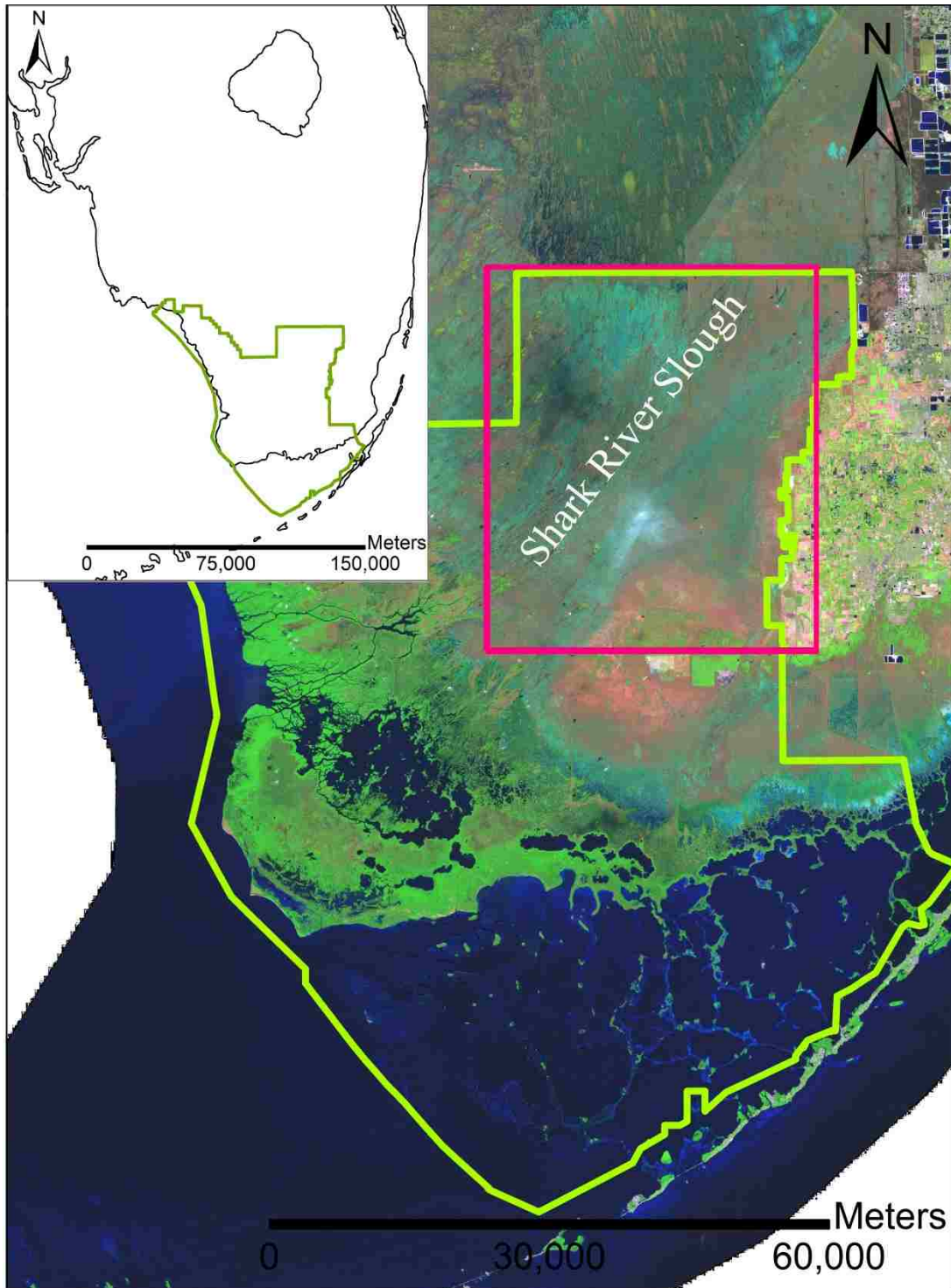
Figure 3.1: Map of south Florida and false color Landsat imagery of Everglades. Green lines mark the boundary of Everglades National Park. Pink quadrat marks the study area. Landsat image was taken on 4/18/2004 and bands shown are band 5, 4 and 3. Image obtained from Florida Coastal Everglades Long Term Ecological Research data network (FCE. LTER, http://fce.lternet.edu/data/GIS/).
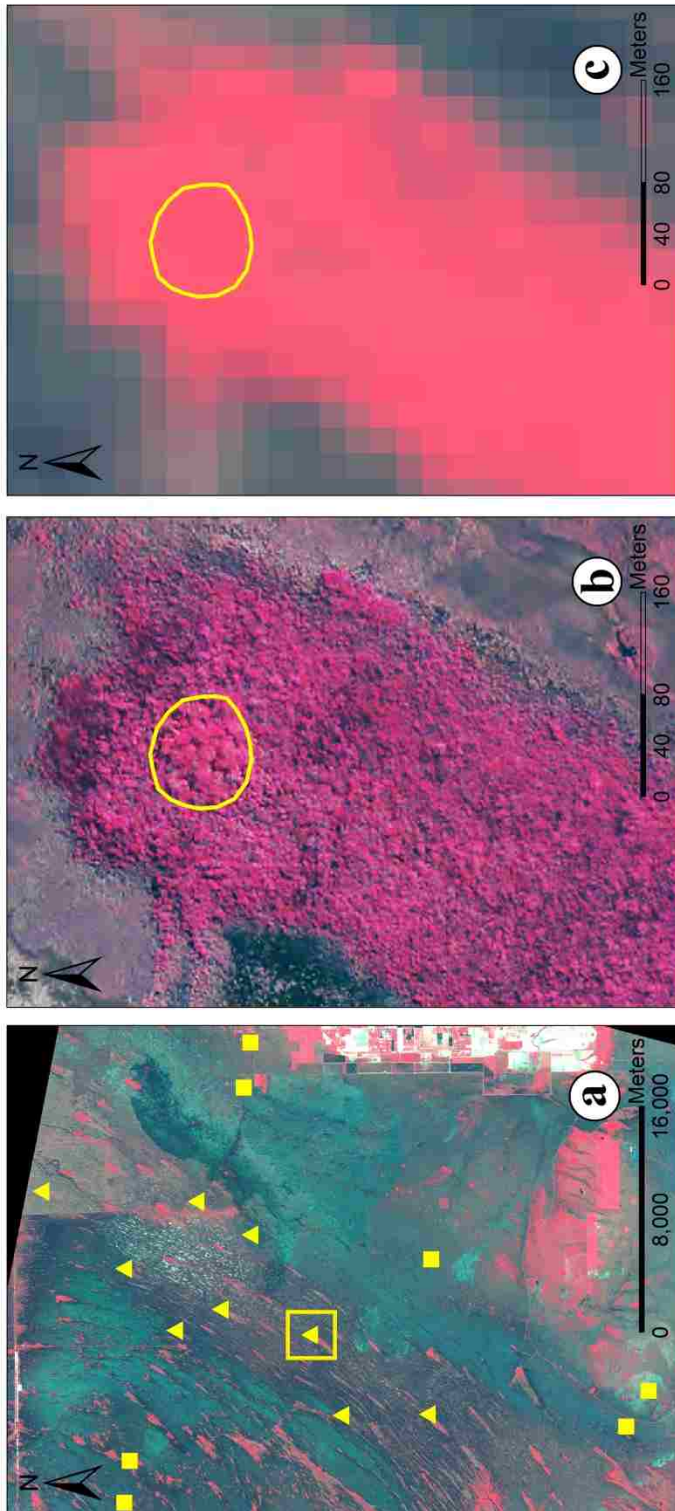
Figure 3.2: a. SPOT 4 satellite image (28-Oct-2008) of the Everglades National Park and selected prairie (■) and slough (▲)tree islands. Orthophoto (b) and SPOT 4 image (c) of one tree island marked in the yellow square of a (Panther Island). Yellow circles in b and c mark the areas where leaf samples and vegetation indices were acquired in upland areas on the tree island.
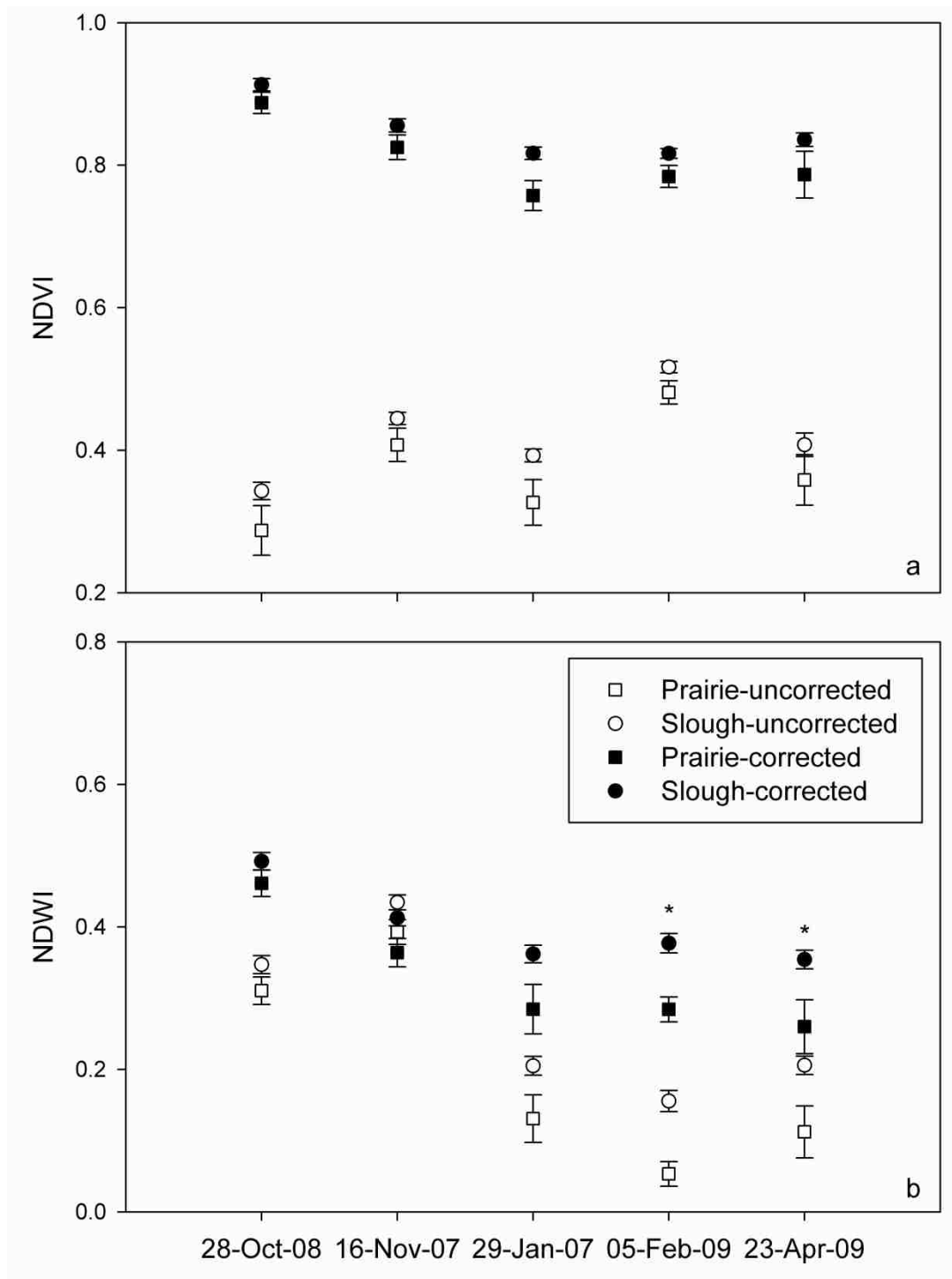
Figure 3.3: Atmospherically corrected (closed) and uncorrected (open) NDVI (a) and NDWI (b) values for prairie (squares) and slough (circles) tree islands. Error bars show the standard error of the mean (SEM). Stars (*) indicate statistically significant differences between prairie and slough tree islands at one date by Mann-Whitney *U* test for atmospherically corrected vegetation indices.
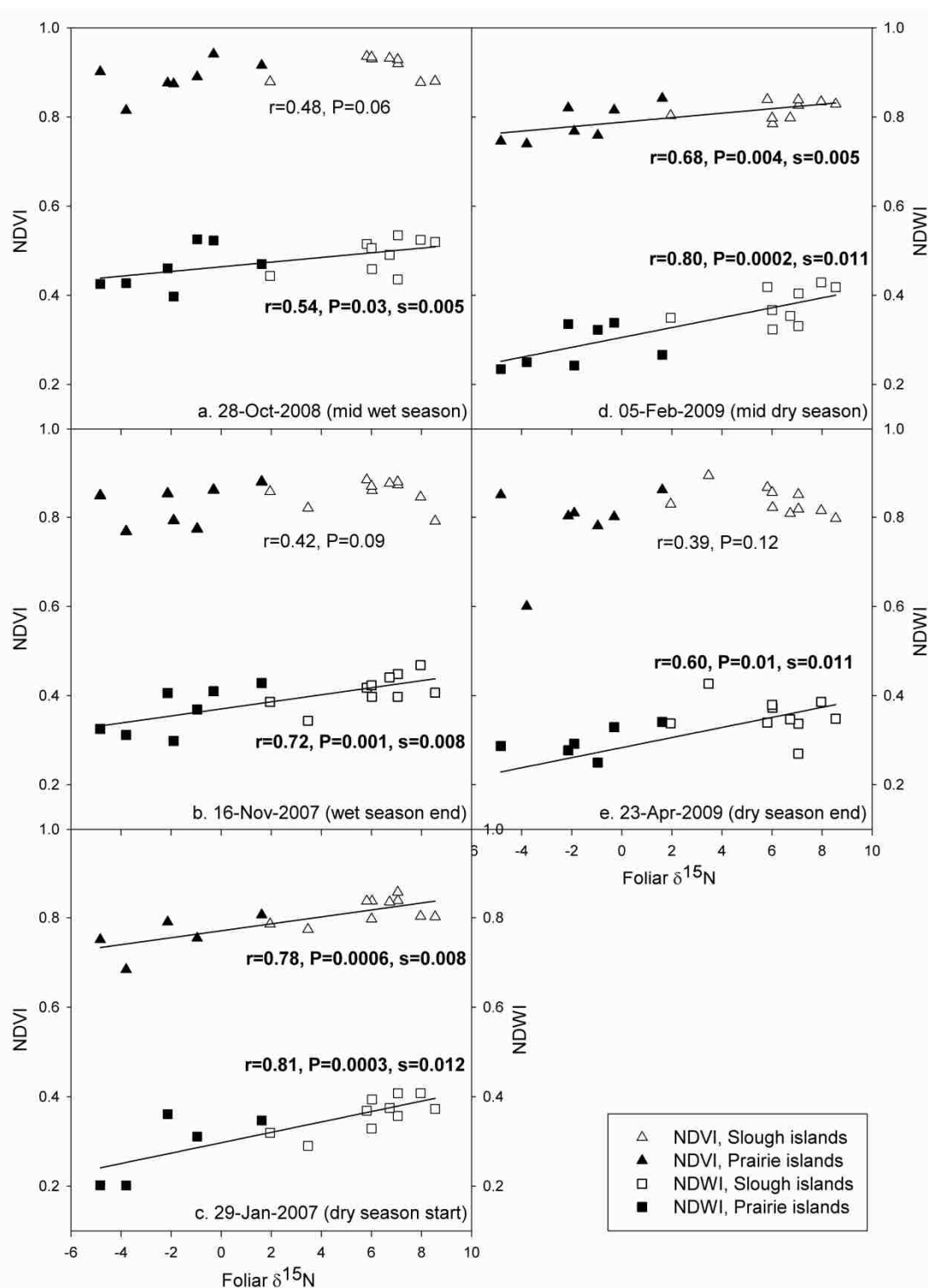
Figure 3.4: Average NDVI (triangles) and NDWI (squares) versus average foliar $\delta^{15}N$ (‰) for each tree island (n=15-17 depending on image extent). Closed symbols represent prairie tree islands, open symbols represent slough tree islands. Lines of best fit represent significant correlation (P<0.05). Statistics shown include Pearson's correlation coefficient (r), possibility (P), and slope (s).
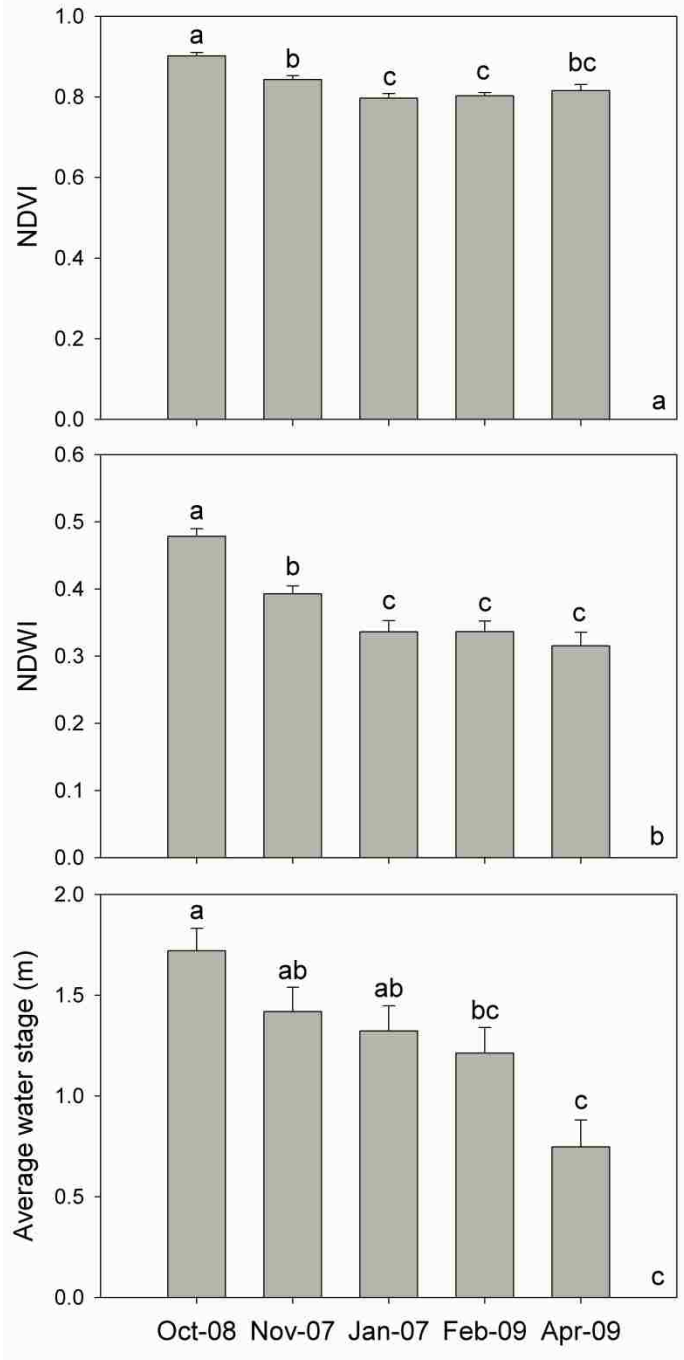
Figure 3.5: Average NDVI (a), NDWI (b), and monthly average water stage (c) of each SPOT 4 image. Error bars show the standard error of the mean (SEM). Bars marked with same letters do not differ statistically by Tukey's post-hoc test following a one-way ANOVA .
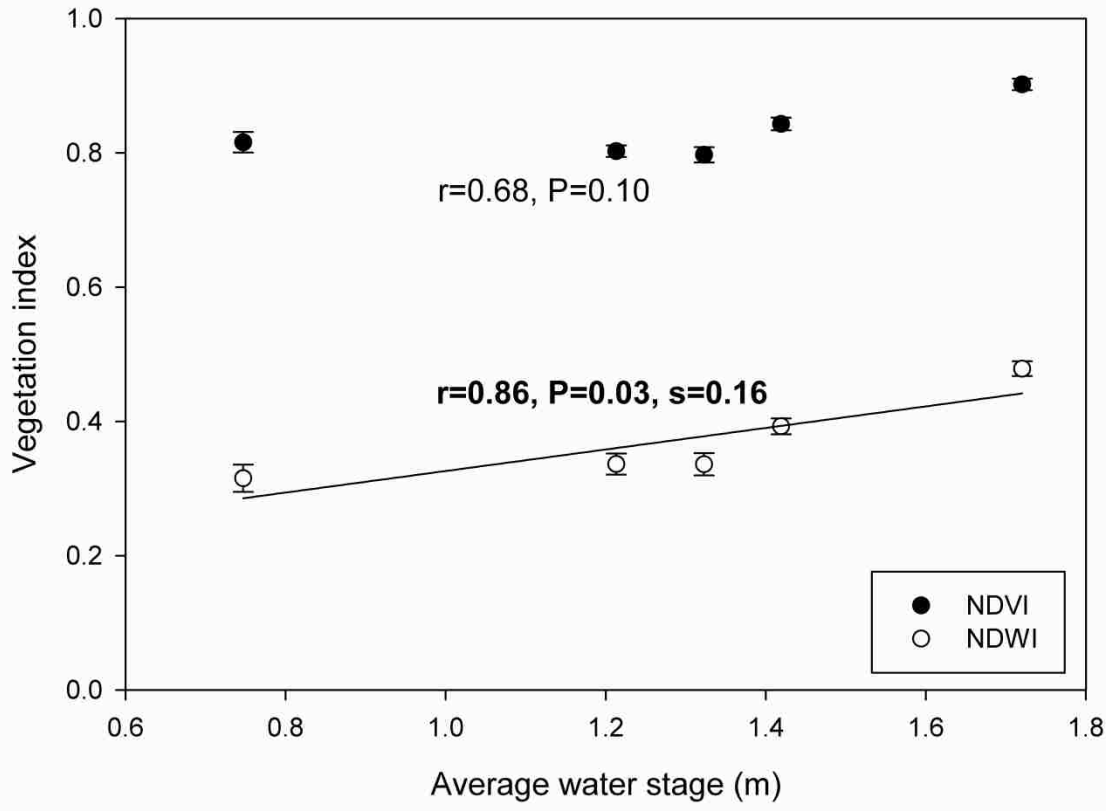
Figure 3.6: Monthly average water stage (m) for the months SPOT 4 images were acquired versus average NDVI (●) and NDWI (○) over all sampled tree islands of each date. Water stage data obtained from the Everglades Depth Estimation Network (EDEN, http://sofia.usgs.gov/eden/). Error bars represent standard error of the mean (SEM). Lines of best fit represent significant correlation (P<0.05). Statistics shown include Pearson's correlation coefficient (r), probability (P), and slope (s).

Chapter 4

Factors determining transpiration rate of hardwood tree species in Everglades tree islands

Summary

The hardwood hammock trees that grow in Everglades tree island habitats have high transpiration rates. These high transpiration rates are important for both water relations and tree island nutrient accumulation. In this study, I monitored transpiration of tree island hardwood plant species by measuring sap flux velocity at four different tree islands for twelve continuous months. I examined the relationships between sap flux velocity and broad climate factors including solar radiation, air temperature, relative humidity, and precipitation, as well as the more localized factor of marsh water depth, in order to determine the primary factors affecting the transpiration rates of tree island plants. Climate factors did not have simple linear effects on sap flux velocity, but affected the transpiration rate episodically, especially under extreme conditions. On the other hand, the localized factor of marsh water depth in different landscapes showed a significant effect on sap flux velocity, which indicates that Everglades hydrology management can also affect tree island plant transpiration activity. Satinleaf tree island, which has the densest canopy among all four monitored tree islands, had the highest transpiration rate in the canopy species *Coccoloba diversifolia*, but the lowest transpiration rate in the understory species *Eugenia axillaris*. I also found that *Eugenia axillaris* had lower transpiration rates and lower seasonal changes than *Coccoloba diversifolia*. This suggests that transpiration of understory species is dampened by the canopy and limited by certain climate factors such as low solar radiation and high relative humidity, especially in communities with dense canopies.

Background

Tree islands are patches of woody vegetation within a freshwater wetland matrix dominated by non-woody species (Wetzel, 2002b). These habitats are unique and important features in many large wetland ecosystems. Tree islands are believed to be a result of ecosystem self-organizing landscape processes and feedback between hydrological and climatic factors after wetland formation (Foster et al., 1983; Glaser, 1987; Wetzel, 2002b; Gumbricht et al., 2004). As the only elevated woody habitats in a non-woody wetland matrix, tree islands can affect local hydrology and redistribution of materials, and are often the focus of nutrient concentration and species richness in wetland ecosystems (Slack et al., 1980; Wetzel, 2002b).

In this study, I focused on tree islands of the South Florida Everglades, which is the largest subtropical wetland ecosystem in the United States. Tree islands in the Everglades exist as upland plant communities scattered in a matrix of fresh water marshes that spread over the Everglades' vast slough and marl prairie landscape. Although they occupy only a small portion of the landscape, tree island habitats constitute biodiversity and nutrient hotspots in the Everglades ecosystem (Slack et al., 1980; Wetzel, 2002b). Everglades tree islands are the focus of nutrient inputs from a wide range of potential sources such as precipitation, surface water surrounding the tree island, groundwater, plant litter and bird guano deposition, and bedrock mineralization by tree exudates (Wetzel et al., 2005). These tree islands also provide essential habitats for wildlife and plant species that do not tolerate flooding, and they have two-to-three times the species richness of surrounding marshes (Willard, 2003).

The plant communities of tree islands have high transpiration rates. According to the chemohydrohynamic nutrient accumulation model, the high transpiration of tree island plant communities is the driving force of tree island nutrient accumulation (Wetzel et al., 2005). In a previous study examining water uptake by tree island plants, Saha et al. (2010a) showed that Everglades tree island plants use soil-trapped rain water during the wet season and ground water associated with the surrounding marsh during the dry season. Water level patterns reported by Ross et al. (2006) suggest that ground water sources contribute significantly to plant water usage during the dry season. In a previous study using stable isotope proxies to look at plant water deficits and nutrient availabilities, Wang et al. (2010) showed that tree islands with high dry season water deficits and high water use efficiency accumulate less P than tree islands with persistent water availability during the dry season. I also have shown, using remote sensing analysis, that the normalized difference water index (NDWI), an indicator of canopy water content, is related to P availability to tree island plants as assessed by stable isotopes (Wang et al., 2011). All the above studies support the chemo-hydrodynamic nutrient accumulation model, and suggest that tree island plant water uptake and transpiration function importantly in both nutrient redistribution and the ground and marsh water budgets of the Everglades ecosystem.

In this study, I looked at tree island transpiration using the direct approach of the Granier sap flux velocity method (Granier, 1987). Sap flux velocity measures the volume of water taken up by a plant per unit sap wood area (Granier, 1987). I assumed that sap flux velocity is proportional to transpiration, and used it as a proxy for transpiration (Small and McConnell, 2008). There are a variety of factors that could affect sap flux

velocity. Among the most commonly analyzed meteorological factors affecting broad areas of the Everglades, solar radiation and air temperature have been shown to have a strong positive effect on transpiration and sap flux velocity in both woody and grass species through effects on photosynthetic activity and stomatal conductance (Briggs and Shantz, 1916; Qu et al., 2007; Xu, 2007; Xia et al., 2008). Relative humidity and vapor pressure deficit also are usually correlated with sap flux velocity, because the diffusion of the water vapor out of the leaf is more rapid when the surrounding air is dry (Qu et al., 2007; Xia et al., 2008). Precipitation, however, has a complex effect on sap flux velocity, because it is related to multiple factors including water availability, solar radiation, and relative humidity (Zhao and Liu, 2010).

An additional factor which may be of importance is the highly managed Everglades hydrology. The water level in the Everglades marshes is affected by surface water flow in canals and rivers, which is controlled and regulated by the South Florida Water Management District (Richardson and Huvane, 2008). According to the chemohydrodynamic model and studies done by Ross et al. (2006) and Saha et al. (2010a), tree island plants take up marsh-associated groundwater during the dry season. Therefore, marsh water level is related to plant water availability in tree islands, especially during the dry season.

In this study, I wanted to determine what are the primary factors affecting the transpiration rate of tree island plants: broad climate factors which affect the entire region relatively homogeneously versus the more local condition of water level, which is subject to water management practices. I examined the sap flux velocity of five different evergreen tree species of Everglades tree island hardwood hammock communities and

their responses to both climate factors and water level during one year. I examined four different broad climate factors, which are solar radiation, air temperature, relative humidity and precipitation, in order to look at the seasonal responses of sap flux velocity to the weather fluctuations of the entire Everglades region. I also examined the more localized effects of marsh water depth in different landscapes on tree island plant sap flux velocity.

Methods

Study site

The study was conducted in the Everglades National Park, which is part of the South Florida Everglades ecosystem. The annual precipitation of the Everglades ecosystem ranges from 1,270 to 1,620 mm, approximately 70-90% of which falls during the wet season, from June to November (McNab and Avers, 1994; Renken et al., 2006). The average annual temperature is 22 to 25 °C, and the frost-free growing season lasts for 330 to 365 days (McNab and Avers, 1994). The region has a gentle elevation gradient of less than 4.5 cm per kilometer with a 48 km-wide sheet flow of surface water concentrated in the Shark River Slough (Fling et al., 2004). The Everglades is a complex wetland ecosystem composed of a variety of terrestrial and marine habitats, including upland pinelands and hammocks, freshwater marshes, tree islands, mangroves, and coral reefs (Lodge, 2004). The freshwater marsh habitat covers about 70% of the Everglades area, and consists of two distinct types of landscape: the mixed ridge-slough matrix (hereafter referred to as slough) and the marl prairies (hereafter referred to as prairie) (Bernhardt and Willard, 2009). The sloughs are flooded throughout the year, with maximum water

depths of approximately 1 m; while the prairies are characterized by shallow water (< 0.5 m) and short (< 180 day) hydroperiods.

Tree islands are common features in both slough and prairie landscapes. Everglades tree islands are often composed of a rarely-flooded upland head dominated by subtropical hardwood hammock plant communities, and a lowland tail dominated by partially flood-tolerant swamp forest (Sklar and van der Valk, 2002; Wetzel, 2002a). In this study, I selected four tree islands from the Shark River Slough and its adjacent marl prairies in the Everglades National Park (Fig. 4.1). As the largest slough in the Everglades National Park, the Shark River Slough serves as the primary flow path that carries surface water sheet flow southwestwards into the Gulf of Mexico (Fig. 4.1). The marshes in the Shark River Slough are flooded throughout the year, while the marshes in the adjacent prairies dry out during the dry season (from January to May). Of the selected tree islands, Satinleaf (25.660 °N, 80. 756 °W) and SS37 (25.553 °N, 80.816 °W) are located in the Shark River Slough, and NP205 (25.689 °N, 80.847 °W) and A4900 (25.692 °N, 80.877 °W) are located in the prairies west of the slough. The selected tree islands are well preserved and do not suffer from degradation or flood. The average elevation of these tree islands is 0.74m above mean water stage (Shamblin et al., 2008).

I also obtained the canopy and soil characteristics of the four selected tree islands. Ruiz et al. (2011) measured the leaf area index (LAI), canopy height, and soil depth of each tree island using methods described by Fraser et al. (1999) and Ross et al. (2004). Island mean LAI, maximum canopy height, and mean soil depth (± 1 S.D.) was recorded for each tree island. In order to measure soil pore water phosphorus concentration, I randomly placed ten 15g anion exchange resin (Amberlite® IRA - 400 OH, Supelco, USA)

bags at 10cm depth in the soil from Aug 28th 2009 to Oct 28th 2009 on each tree island. I

extracted the exchangeable P from each resin bag using 80 ml, 1 molar potassium

chloride (KCl) solution, and then diluted the extract with distilled water to 150 ml. The

diluted sample was analyzed by an Alkem 3000 Phosphorus analyzer (Alpkem, OI

Analytical, Texas, USA) using the USEPA method 365.1 (USEPA, 1984) by the

molybdate blue colorimetric approach (Fiske and Subbarow, 1925). P concentration was

measured as milligrams per liter diluted solution. Average pore water P concentration of

each tree island was recorded.

Sap flux velocity measurement:

    The hardwood hammock community on the head of each tree island is dominated by

about 5 to 10 evergreen or deciduous subtropical tree species. Some common species that

appear in most tree islands include *Eugenia axillaris*, *Myrsine floridana*, *Bursera

simaruba*, *Coccoloba diversifolia*, *Celtis laevigata* and *Sideroxylon foetidissimum*. These

tree island hardwood species are intolerant of prolonged flooding (Saha et al., 2010a).

The deciduous species (*Bursera simaruba* and *Celtis laevigata*) lose their leaves during

the January to May dry season, with a leafless period of about one month duration.

Therefore, I selected only the evergreen species for sap flow measurement to better assess

the annual pattern.

    For each tree island, species were ranked with Importance Values based on relative

density and basal area (Shamblin et al., 2008). At each tree island, I selected ten

individual trees (twelve trees for Satinleaf island) from the three evergreen species with

the highest Importance Values for insertion of Granier sap flow sensors (Dynamax,

United States). The sap flow sensors were inserted during August (NP205 and Satinleaf)

and September (A4900 and SS37) of 2009. I used sap flow sensors 10mm or 30mm in
length. Diameter at breast height (dbh) values were measured for each tree at time of
insertion in order to determine the size of sap flow sensors to be inserted (Table. 4. 1).
Temperature differences between two probes were measured every minute and averaged
and recorded every 60 minutes by a CR1000 data logger (Campbell Scientific, United
States) and converted to sap flux according to the equation

$$F = 119((T_{diff,max}-T_{diff})/T_{diff})^{1.23} ,$$

in which F is the sap flux velocity (μm/s), $T_{diff,max}$ is the maximum temperature difference
between sensors on each day, which usually occurs during the night when there is no
transpiration, and T_{diff} is the temperature difference of the minute when the velocity is
calculated (Granier, 1987; Saugier et al., 1997). The sap flux velocity was measured
continuously for one year until July (NP205and A4900) or September (Satinleaf and
SS37) of 2010.

Water depth and climate data

I obtained climate data from the Florida Automated Weather Network
(http://fawn.ifas.ufl.edu/data/) Homestead, FL station (25.510°N, 80.498°W), which is
the closest station to my study sites. Parameters recorded include daily average solar
radiation rate as Radiant Flux Density (Wm^{-2}), daily average precipitation (cm), daily
average relative humidity, and daily average temperature (°C). I calculated the monthly
average solar radiation, average temperature, relative humidity, and monthly total
precipitation. I assumed that the regional variation of these parameters between my four
study sites is negligible on a monthly basis. I also obtained daily water gage data between
August 1st 2009 and September 30th 2010 using the Everglades Depth Estimation

Network (EDEN, http://sofia.usgs.gov/eden/) from four monitoring sites. Monthly

average water depth at each location was calculated.

<u>Data analysis</u>

I calculated the daily total sap flux velocity (mm/day) of each individual tree by

adding up hourly averages calculated from the temperature differences recorded by the

data loggers. November data from the NP205 island were missing because the data logger

malfunctioned from October 14th 2009 to Dec 1st 2009. January data from *Coccoloba*

diversifolia at Satinleaf island were missing because sap flow probes malfunctioned.

Monthly average sap flux velocity was then calculated for each species at each tree island.

Among all selected species, *Eugenia axillaris* and *Coccoloba diversifolia* appear in

all four tree islands; therefore I performed most of the comparative analyses with these

two species which represent an understory and a canopy species, respectively. I

calculated average monthly sap flux velocity of *Eugenia axillaris* and *Coccoloba*

diversifolia across Satinleaf and SS37 islands to represent slough tree islands and across

NP205 and A4900 islands to represent prairie tree islands. In order to determine the

effects of climate factors on sap flux velocity, I performed a series of multiple regression

analyses using sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* of

slough and prairie tree islands separately as dependent variables. I performed a

correlation analysis on the four climate factors: monthly average solar radiation, monthly

average air temperature, monthly average relative humidity, and monthly total

precipitation as rainfall. I found that solar radiation, air temperature, and rainfall were

highly correlated to each other (Table. 4.2), and could not be used as independent

variables in the multiple regression analysis at the same time. Therefore, only solar

radiation and relative humidity were used in the multiple regression analysis so that the independent variables were independent from each other (Sokal and Rohlf, 1995). Air temperature and rainfall were dropped because they affect transpiration indirectly through solar radiation and relative humidity. The significance level of each multiple regression was adjusted by a Bonferroni correction (Sokal and Rohlf, 1995). For each monitoring tree island, I examined the effect of seasonal water depth fluctuations on sap flux velocity of both *Eugenia axillaris* and *Coccoloba diversifolia* using linear regression analysis. I also examined the relationship between *Eugenia axillaris* and *Coccoloba diversifolia* at slough and prairie tree islands separately. I performed a separate One-way ANOVA to examine the differences of sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* among four tree islands, followed by a Tukey's post-hoc test to determine the differences between each site.

Results

I found that Satinleaf tree island had the highest LAI and maximum canopy height among all four monitored tree islands (Table. 4. 3). The average soil depth also differed among tree islands. Satinleaf tree island, located in the slough, had the greatest soil depth of 0.407 ± 0.176m; while A4900 island, located in the prairie, had the lowest soil depth of 0.134 ± 0.131m (Table. 4. 3). For soil pore water exchangeable P concentration, Satinleaf tree island had higher P than all the other tree islands. The average P concentration of the final diluted solution of Satinleaf island was 6.47 ± 1.42 mg/L, while the second highest SS37 island had only 1.34 ± 0.4 mg/L (Table. 4. 3).

Figure 4.2 shows the monthly average solar radiation, air temperature, relative humidity and monthly total precipitation from August 2009 to September 2010, with a

full dry season from January 2010 to May 2010. Solar radiation decreased during the wet season of 2009 with the minimum value of 125 Wm^{-2} in December 2009, and increased during the dry season of 2010 with the maximum value of 253 Wm^{-2} in May 2010 (Fig. 4.2a). Similar to solar radiation, average air temperature also decreased from August 2009 to January 2010, and increased during the dry season of 2010. June, July, August, and September of both years have the highest average temperature of around 28 °C (Fig. 4.2b). Relative humidity ranged from 80% to 86% during the wet season of 2009, and fluctuated from August to December. January, February and March of 2010 had the lowest relative humidity of approximately 78%. Relative humidity increased during the second half of dry season 2010 and continued to increase through the start of wet season 2010 in June through August 2010 (Fig. 4.2c). Wet season 2009 had monthly precipitation ranging from 5 cm to 15 cm. January 2010 had only 2.3 cm of precipitation, which was the minimum for the year. However, the rest of the dry season 2010 had much higher precipitation than January, ranging from 5 cm to 11 cm (Fig. 4.2d). Water depth was found to be higher at the slough water stations than the prairie stations. The lowest water level in the slough marshes, 0.37 m depth, appeared in February 2010. For the prairie marshes, the water level dropped below ground between March and May 2010, with the lowest water depth in April 2010 of -0.13 m (Fig. 4.3).

The seasonal pattern of sap flux velocity was consistent across all monitored species and tree islands. Most species showed an increase in sap flux velocity from August to October 2009, a decrease from October 2009 with the lowest point in January 2010, and a constant increase afterwards (Fig. 4.4). *Coccoloba diversifolia* showed the highest sap flux velocity in all 4 tree islands, while understory species such as *Eugenia axillaris* and

Myrsine floridana had relatively low sap flux velocity (Fig. 4.4). I found a significant correlation between the sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* in the prairie tree islands (r = 0.78, P = 0.005), but not in the slough tree islands (r = 0.39, P = 0.208) (Fig. 4.5).

In the multiple regression analysis, solar radiation was found to have a significant effect on sap flux velocity of both *Eugenia axillaris* and *Coccoloba diversifolia* in the slough tree islands, but not in the prairie tree islands (Table. 4.4). I found no significant effect of relative humidity on sap flux velocity in all four separate multiple regression analyses (Table. 4.4). Seasonal water depth fluctuations was found to have no significant effect on sap flux velocity. The sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* differ among the four monitoring sites. Satinleaf island was found to have the highest sap flux velocity in *Coccoloba diversifolia* among all four sites (Fig. 4.6). On the other hand, for *Eugenia axillaris*, A4900 island had the highest sap flux velocity, and Satinleaf island had the lowest sap flux velocity (Fig. 4.6).

Discussion

The evergreen canopy species in all four monitored tree islands, *Coccoloba diversifolia*, showed the highest sap flux velocity as well as the most dramatic seasonal changes of all monitored species. On the other hand, the two most common understory species, *Eugenia axillaris* and *Myrsine floridana*, had low sap flux velocity. Although these two species showed similar seasonal patterns to *Coccoloba diversifolia*, they had much smaller seasonal changes than *Coccoloba diversifolia* (Fig. 4.4). This is most likely because the understory trees are more limited to certain microhabitat conditions of the understory than canopy trees, which would dampen their sap flux velocity as well as the

seasonal differences. For example, understory tree species generally receive low solar radiation that can limit photosynthetic activity and therefore transpiration and sap flux velocity. Moreover, understory trees are exposed to high relative humidity which also decreases transpiration. Both factors could explain the low sap flux velocity found in *Eugenia axillaris* and *Myrsine floridana*. On the other hand, the transpiration of canopy trees generally is not limited by solar radiation or vapor pressure gradient, and therefore can have high sap flux velocity and large seasonal differences.

The sap flux velocity of *Coccoloba diversifolia* was much higher in Satinleaf tree island than the other three tree islands (Fig. 4.4). Satinleaf island also has the highest LAI and maximum canopy height among all four tree islands (Table. 4.1), which indicates that Satinleaf tree island has the densest canopy. If the high density is caused by high foliage leaf area of individual canopy trees, including *Coccoloba diversifolia*, then one may expect high sap flux velocity of *Coccoloba diversifolia* at this island. *Eugenia axillaris*, however, showed the lowest sap flux velocity at Satinleaf tree island (Fig. 4.4). This is most likely because *Eugenia axillaris*, as an understory species, is more severely overshadowed by the dense, tall canopy of Satinleaf tree island than it is at other tree islands with lower LAI and canopy height. Moreover, I found significant correlation between the sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* only in the prairie tree islands but not in the slough tree islands (Fig. 4.5). This again indicates that sap flux velocity for *Eugenia axillaris* was less dampened in the prairie tree islands than in the slough tree islands. Although both species are affected by some common factors such as water availability, air temperature, relative humidity, and solar radiation, slough tree islands can have dense canopy, and the understory species on average are exposed to

relatively constant conditions with low solar radiation and high relative humidity, and therefore show different patterns from *Coccoloba diversifolia*.

Average soil depth and soil pore water phosphorus concentration was the highest at Satinleaf island among the four monitored tree islands (Table. 4. 1). According to the chemohydrodynamic nutrient accumulation model, transpiration is the driving force for tree island nutrient accumulation (Wetzel, 2002a; Wang et al., 2010). Therefore, the high sap flux velocity of *Coccoloba diversifolia* and high nutrient accumulation in Satinleaf tree island are consistent with this model. Deep soil and more available P might have resulted in greater growth of the hardwood tree species on the tree island than on others. Therefore, higher transpiration-driven nutrient accumulation may reflect a positive feedback system.

The seasonal patterns of sap flux velocity during the year were most likely affected by the fluctuations in water level and climate conditions. However, in the multiple regression analysis, I did not find a clear linear pattern between climate conditions and sap flux velocity. Only solar radiation showed significant linear effects on sap flux velocity only in the slough tree islands (Table. 4.4). Most species I monitored showed a drop in sap flux velocity beginning in November 2009, with the minimum sap flux velocity in January 2010, and a constant increase afterwards during the entire dry season (Fig. 4.4). South Florida had an unusual cold spell during December 2009 and most of January 2010 (Fig. 4.2b); many evergreen hardwood trees partially lost their leaves because of this extreme weather condition. This might be an explanation for the decrease of sap flux velocity during the late wet season and the minimum values in January. Also, low solar radiation associated with the cold spell might also contribute to the low

transpiration (Fig. 4.2a). The increase of sap flux velocity during the dry season was opposite from what I expected before the study. There could be two reasons for this. First, after losing leaves during the cold spell in January, the hardwood tree species in Everglades tree islands produced new leaves to recover to normal photosynthetic activities, which resulted in the recovery of transpiration and water uptake. Second, the dry season of 2010 was extremely wet. The total precipitation From November 2009 to April 2010 was 54 cm (Fig. 4.2d), which is much higher than the average of 30-40 cm precipitation during a normal dry seasons (Duever et al., 1994). Water availability never appeared to be an issue for tree island plants, therefore it is most likely that high solar radiation (Fig. 4.2a) and low relative humidity (Fig. 4.2c) caused the increase of sap flux velocity from winter to spring. So, I conclude that although sap flux velocity was not determined by the climate factors across the entire year, it probably was episodically affected during part of the year, especially by extreme conditions.

Similar to the climate factors, monthly average water depth did now show any seasonal effect on sap flux velocity of *Eugenia axillaris* or *Coccoloba diversifolia*. The different locations, however, did have a significant effect on sap flux velocity of both *Eugenia axillaris* and *Coccoloba diversifolia* at slough and prairie tree islands (Fig. 4.6). *Coccoloba diversifolia* had the highest sap flux velocity in Satinleaf tree islands where marsh water depth was much higher than the other three tree islands during the entire year (Fig. 4.3, Fig. 4.6). This is consistent with what I expected because high water depth around the tree island means the plants would have higher water availability and therefore greater transpiration and higher sap flux velocity during dry spells than in islands surrounded by marshes with low water depth. *Eugenia axillaris*, however, had

lower sap flux velocity at the slough tree islands (Satinleaf island and SS37 island), than at the prairie tree islands (A4900 island and NP205 island), which is opposite to the expected pattern (Fig. 4.6). As an understory species that experiences high relative humidity and low solar radiation, *Eugenia axillaris* has a lower demand for water than *Coccoloba diversifolia*. Therefore, high marsh water depth in the slough is not as important a factor to *Eugenia axillaris* as to *Coccoloba diversifolia*. The high sap flux velocity of canopy species at the slough tree islands means that dense canopy retards the transpiration of *Eugenia axillaris*, which might explain its lower sap flux velocity found in slough tree islands than prairie tree islands.

Overall, my results show that sap flux velocity of Everglades tree island plants is affected by a combination of different factors. Climate factors did not show simple linear effects on sap flux velocity. Sap flux velocity is likely to be affected by the climate factors only episodically, especially by extreme conditions such as low temperature at the beginning of 2010 and the unusually high dry season precipitation. Similar to climate factors, seasonal changes of marsh water depth did not have any effect on sap flux velocity. However, different marsh water depth at slough and prairie landscapes had a significant effect on sap flux velocity. Therefore, I conclude tree island plant transpiration is affected by both regional climate factors and local water management practice. The understory species, *Eugenia axillaris* showed different patterns of sap flux velocity from the canopy species, *Coccoloba diversifolia*, especially in the slough tree islands. The understory species are more limited by solar radiation and relative humidity, and less limited by water availability than the canopy species.

Table 4.1: List of trees selected for sap flow sensor insertion at each tree island. Species name abbreviations represent: *Eugenia axillaris* (EUGAXI), *Coccoloba diversifolia* (COCDIV), *Myrsine floridana* (MYRFLO), *Sideroxylon foetidissimum* (SIDFOE), and *Chrysophyllum oliviforme* (CHYOLI). DBH values represent diameter at breast height measured at the time of sensor insertion. TDP values represent length of sap flow probe inserted.

Satinleaf (slough)			SS37 island (slough)			A4900 island (slough)			NP205 island (slough)		
Species	DBH (cm)	TDP (mm)	Species	DBH (cm)	TDP (mm)	Species	DBH (cm)	TDP (mm)	Species	DBH (cm)	TDP (mm)
EUGAXI	4.85	30	EUGAXI	2.91	10	EUGAXI	4.29	10	EUGAXI	4.85	10
EUGAXI	5.66	30	EUGAXI	3.15	10	EUGAXI	3.24	10	EUGAXI	3.72	10
EUGAXI	5.26	30	EUGAXI	2.91	10	EUGAXI	4.29	10	EUGAXI	4.53	10
EUGAXI	5.10	30	COCDIV	10.52	30	COCDIV	5.66	30	EUGAXI	3.40	10
EUGAXI	7.04	30	COCDIV	7.93	30	COCDIV	7.44	30	COCDIV	7.52	30
EUGAXI	5.26	30	COCDIV	5.58	30	COCDIV	5.99	30	COCDIV	8.66	30
COCDIV	9.55	30	COCDIV	6.47	30	COCDIV	5.42	30	COCDIV	8.90	30
COCDIV	10.11	30	MYRFLO	4.93	30	MYRFLO	2.99	10	COCDIV	7.52	30
COCDIV	5.91	30	MYRFLO	5.34	30	MYRFLO	4.45	10	SIDFOE	16.58	30
CHROLI	9.14	30	MYRFLO	4.85	10	MYRFLO	3.32	10	SIDFOE	21.19	30
CHROLI	7.85	30									
CHROLI	14.80	30									

Table 4.2: Correlation matrix of climate factors: Monthly average solar radiation (Wm^{-2}),
monthly average air temperature (°C), monthly total precipitation as rainfall (cm), monthly
average relative humidity (%). Statistics shown include Pearson's correlation coefficient (R), P
values, and sample size (n). Bold R values indicate significant correlation at α=0.05.

Source	Statistics	Solar radiation	Air temperature	Rainfall
Air temperature	R	**0.555**		
	P	0.039		
	n	14		
Rainfall	R	0.210	0.525	
	P	0.472	0.054	
	n	14	14	
Relative humidity	R	-0.074	**0.727**	**0.566**
	P	0.800	0.003	0.035
	n	14	14	14

Table 4.3: Canopy and soil attributes of monitored tree islands measured in 2009. Parameters include leaf area index (LAI), maximum canopy height (m), mean soil depth (m), and mean soil pore water phosphorus concentration (mg/L).

Region	Tree island	LAI	Maximum canopy height (m)	Mean (± 1 S.D.) soil depth (m)	Mean (± 1 SEM) soil pore water P concentration (mg/L)
Slough	Satinleaf	2.92	13	0.407 ± 0.176	6.47 ± 1.42
Slough	SS37	2.56	8	0.240 ± 0.136	1.34 ± 0.4
Prairie	A4900	2.57	11	0.134 ± 0.131	0.28 ± 0.03
Prairie	NP205	2.68	12	0.304 ± 0.170	0.34 ± 0.03

Table 4.4: Results of multiple regression analysis of climate factors: monthly average solar radiation (wm^{-2}) and monthly average relative humidity (%) on sap flux velocity of *Coccoloba diversifolia* (COCDIV)and *Eugenia axillaris* (EUGAXI) in slough and prairie tree islands. Statistics shown include degrees of freedom (df), *F* values, and P values of overall ANOVA, and standardized coefficient of determination (r^2), t values, and P values of each climate factor. Bold P values indicate significant regression at α=0.025 after Bonferroni correction.

a. Dependent Variable: COCDIV_slough

ANOVA	df	*F*	P	Coefficients Factors	r^2	t	P
Regression	2	3.957	0.054	solar radiation	0.661	2.787	**0.019**
Residual	10			relative humidity	0.147	0.618	0.550

b. Dependent Variable: EUGAXI_slough

ANOVA	df	*F*	P	Coefficients Factors	r^2	t	P
Regression	2	5.970	**0.020**	solar radiation	0.737	3.438	**0.006**
Residual	10			relative humidity	-0.012	-0.057	0.956

c. Dependent Variable: COCDIV_prairie

ANOVA	df	*F*	P	Coefficients Factors	r^2	t	P
Regression	2	1.429	0.295	solar radiation	0.478	1.558	0.158
Residual	8			relative humidity	0.269	0.876	0.407

d. Dependent Variable: EUGAXI_prairie

ANOVA	df	*F*	P	Coefficients Factors	r^2	t	P
Regression	2	0.882	0.451	solar radiation	0.420	1.297	0.231
Residual	8			relative humidity	0.152	0.471	0.650
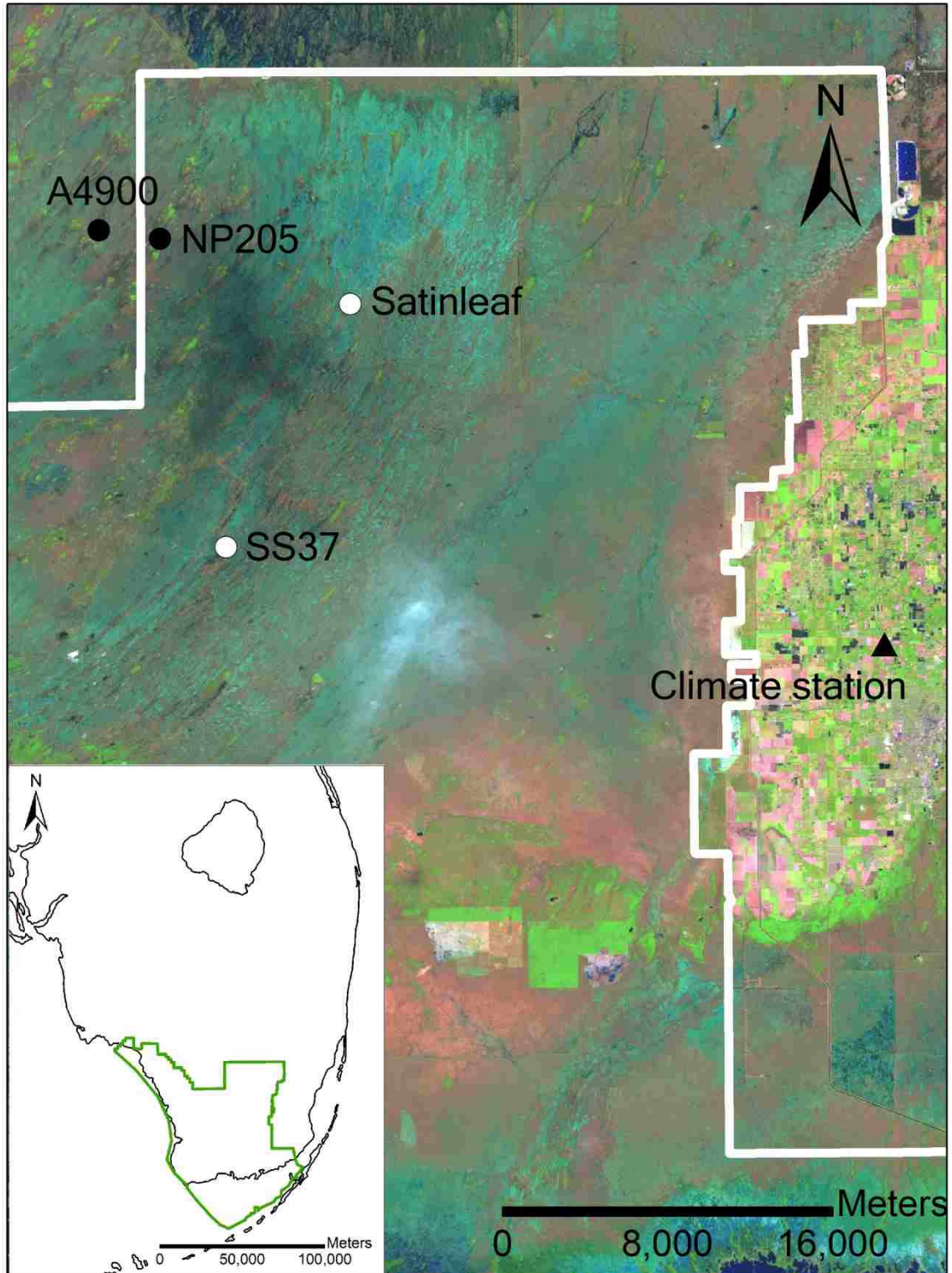
Figure 4.1: Map of a portion of south Florida Everglades. Bold lines represent the boundary of Everglades National Park. Selected tree islands marked as ○ (slough) and ● (prairie). Climate station marked as ▲.
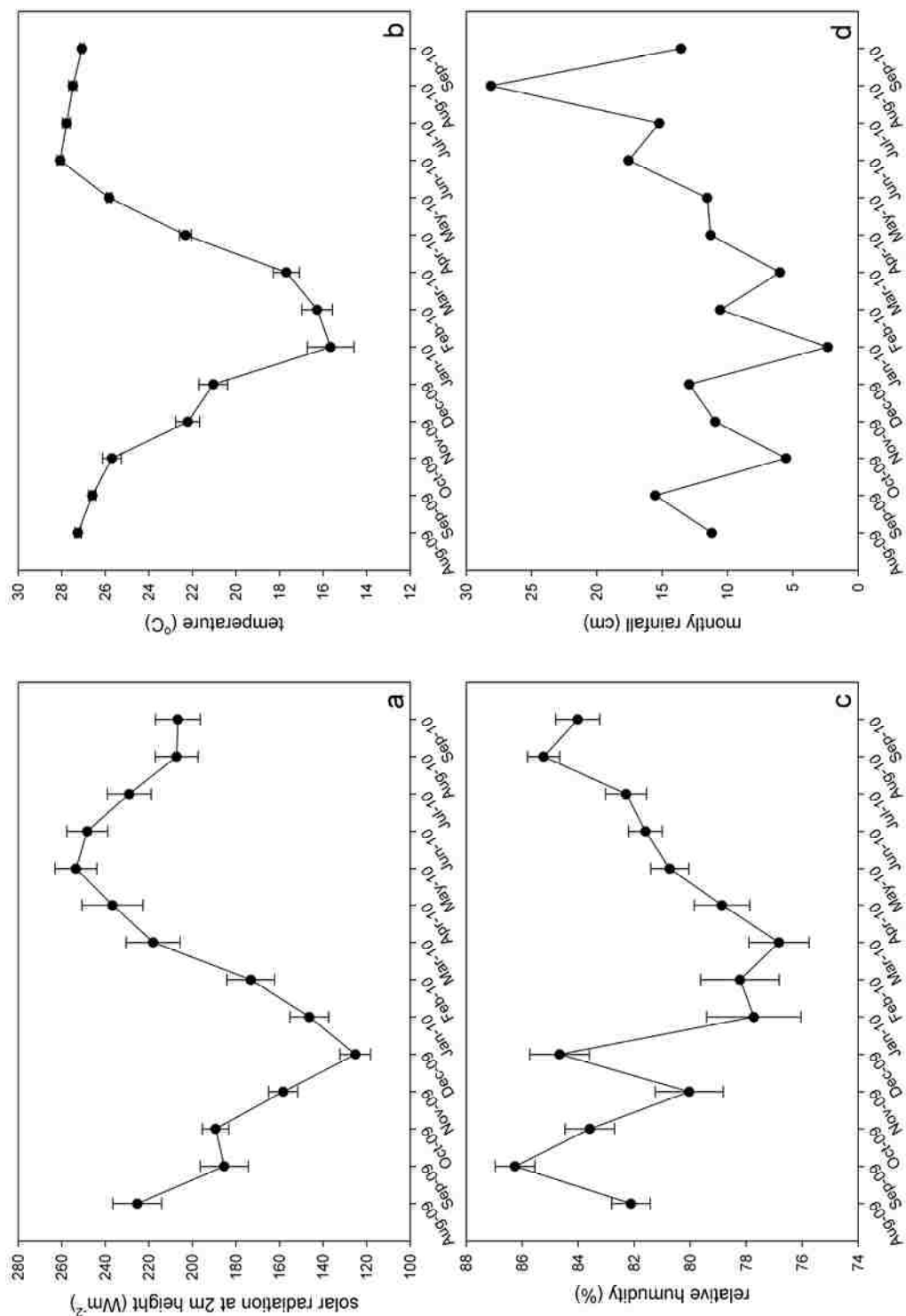
Figure 4.2: Climate parameters taken from FAWN (http://fawn.ifas.ufl.edu/data/) Homestead, FL station from Aug 1st 2009 to Sep 30th 2010: a. monthly average solar radiation measured at 2m height (wm-2), b. monthly average air temperature measured at 2m height (°C), c. monthly average relative humidity measured at 2m height (%), and d. monthly total precipitation as rainfall (cm). Error bars represent ± 1 SEM.
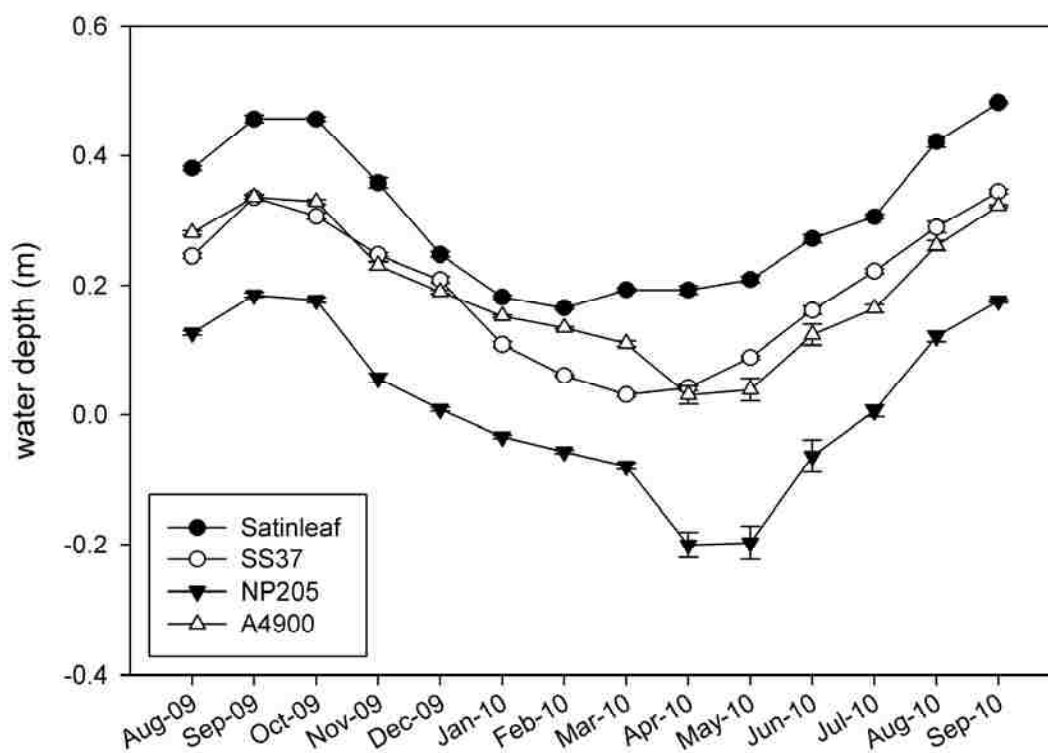
Figure 4.3: Monthly average marsh water level (m) as measured by Everglades Depth Estimation Network (EDEN, http://sofia.usgs.gov/eden/) of each monitoring tree island. Error bars represent ± 1 SEM.
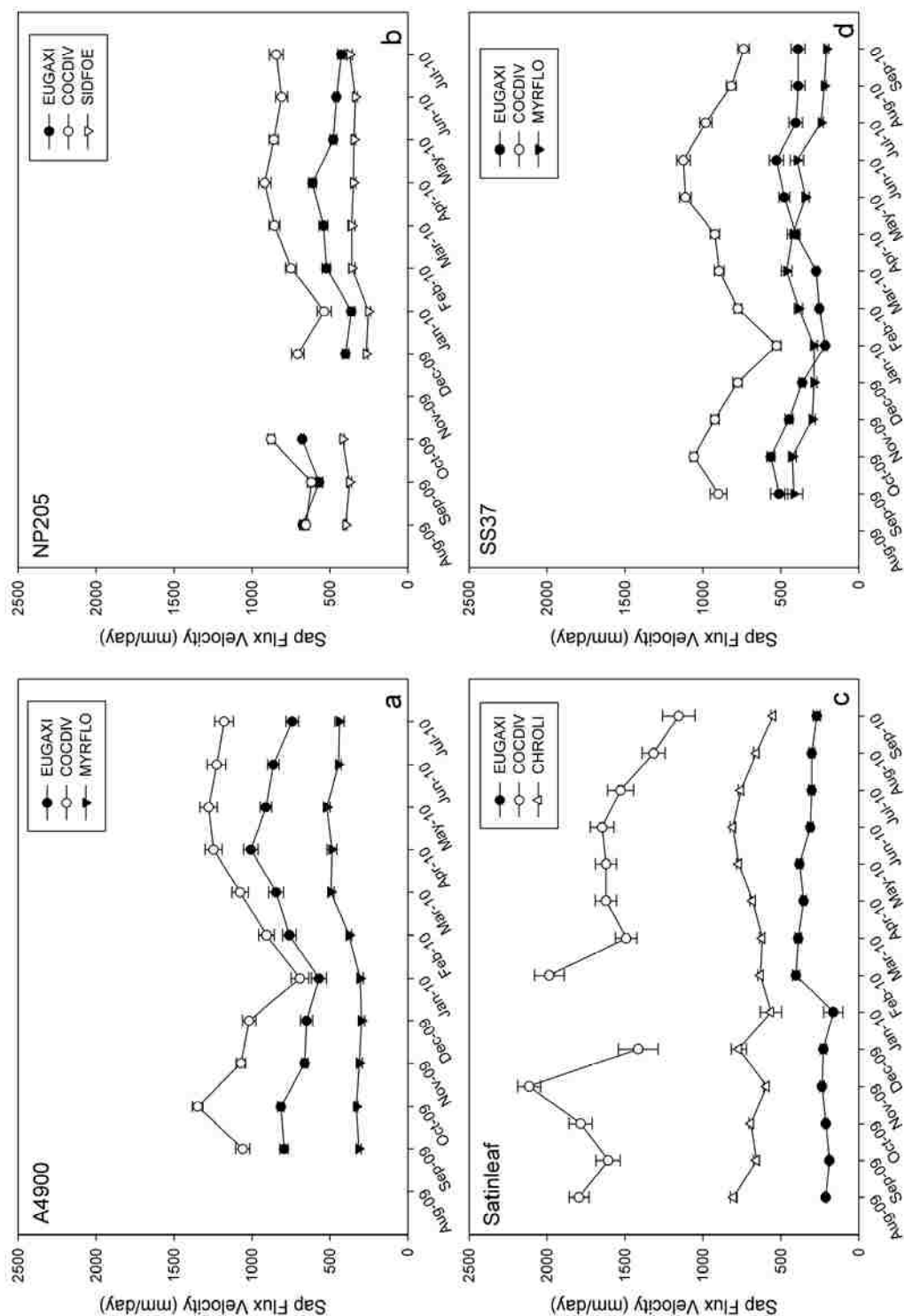
Figure 4.4: Monthly average daily sap flux velocity (mm/day) for *Eugenia axillaris* (●), *Coccoloba diversifolia* (○), *Myrsine floridana* (▼), *Sideroxylon foetidissimum* (▽), and *Chrysophyllum oliviforme* (△) in 4 monitored tree islands. Missing data points were because of data logger malfunction. Error bars represent ± 1 SEM.
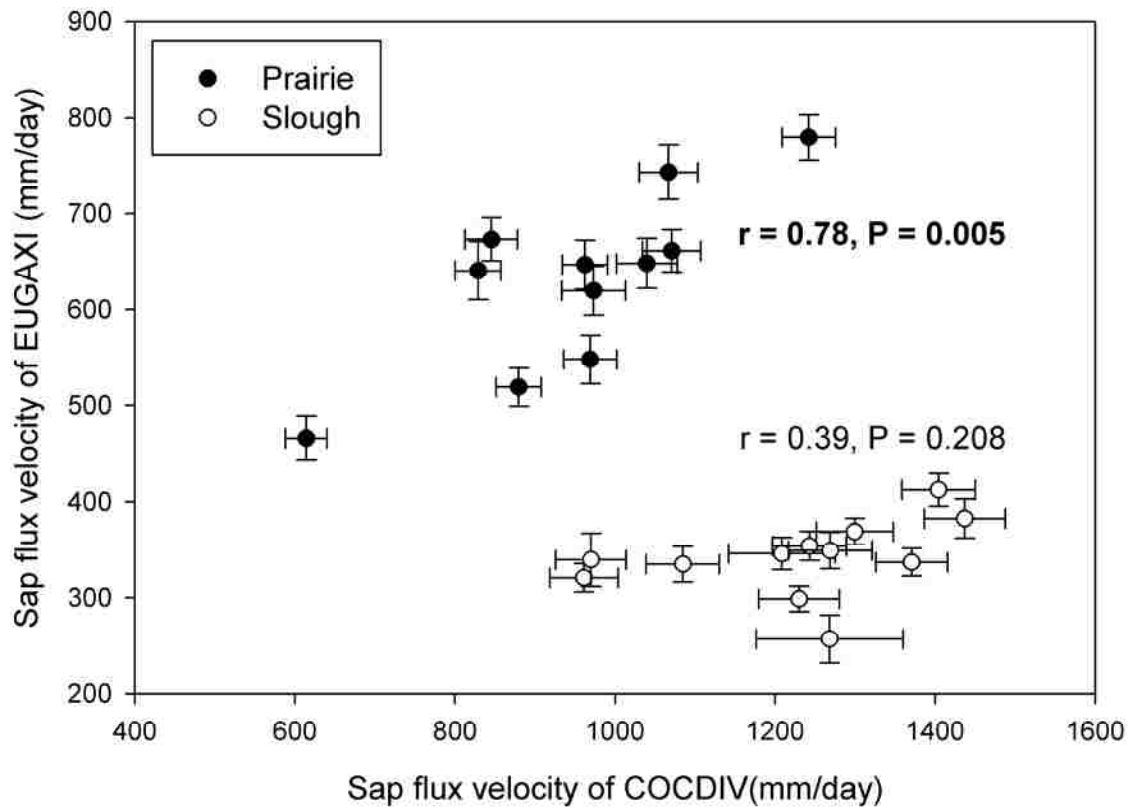
Figure 4.5: The correlation between monthly sap flux velocity of *Eugenia axillaris* and *Coccoloba diversifolia* in slough (○) and prairie (●) tree islands. Error bars in both directions represent ± 1 SEM. Statistics shown include Pearson's correlation coefficient (r) and P values. Bold r and P values represent significant correlation.
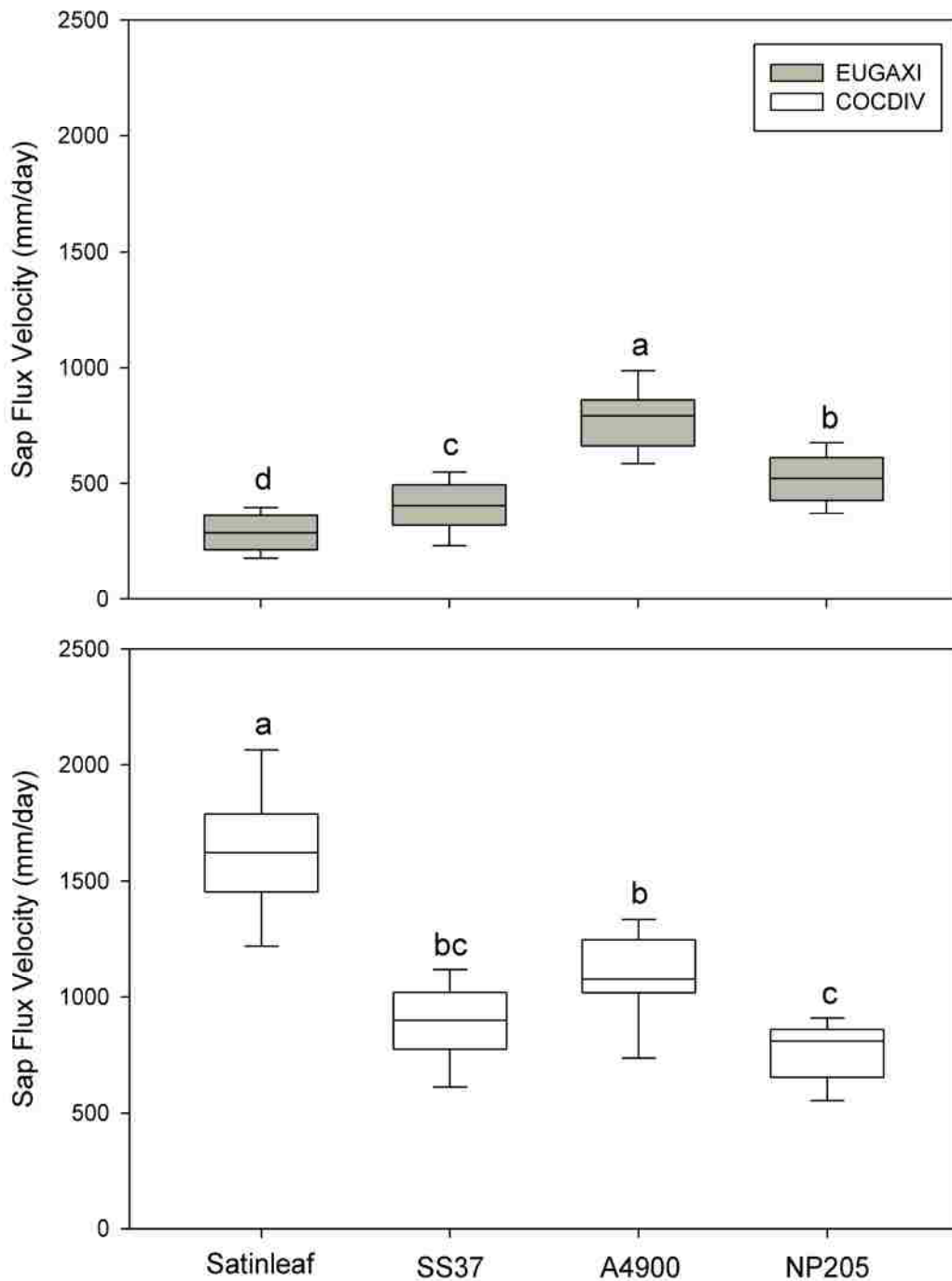
Figure 4.6: Box and whisker plot showing sap flux velocity of *Eugenia axillaris* (grey) and *Coccoloba diversifolia* (white) on four monitored tree islands. The line within the box represents the median, upper and lower boundary of the box represent the 75th to 25th percentiles, and the whiskers above and below the box represent the 95th and 5th percentiles. Boxes topped with same letters do not differ statistically by Tukey's post-hoc test following a one-way ANOVA .

Chapter 5

Overall Conclusions

The research in this dissertation examined water and nutrient status of woody plant species of Everglades tree island habitats in two distinct landscapes of slough and prairies. I assessed plant physiological attributes, including water deficit, canopy water content, transpiration rate, foliar and soil nutrient concentration, nutrient availability, etc. By looking at these variables, I was able to test two hypotheses associated with the chemohydrodynamic transpiration-driven nutrient accumulation model of tree islands in the Everglades (Wetzel et al., 2005). Tree islands located in the Shark River Slough, with marshes flooded during the entire year, were hypothesized to have higher water availability and higher nutrient availability than tree islands located in the nearby marl prairies, with marshes flooded only during the dry season. I tested these two hypotheses with different methods. Here I summarize the results of each method and discuss the how these results establish a link between hydroperiod, water use, and nutrient accumulation of Everglades tree islands.

Slough tree islands have higher water availability than prairie tree islands

I tested this hypothesis in three different methods: using foliar $\delta^{13}C$ as a proxy to look at dry season water deficit, using satellite remote sensed vegetation indices to assess canopy water content, and using Granier sap flow probes to measure transpiration directly. Foliar $\delta^{13}C$ was used as a proxy for water use efficiency. In the Everglades tree islands, plants generally have plenty of water available and thus low water use efficiency during the wet season. Therefore, an increase of foliar $\delta^{13}C$ from wet season to dry season means plants suffer plant water deficit during the dry season. I found that woody tree species

growing in prairie tree islands suffer from water deficit during the dry season, while those growing in slough tree islands do not (Chapter 2). According to Saha et al (2010b), tree island plants switch their water source from rain water to marsh associated groundwater during the dry season. In this case, slough tree island plants have more water available than prairie tree island plants because of high groundwater level associated with marsh surface water during the dry season; while in the prairies, the surrounding marsh dries out and ground water level is relatively low, resulting in less water available for prairie tree island plants than for slough tree island plants.

By using NDWI derived from SPOT 4 satellite images as an indicator for canopy water content, I found that the upland hammock woody plant communities in the slough tree islands have higher canopy water content than those in the prairie tree islands, especially during the dry season (Chapter 3). This result agrees with the findings from the foliar $\delta^{13}C$ analysis in Chapter 2. Unlike the prairie tree island plants, the slough tree island plants do not suffer from water deficit during the dry season, and therefore have higher canopy water content than prairie tree island plants.

In Chapter 2 and Chapter 3, I examined water availability of tree island plants at small and large scales, and they both support the hypothesis that slough tree island plants have higher water availability than prairie tree island plants. In Chapter 4, I tested this hypothesis with the direct approach of comparing transpiration rates of common tree species in different tree islands by measuring sap flux velocity of individual trees. I found that different marsh water depth in slough and prairie landscapes have a significant effect on tree island plant transpiration. The canopy species, *Coccoloba diversifolia* has higher transpiration rate in slough tree islands than in prairie tree islands; while the understory

species, *Eugenia axillaris* has lower transpiration rate in slough tree islands than in prairie tree islands (Chapter 4). The high transpiration of *Coccoloba diversifolia* in slough tree islands, as well as high LAI and high canopy height, might be explained by less limitation of water availability in the slough landscape. Further, transpiration of *Eugenia axillaris* is dampened by the dense canopy and is much lower than that of *Coccoloba diversifolia*. I did not find, however, significant effects of seasonal variation of marsh water depth on tree island plant transpiration, which might be partly caused by an unusually wet dry season in 2010 when the sap flux velocity data were collected.

Slough tree islands have higher nutrient availability than prairie tree islands

Along with tree island water status, the other aspect of the chemohydrodynamic transpiration-driven nutrient accumulation model that I examined is tree island nutrient status. Again, I tested this hypothesis with four different methods: using foliar $\delta^{15}N$ as a proxy of P availability at the community level of each tree island, measuring soil total P concentration of each island, using anion exchange resin bags to measure soil pore water P concentration directly, and using foliar N/P ratio as an indicator of N or P limitation to plants.

I used Island average foliar $\delta^{15}N$ as a proxy of P availability at the community level, and found that slough tree islands generally have higher P availability than prairie tree islands (Chapter 2). Soil total P concentration showed the same pattern; slough tree islands have much higher soil total P than prairie tree islands (Chapter 2). I also measured soil pore water P concentration to assess P in available format for plant uptake. I found the highest soil pore water P concentration in Satinleaf tree island, which is a slough tree island

(Chapter 4). These results support my hypothesis that slough tree islands have more P available than prairie tree islands.

I also measured N and P concentration in leaf tissue and used foliar N/P ratio as an indicator of N or P limitation at the species level of each tree island. I found that for the same species that grow in both slough and prairie tree islands, they show P limitation in the prairie tree islands but no P limitation in the slough tree islands (Chapter 2). Again, this indicates that prairie tree islands have lower P availability than slough tree islands and therefore P is limiting plant growth in prairie tree islands.

A chemohydrodynamic link between water and nutrient status of Everglades tree islands

As well as testing these two hypotheses separately, in this dissertation research, I also tried to establish a link between tree island plant water use and nutrient accumulation. I have shown that island average NDWI, the proxy for community level water availability, is positively correlated with island average foliar δ^{15}N, the proxy for community level P availability (Chapter 3). This supports the transpiration-driven nutrient accumulation model that tree islands with high water availability can accumulate more P than tree islands with low water availability. I found that Satinleaf tree island, which is a slough tree island, has the highest transpiration rates in canopy species among all four islands studied in Chapter 4 as well as highest soil pore water P concentration. Satinleaf island also has the greatest soil depth, LAI and canopy height among the four monitored tree islands (Chapter 4). These findings indicate a possible positive feedback mechanism that high transpiration-driven nutrient accumulation leads to high soil sedimentation and P

availability, which in turn results in enhanced growth of woody tree species and elevated

transpiration in the future.

Techniques introduced in this research and possible applications

In this dissertation research, I studied the tree island habitat, which is the most remote

habitat in the Everglades ecosystem. It is extremely difficult to access these study sites,

most of the islands are only approachable by helicopter, which limits the equipment in

the study and requires high input of both funds and labor. Therefore, in this research, I

introduced a variety of proxies and remotely-monitored measurements which facilitated

monitoring of the status of these islands.

I used two stable isotope proxies in this research. I showed that foliar $\delta^{15}N$ is a superior

index for long-term, community level measurements of P availability than soil or foliar P

concentrations that often show a large variation with time and sampling locations

(Chapter 2). Similarly, comparison of foliar $\delta^{13}C$ between the wet and dry seasons

provides an easy measurement of the annual pattern of plant water deficit. In study sites

like the tree islands, these proxies are much more practical than continuous

measurements of soil or foliar P concentration and plant water use efficiency, and can

therefore be used in future long-term monitoring studies.

Satellite remote sensing analysis has been used most commonly in studies asking

generalized questions at the landscape scale. In the Everglades, previous remote sensing

studies mostly focused on the freshwater marshes. In this research, I applied this

technique specifically in tree island habitats, which are relatively small objects for remote

sensing studies (Chapter 3). By combining two types of aerial surveys, satellite and

orthophotos, I show the potential of using remote sensing analysis to solve specific questions in the future.

In this study, I also performed measurements of sap flux velocity. I was able to set up the system of data transfer so that I could monitor the data logger remotely by wireless access (Chapter 4). In this way, one can have real time measurements of remote study sites for long-term monitoring purposes.

Future directions

Using the above techniques, this dissertation research shows the potential for a long term monitoring program of the Everglades tree islands. Similar to the water level and weather stations of the EDEN network in the Everglades marshes and canals, one can have monitoring stations in the tree islands that measure real-time transpiration data of woody plants. Carbon and Nitrogen stable isotope ratios can be measured twice a year to keep a long term database of dry season and wet season water and nutrient status of tree islands. One can also expand the satellite remote sensing surveys, possibly including the degraded tree islands in the Water Management Areas north of Everglades National Park in order to compare healthy tree islands with the disturbed ones.

In this dissertation research, I tested the two hypotheses regarding water and nutrient availability associated with the chemohydrodynamic transpiration-driven nutrient accumulation model, and established a link between hydroperiod and water and nutrient status of tree island habitats. However, I was not able to draw any conclusion about a causal relationship between water availability and nutrient accumulation. In order to answer the question regarding causality, one can possibly conduct some manipulative experiments at the Everglades laboratory: the Loxahatchee Impoundment Landscape

Assessment (LILA) in Boynton Beach, Florida. LILA is a manmade model of the

Everglades ecosystem with human-transpiration-drivenconstructed features including tree

islands, ridges and sloughs. Hydrology is completely human controlled in LILA. One can

reconstruct the slough and prairie tree islands in LILA by controlling the marsh

hydroperiod, and keep the other physical attributes and plant community composition the

same between two groups. Plant water use patterns and nutrient status can then be

monitored. Although the nutrient accumulation process takes thousands of years, one can

use isotopic tracers to trace the process of mineral nutrient uptake and accumulation in

the tree islands.

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