

2010

Landscape patterns of community structure, biomass and net primary productivity of mangrove forests in the Florida Coastal Everglades as a function of resource, regulators, hydroperiod, and hurricane disturbance

Edward Castaneda

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_dissertations



Part of the [Oceanography and Atmospheric Sciences and Meteorology Commons](#)

Recommended Citation

Castaneda, Edward, "Landscape patterns of community structure, biomass and net primary productivity of mangrove forests in the Florida Coastal Everglades as a function of resource, regulators, hydroperiod, and hurricane disturbance" (2010). *LSU Doctoral Dissertations*. 2823.

https://digitalcommons.lsu.edu/gradschool_dissertations/2823

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

**LANDSCAPE PATTERNS OF COMMUNITY STRUCTURE, BIOMASS AND NET
PRIMARY PRODUCTIVITY OF MANGROVE FORESTS IN THE FLORIDA
COASTAL EVERGLADES AS A FUNCTION OF RESOURCES, REGULATORS,
HYDROPERIOD, AND HURRICANE DISTURBANCE**

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
Edward Castaneda
B.S. Universidad Jorge Tadeo Lozano, 1998
M.S. University of Louisiana at Lafayette, 2003
August 2010

ACKNOWLEDGEMENTS

This study was conducted as part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program funded by the National Science Foundation (Grant #DBI-0620409).

I am deeply grateful to my mentor Dr. Robert R. Twilley for his guidance, support, and encouragement during the development of my mangrove research. I would also like to thank my committee members, Dr. John W. Day, Dr. John R. White, Dr. Victor H. Rivera-Monroy, and Dr. Brian Marx for their valuable guidance and support. I would like to express my sincere appreciation to Dr. Victor H. Rivera-Monroy for his friendship, support, dedication, and valuable advice during these past years of my career.

Special thanks to Florida International University, center of the FCE-LTER program and the Florida Bay Interagency Science Center-Everglades National Park for their logistic support during the study. I also thank Dan Bond, Leigh Anne Sharp, Jennifer Overton, Matthew Heels, Leander J. Lavergne, Peter Lenaker, Greg Losada, Dr Carlos Coronado-Molina, and Dr. Kim de Mutsert for their valuable assistance during field trips and laboratory work.

Finally, I dedicate this dissertation to my parents Eduardo and Julia for their continued love, wisdom, support, and encouragement in all my endeavors over the years.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	v
CHAPTER 1. INTRODUCTION.....	1
REFERENCES.....	4
CHAPTER 2. PATTERNS OF ROOT DYNAMICS IN MANGROVE FORESTS ALONG NUTRIENT GRADIENTS IN THE FLORIDA COASTAL EVERGLADES, USA.....	8
INTRODUCTION.....	8
MATERIALS AND METHODS.....	14
Study Sites.....	14
Root Biomass.....	16
Root Productivity.....	17
Root Nutrient Content.....	18
Statistical Analyses.....	19
RESULTS.....	20
Root Biomass.....	20
Root Productivity.....	24
Root Turnover and Longevity.....	26
Root Nutrient Content.....	28
DISCUSSION.....	30
Landscape Patterns of Root Allocation.....	30
Simulation Models of Root Allocation.....	51
SUMMARY.....	55
REFERENCES.....	56
CHAPTER 3. SEDIMENT AND NUTRIENT DEPOSITION ASSOCIATED WITH HURRICANE WILMA IN MANGROVES OF THE FLORIDA COASTAL EVERGLADES.....	67
INTRODUCTION.....	67
MATERIALS AND METHODS.....	71
Study Sites.....	71
Hydrology and Storm Surge.....	74
Sediment Core Collection and Analyses.....	74
Statistical Analyses.....	76
RESULTS.....	77
Hydrology and Storm Surge.....	77
Soil and Sediment Properties.....	78
DISCUSSION.....	88
Storm Surge and Soil Vertical Accretion.....	88
Soil Nutrient Inputs.....	91
SUMMARY.....	95
REFERENCES.....	96

CHAPTER 4. PATTERNS OF COMMUNITY STRUCTURE AND TOTAL NET PRIMARY PRODUCTIVITY OF MANGROVE FORESTS IN THE FLORIDA COASTAL EVERGLADES, USA.....	101
INTRODUCTION.....	101
MATERIALS AND METHODS.....	107
Experimental Design.....	107
Hydroperiod.....	108
Soil Properties.....	109
Forest Structure, Aboveground Biomass and Wood Production.....	110
Litterfall Production.....	112
Belowground Biomass and Production.....	112
Statistical Analyses.....	113
RESULTS.....	114
Hydroperiod.....	114
Soil Properties.....	115
Forest Structure, Aboveground Biomass and Wood Production.....	123
Litterfall Production.....	131
Total Annual Net Primary Productivity (NPP _T).....	137
DISCUSSION.....	140
SUMMARY.....	148
REFERENCES.....	150
CHAPTER 5. SUMMARY.....	158
APPENDIX A. LETTER OF PERMISSION.....	163
APPENDIX B. HYDROPERIOD IN MANGROVE FORESTS OF THE FLORIDA COASTAL EVERGLADES.....	167
APPENDIX C. SUMMARY OF ABOVEGROUND BIOMASS, LITTERFALL, AND WOOD PRODUCTION OF NEOTROPICAL MANGROVE FORESTS.....	168
VITA.....	171

ABSTRACT

Spatial and temporal patterns of mangrove vegetation in the Florida Coastal Everglades (FCE) reflect a major interplay of resources, regulators and hydroperiod gradients. I investigated landscape patterns of community structure, biomass and NPP of mangroves along two FCE estuaries: Shark River and Taylor River. I also evaluated whether pulsing events such as Hurricane Wilma are significant to soil nutrient inventories and vertical accretion of mangroves in FCE. There was a higher forest structural complexity of mangroves in Shark River relative to Taylor River. The biomass root:shoot ratio was 17 times higher in Taylor River relative to Shark River, indicating that scrub mangroves allocate a larger proportion of their total biomass to belowground. Root turnover rates consistently decreased as the root size classes increased from fine to coarse roots, indicating differences in longevity. Fine root biomass was negatively correlated with soil P density and frequency of inundation. Average total NPP was twice in Shark River compared to Taylor River. Aboveground production accounted for 68% (Shark River) and 42% (Taylor River) of the total NPP. Total root production contributed 32% (Shark River) and 58% (Taylor River) of the total. Sediment deposition from Wilma decreased with distance inland at each site. Vertical accretion resulting from this hurricane was one order of magnitude greater than the long-term accretion rate. Total P inputs from hurricane sediments were equivalent to twice the average soil P density (0.19 mg cm^{-3}). Results from this study indicate that scrub mangroves of Taylor River have adapted to P limitation and flooded hydroperiods by allocating more biomass and production belowground relative to aboveground. Allochthonous mineral inputs from Hurricane Wilma represent a significant source of sediment to vertical accretion rates and nutrient resources in mangroves of southwestern Everglades. This source of P is significant to forest development due to the P-limited condition of this carbonate

ecosystem. This information on how mangrove biomass and NPP are distinctly allocated between above- and belowground in response to environmental gradients across the FCE will be used to develop carbon budgets before and after hurricanes and to improve our understanding of carbon dynamics in neotropical mangrove forests.

CHAPTER 1

INTRODUCTION

Vegetation patterns in forested and wetland ecosystems result from the interaction of complex environmental gradients and natural disturbances (i.e., hurricanes, fire) that operate at different spatial and temporal scales, creating an array of either monospecific or mixed communities across the continuum landscape, depending on the competitive ability of the species (Huston 1994). Mangrove forests thriving along tropical and subtropical coastlines are ideal for investigating vegetation patterns because their position along the intertidal zone is influenced by sharp environmental gradients, resulting in different patterns of community structure and productivity (Lugo and Snedaker 1974). On a global perspective, the distribution of mangrove species and aboveground biomass is correlated with gradients in climatic factors including temperature, precipitation, and solar radiation (Blasco 1984; Twilley et al. 1992; Saenger and Snedaker 1993). Variability in the geophysical processes (river, tide, and waves) within a coastal landform control the basic patterns in mangrove forest structure and productivity and determine in large part the network in energy flow and material cycling (Thom 1982, Twilley 1995; Woodroffe 2002). At the local scale, ecological processes of resource competition (light and nutrients) and tolerance to regulator gradients (salinity and sulfide) control vegetation patterns depending on site-specific conditions of topography and hydrology, resulting in the development of distinct ecological types of mangroves such as riverine, fringe, basin, scrub, and overwash (Lugo and Snedaker 1974). The interaction and degree of these resources and regulators along with hydroperiod gradients across the intertidal zone define a constraint envelope for determining the structure and productivity of mangrove wetlands within a coastal setting (Twilley and Rivera-Monroy 2005). The significance of these three environmental gradients in controlling mangrove vegetation patterns in neotropical regions has been extensively

demonstrated with field and greenhouse studies (Lugo and Snedaker 1974; McKee 1993; Chen and Twilley 1999b; Feller et al. 2003a, b; Cardona-Olarte et al. 2006; Castañeda-Moya et al. 2006; Krauss et al. 2006).

Hurricanes and tropical storms are also a common feature in the Caribbean-Gulf of Mexico region, and their influence in the community structure and function of tropical and subtropical forest ecosystems have been documented in the literature (Michener et al. 1997; Lugo 2000, 2008). Mangrove forests are more susceptible to the direct influence of these pulsing events due to their position in the intertidal zone (Sherman et al. 2001; Piou et al. 2006). Despite their low floristic complexity relative to rainforests, neotropical mangrove forests are highly resilient to natural disturbances such hurricanes, and have developed life history traits that allow trajectories in ecosystem structure and function at decadal time scales depending on the frequency and intensity of the storm (Smith et al. 1994; Alongi 2008). The ecological effects of these pulsing events on landscape patterns of forest structure and development in neotropical mangrove forests is well documented in the literature (Smith et al. 1994, 2009; Ross et al. 2006; Ward et al. 2006; Zhang et al. 2008). Yet, few studies have documented the positive role of hurricane deposition in controlling soil vertical accretion and nutrient biogeochemistry of mangroves in zones of high disturbance frequency such as south Florida (Whelan et al. 2009; Castañeda-Moya et al. 2010).

The Florida Coastal Everglades (FCE) in south Florida is a unique ecosystem characterized with a high recurrence of tropical storms and hurricanes (Duever et al. 1994) and strong environmental gradients (Fourqurean et al. 1992; Koch 1997; Chen and Twilley 1999b; Childers et al. 2006; Ewe et al. 2006). These conditions determine different habitats and landscape vegetation patterns from freshwater dominated marshes, to different mangrove

ecotypes (i.e., riverine and scrub) in the estuarine region, and seagrass communities in Florida Bay (Ewe et al. 2006). Therefore, this ecosystem offers an opportunity to study landscape mangrove vegetation patterns in response to environmental gradients and hurricane disturbances.

The goal of this research is to determine the spatial and temporal landscape patterns of community structure, above- and belowground biomass and net primary productivity (NPP) of mangrove forests, and to evaluate the environmental factors controlling these patterns along two FCE estuaries, Shark River and Taylor River. In addition, the passage of Hurricane Wilma across FCE in October 2005 provided an excellent opportunity to evaluate the role of these pulsing events on community structure, productivity, and soil nutrient biogeochemistry. In this study, I only report on the quantity of sediment deposition and changes in soil nutrient pools across FCE mangroves to evaluate whether pulsing events such as Hurricane Wilma are significant to soil nutrient inventories and vertical accretion of mangrove forests in FCE.

In Chapter 2, I evaluated the spatial and temporal patterns of root dynamics across FCE mangroves. I characterized the distribution of root biomass and productivity with soil depth and root size distribution. I also evaluated how resource and hydroperiod gradients control belowground biomass allocation, productivity, and root turnover across FCE mangroves.

In Chapter 3, I quantified storm surge and sediment and nutrient deposition from Hurricane Wilma. I characterized the physicochemical properties of storm-derived deposits and compared to those of mangrove soils. I also evaluated the role of hurricane sediment deposition in maintaining landscape patterns of soil fertility and vertical accretion of mangroves in FCE.

In Chapter 4, I evaluated the long-term spatial and temporal patterns of community structure and above- and belowground biomass and total (litterfall, wood, roots) NPP along Shark River and Taylor River. I also characterized the long-term spatial and temporal variation

in mangrove soil properties and hydroperiod along these two estuaries, and evaluated what are the relative factors controlling rates of biomass and total NPP between these two areas.

Finally, Chapter 5 provides a synthesis of the landscape patterns of mangrove community structure and above- and belowground biomass and productivity in response to the interaction of environmental gradients, and the role that hurricanes play in the nutrient biogeochemistry and vertical accretion of mangroves in the Florida Everglades.

REFERENCES

- Alongi, D.M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science* 76: 1-13.
- Blasco, F. 1984. Climatic factors and the biology of mangrove plants. In *The Mangrove Ecosystem Research Methods*, eds. S. C. Snedaker and J. G. Snedaker, 18-35. Paris, France: UNESCO.
- Cardona-Olarte, P., R.R. Twilley, K.W. Krauss, and V.H. Rivera-Monroy. 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. *Hydrobiologia* 569: 325-341.
- Castañeda-Moya, E., V.H. Rivera-Monroy, and R.R. Twilley. 2006. Mangrove zonation in the dry life zone of the Gulf of Fonseca, Honduras. *Estuaries and Coasts* 29: 751-764.
- Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, K. Zhang, S.E. Davis, III., and M. Ross. 2010. Sediment and nutrient deposition associated with Hurricane Wilma in mangroves of the Florida Coastal Everglades. *Estuaries and Coasts* 33: 45-58.
- Chen, R., and R.R. Twilley. 1999b. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955-970.
- Childers, D.L., J.N. Boyer, S.E. Davis, C.J. Madden, and D.T. Rudnick. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades. *Limnology and Oceanography* 51: 602-616.
- Duever, M.J., J.F. Meeder, L.C. Meeder, and J.M. McCollom. 1994. The climate of South Florida and its role in shaping the Everglades ecosystem. In *Everglades: The Ecosystem and Its Restoration*, eds. S. M. Davis and J. C. Ogden, 225-248. Delray Beach, Florida: St. Lucie Press.

- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, D. Iwaniec, V. Rivera-Monroy, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along tow freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569: 459-474.
- Feller, I.C., K.L. McKee, D.F. Whigham, and J.P. O'Neill. 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145-175.
- Feller, I.C., D.F. Whigham, K.L. McKee, and C.E. Lovelock. 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia* 134: 405-414.
- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.
- Huston, M.A. 1994. *Biological Diversity*. Cambridge University Press, Cambridge.
- Koch, M.S. 1997. *Rhizophora mangle* L. seedling development into the sapling stage across resource and stress gradients in subtropical Florida. *Biotropica* 29: 427-439.
- Krauss, K.W., T.W. Doyle, R.R. Twilley, V. Rivera-Monroy, and J.K. Sullivan. 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia* 569: 311-324.
- Lugo, A.E. 2000. Effects and outcomes of Caribbean hurricanes in a climatic change scenario. *The Science of the Total Environment* 262: 243-251.
- Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology* 33: 368-398.
- Lugo, A.E., and S.C. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5: 39-64.
- McKee, K.L. 1993. Soil physicochemical patterns and mangrove species distribution - reciprocal effects? *Journal of Ecology* 81: 477-487.
- Michener, W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climatic change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770-801.
- Piou, C., I.C. Feller, U. Berger, and F. Chi. 2006. Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. *Biotropica* 38: 365-374.

- Ross, M.S., P.L. Ruiz, J.P. Sah, D.L. Reed, J. Walters, and J.F. Meeder. 2006. Early post-hurricane stand development in fringe mangrove forests of contrasting productivity. *Plant Ecology* 185: 283-297.
- Saenger, P., and S.C. Snedaker. 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* 96: 293-299.
- Sherman, R.E., T.J. Fahey, and P. Martinez. 2001. Hurricane impacts on a mangrove forest in the Dominican Republic: Damage patterns and early recovery. *Biotropica* 33: 393-408.
- Smith, T.J.I., G.H. Anderson, K. Balentine, G. Tiling, G.A. Ward, and K.R.T. Whelan. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: Sediment deposition, storm surges and vegetation. *Wetlands* 29: 24-34.
- Smith, T.J.I., M.B. Robblee, H.R. Wanless, and T.W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44: 256-262.
- Thom, B.G. 1982. Mangrove ecology - a geomorphological perspective. In *Mangrove Ecosystems in Australia*, eds. B. F. Clough, 3-17. Canberra: Australian National University Press.
- Twilley, R.R. 1995. Properties of mangrove ecosystems related to the energy signature of coastal environments. In *Maximum power: the ideas and applications of H. T. Odum*, eds. C. A. S. Hall, 43-62. Niwot, Colorado: University Press of Colorado.
- Twilley, R.R., R.H. Chen, and T. Hargis. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air, and Soil Pollution* 64: 265-288.
- Twilley, R.R., and V. Rivera-Monroy. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research* 40: 79-93.
- Ward, G.A., T.J.I. Smith, K.R.T. Whelan, and T.W. Doyle. 2006. Regional processes in mangrove ecosystems: spatial scaling relationships, biomass, and turnover rates following catastrophic disturbance. *Hydrobiologia* 569: 517-527.
- Whelan, K.R.T., T.J.I. Smith, G.H. Anderson, and M.L. Ouellette. 2009. Hurricane Wilma's impact on overall soil elevation and zones within the soil profile in a mangrove forest. *Wetlands* 29: 16-23.
- Woodroffe, C.D. 2002. *Coasts: Form, Process, Evolution*. Cambridge University Press, Cambridge, UK.
- Zhang, K., M. Simard, M.S. Ross, V. Rivera-Monroy, P. Houle, P.L. Ruiz, R.R. Twilley, and K.R.T. Whelan. 2008. Airborne laser scanning quantification of disturbances from

hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA.
Sensors 8: 2262-2292.

CHAPTER 2

PATTERNS OF ROOT DYNAMICS IN MANGROVE FORESTS ALONG NUTRIENT GRADIENTS IN THE FLORIDA COASTAL EVERGLADES, USA

INTRODUCTION

Plants respond to resource imbalance by allocating new biomass to acquisition of resources that most strongly limit growth (Chapin et al. 1987; Gleeson and Tilman 1992; Bazzaz 1997). For instance, plants will allocate more biomass to aboveground structures compare to belowground roots in response to intense shading or herbivory (Chapin 1980; Bloom et al. 1985). The resulting decrease in root:shoot ratio reduces carbon stress and returns carbon and nutrient reserves to a balance more favorable for growth (Chapin et al. 1987). Conversely, in soil nutrient-poor environments plants tend to allocate more biomass to roots to acquire limiting resources from within the soil, leading to a more favorable carbon:nutrient balance (Grime 1977; Chapin 1980; Tilman 1985; Chapin et al. 1987). Accordingly, plants have the ability to adjust biomass allocation to roots or shoots in response to limitation in resource availability. This physiological and morphological plasticity avoid excess foraging for a non-limiting resource and maximize efficiency for capturing the most strongly limiting resource (Gleeson and Tilman 1992). We define phenotypic plasticity as the ability of plants to modify their morphology or physiology in response to changes in environmental conditions (Schlichting 1986). These plastic responses represent changes in typical developmental sequences due to the interaction of the plant's genotype with the environment, and thus are an adaptive mechanism under genetic control (Schlichting 1986).

Biomass allocation can also have significant importance to ecological processes associated with carbon budgets of ecosystems (Nadelhoffer et al. 1985; Jackson et al. 1997; Bouillon et al. 2008). Belowground biomass allocation in forest and wetland ecosystems is

considered significant to soil formation and vertical accretion (Chen and Twilley 1999a; Turner et al. 2004; McKee et al. 2007), nutrient cycling (Nadelhoffer et al. 1985), and nutrient uptake, transport, and storage (Eissenstat et al. 2000). Moreover, the contribution of roots to the global carbon budget and nutrient economy of forest and wetland ecosystems is significant due to the high proportion of biomass allocated belowground relative to aboveground tissues (Nadelhoffer and Raich 1992; Vogt et al. 1996; Chmura et al. 2003; Bouillon et al. 2008). It is estimated that fine roots account for 10-30% of total forest tree biomass (Santantonio et al. 1977; Sanford and Cuevas 1996) and from 30 to 50% of total net primary production in forest ecosystems (Vogt 1991; Jackson et al. 1997). Thus, resource limitation of forested ecosystems may be significant in the ecological patterns of carbon storage and soil formation as to how plants respond differently to short- and long-term changes in nutrient resources due to background soil conditions and species-specific evolutionary life history traits (Chapin et al. 1986).

Mangroves are forested wetlands that are adapted to a variety of environmental settings characterized by high stress conditions associated with gradients in resources, regulators, and hydroperiod (Twilley and Rivera-Monroy 2005). Mangrove species have the ability to adjust morphological and physiological traits in response to the interaction of these gradients as a mechanism that determines trajectories in ecosystem structure and function across the coastal landscape, depending of the degree of stress among these three gradients (Ellison 2002; Feller et al. 2003a, 2007; Lovelock et al. 2004; Twilley and Rivera-Monroy 2009).

Simulation models of organic matter content and bulk density suggest that root production is a critical process in controlling organic matter accumulation and distribution in mangrove soils in the neotropics (Chen and Twilley 1999a). These models also predicted that variations in root turnover have a more significant effect on these soil characteristics rather than

variation in litterfall, as has been observed in a few empirical studies (McKee and Faulkner 2000; Middleton and McKee 2001). Mangroves are highly adapted species that can allocate a large proportion of their total biomass to belowground in response to nutrient limitation (Saenger 1982; Lugo 1990; Komiyama et al. 2000). Estimates of root biomass in old world mangrove forests indicate that root allocation accounts for up to 40-60% of total standing biomass (Briggs 1977; Komiyama et al. 1987; Mackey 1993; Alongi et al. 2003; Comley and McGuinness 2005; Khan et al. 2007; Tamooch et al. 2008). In neotropical mangrove forests, few data exist to describe root biomass allocation (Golley et al. 1962; Golley et al. 1975; Fiala and Hernandez 1993; Sherman et al. 2003; Giraldo 2005), although root biomass allocation estimates in mangrove forests of Florida and Panama are 50% of the total biomass (Golley et al. 1962; Golley et al. 1975). Few direct measurements of root production and turnover are also scarce (McKee and Faulkner 2000, Cahoon et al. 2003; Giraldo 2005; McKee et al. 2007), and thus there is no clear pattern with nutrient gradients. But in general there are few complete estimates of root biomass, productivity and turnover to test models of biomass allocation and how these allocations of biomass may respond to environmental gradients.

Patterns in productivity and biomass allocation of mangrove forests have been extensively attributable to gradients in resources, regulators and hydroperiod (Lugo and Snedaker 1974; Chen and Twilley 1999b; Feller et al. 2003a, b; Twilley and Rivera-Monroy 2005; Krauss et al. 2006). Recent studies of belowground carbon allocation in mangrove forests around tropical and subtropical latitudes, using a mass balance approach suggest that dwarf mangroves allocate relatively more carbon belowground than do taller mangrove forests in response to low nutrient availability and anaerobic conditions (Lovelock 2008). Mangrove species respond to low nutrient availability with morphological and physiological plasticity

(Feller et al. 2003a, b; Lovelock et al. 2004; Lovelock et al. 2006). In addition, nutrient availability has a significant role in the ability of plants to cope with environmental stress (Murphy and Lugo 1986; Wood et al. 2006). Long-term fertilization of oligotrophic mangrove forests in Belize and Florida increased aboveground wood biomass relative to leaf biomass allocation in response to nutrient additions (Feller et al. 2007). Although, they did not directly measure root biomass allocation, nutrient availability would tend to reduce root biomass allocation based on several fertilization studies in other forest types (Haynes and Gower 1995; Pregitzer et al. 1995; Majdi and Kangas 1997) and wetland ecosystems (Darby and Turner 2008a). For instance, a recent field study demonstrated that long-term fertilization of dwarf *Avicennia marina* mangroves in South Africa shifts resource allocation from roots to shoots increasing growth and aboveground productivity (Naidoo 2009).

The allocation of biomass among mangrove species also responds to changes in hydroperiod with distinct growth, productivity, and species zonation patterns along the intertidal zone (Twilley et al. 1986; Delgado et al. 2001; Castañeda-Moya et al. 2006). For instance, flooded hydroperiods can restrict aboveground mangrove growth (Cardona-Olarte et al. 2006; Castañeda-Moya et al. 2006), but moderate flood durations can maximize growth and productivity (Twilley et al. 1986; Delgado et al. 2001). Yet, there are few studies that have addressed the influence of hydroperiod (duration, frequency, and depth of flooding) on mangrove root dynamics (Cardona-Olarte et al. 2006; Krauss et al. 2006). For instance, greenhouse studies have documented significant shifts in biomass allocation between roots and shoots in neotropical mangrove seedlings under different hydroperiod conditions. (Krauss et al. 2006). In addition, a recent field study of mangrove forests in Belize has shown that root production responds to different hydroperiod conditions from tall fringe to scrub interior mangroves, and parallels the

aboveground productivity gradient (McKee et al. 2007). These studies support the general model that differential patterns in productivity and biomass allocation between above- and belowground mangrove components will respond to three environmental gradients of the intertidal zone including nutrient resources, stressors and hydroperiod (Twilley and Rivera-Monroy 2005). This multigradient model is based mainly on greenhouse studies and patterns across short gradients in oligotrophic systems manipulated with nutrient fertilizers.

In this study, I investigate the landscape patterns of belowground biomass and productivity of mangroves at sites along two Florida Coastal Everglades (FCE) estuaries, Shark River estuary and Taylor River Slough, to test the generality of these allocation models associated with distinct forest productivity gradients (Ewe et al. 2006). These two estuaries are characterized by strong contrasting hydrologic regimes and nutrient resource gradients (Chen and Twilley 1999b; Mancera-Pineda et al. 2009; Castañeda-Moya et al. 2010) resulting in distinct riverine and scrub mangroves within an oligotrophic (i.e., P-limited) carbonate platform. Mangroves along Shark River are fertilized by storm deposits and exhibit elevated aboveground productivity associated with soil P availability that decreases with distance inland from the mouth of the estuary (Chen and Twilley 1999a, b; Krauss et al. 2006; Castañeda-Moya et al. 2010). These allochthonous mineral inputs enhance P concentrations and lower N:P ratios in mangroves at the mouth of Shark River estuary, where soil properties are strongly associated with higher aboveground biomass ($150\text{-}200\text{ Mg ha}^{-1}$) and tree height (18-20 m) compared to upstream sites of this estuary and other regions of southeastern Florida (biomass $<50\text{ Mg ha}^{-1}$; tree height $<5\text{ m}$; Ewe et al. 2006; Simard et al. 2006). Mangrove forests along Taylor River receive less inorganic sediments during storm events due to a geologic barrier called the “Buttonwood Ridge”. This depositional feature ($\sim 1\text{ km}$ wide, $\sim 0.5\text{ m}$ in height) that stretches

roughly 60 km across the southern tip of Florida isolates these mangrove forests from storm deposits of P from Florida Bay (Davis et al. 2004; Castañeda-Moya et al. 2010). Mangroves to the east of the southeastern shore of Florida Bay (e.g., Joe Bay) do receive these storm deposits during a storm event, but they are low in P concentration compared to mangroves areas adjacent to the mouth of Shark River estuary (Castañeda-Moya et al. 2010).

I hypothesized that patterns of belowground root allocation will follow these P-limited conditions and flooded hydroperiods at the Taylor River sites compared to Shark River sites. I expected that mangrove forests along Taylor would have greater root biomass allocation and lower root production due to increased root longevity resulting in lower root turnover rates. I also expected greater root biomass in the top 45 cm of the soil profile, because roots tend to concentrate where soil nutrient resources are more abundant. I addressed the following questions: (1) What are the spatial and temporal patterns of belowground biomass and productivity across the P-limited conditions of Florida Coastal Everglades? (2) How do root biomass and productivity change with soil depth and root size distribution across this nutrient gradient? (3) How does root turnover vary with root size across mangrove sites with nutrient gradients? (4) How do soil nutrient resource and hydroperiod gradients control belowground biomass allocation, productivity, and root turnover across FCE mangrove sites? I focused only in these two environmental gradients since salinity did not explain the variation in community structure and function across our mangrove sites (Mancera-Pineda et al. 2009), and thus I removed salinity stress as a factor influencing patterns in belowground allocation across these sites.

MATERIALS AND METHODS

Study Site

This study was conducted in the southern region of Everglades National Park (ENP; Fig 2.1) in a zone referenced as the Florida Coastal Everglades (FCE). Mangrove forests are distributed along the coastal margin with an estimated total area of 144,447 ha (Simard et al. 2006), which represents approximately two-thirds of all mangrove cover in south Florida (Lodge 2005; see Chen and Twilley 1999b and Castañeda-Moya et al. 2010 for a full site description). In 2000, three mangrove sites were established each along Shark River (SRS-4, SRS-5, and SRS-6) and Taylor River (TS/Ph-6, TS/Ph-7, and TS/Ph-8) estuaries as part of the FCE Long Term Ecological Research (LTER) program (Childers 2006; <http://fcelter.fiu.edu/>). In each site, two 20 x 20 m permanent vegetation plots (20-m apart) were established approximately between 30-50 m from the shoreline to monitor forest structural attributes and soil biogeochemical properties. Mangrove forests along Shark River are considered riverine mangroves consisting of *Rhizophora mangle* (L.), *Avicennia germinans* (L.), *Laguncularia racemosa* (Gaertn) and *Conocarpus erectus* L. SRS-6 is located approximately 4.1 km from the mouth of the estuary, while SRS-5, and SRS-4 are approximately 9.9 and 18.2 km, respectively (Fig. 2.1). Lower Shark River sites (SRS-5 & 6) are tide-dominated, while SRS-4 is influenced by runoff although a tidal influence is observed, particularly in the dry season (Chen and Twilley 1999b). Mangrove sites along Taylor River (TS/Ph-6 & TS/Ph-7) are located approximately 4 and 1.5 km inland from Florida Bay. Mangrove zones are dominated by *R. mangle* scrub forest (tree heights ≤ 1.5 m) with clusters of *C. erectus* and freshwater *Cladium jamaicense*-*Eleocharis* sp. TS/Ph-8 is located near Snook Creek, a tributary of Joe Bay, east of the Taylor River mouth (Fig. 2.1). This site supports a mixed community of *C. jamaicense* and mangroves, with mangrove tree heights of about 3-4

m. *Rhizophora mangle* dominates fringe areas and tidal creeks, whereas *C. erectus* is found in the interior parts (Ewe et al. 2006). Mangrove waterways of this southeastern Everglades region are non-tidal systems with flooded hydroperiods (mainly TS/Ph-6 & 7) compared to Shark River, and water flow is determined by the interactions of seasonal precipitation, upland runoff, and wind (Sutula 1999; Davis et al. 2001).

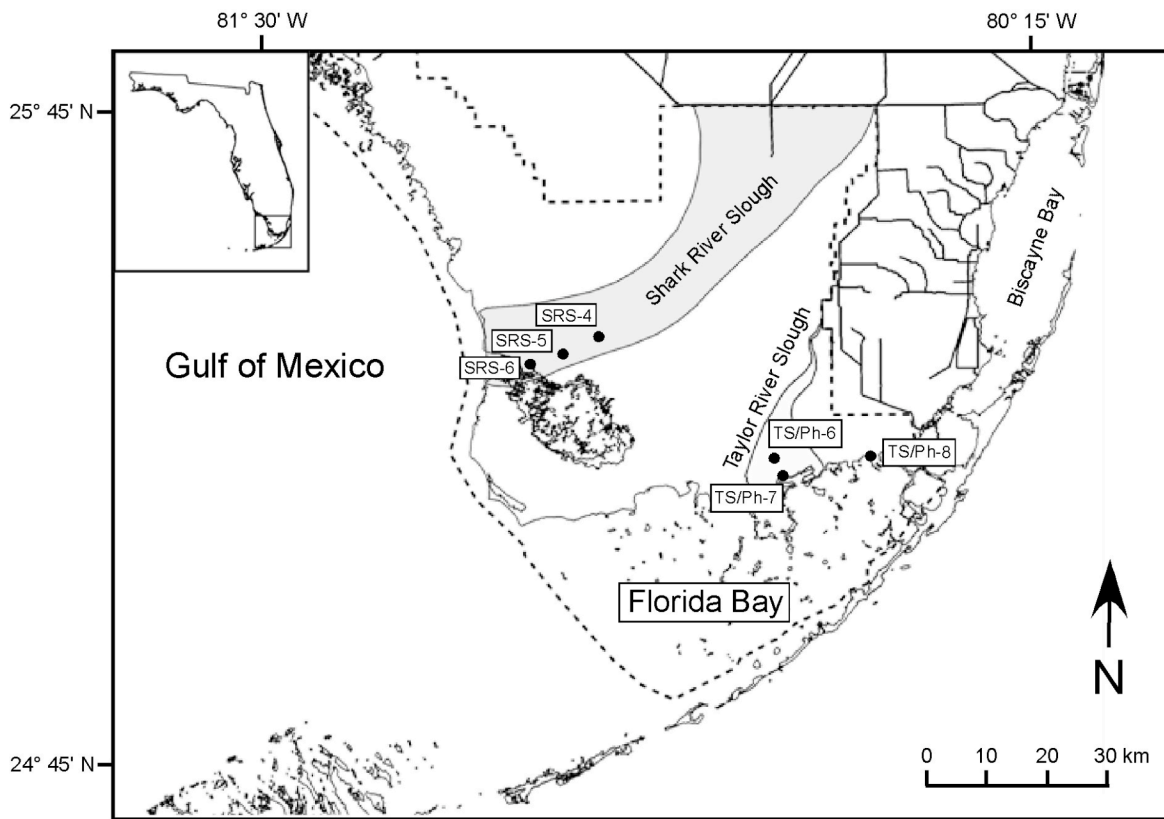


Fig. 2.1 Location of the study sites in the Everglades National Park (ENP), south Florida, USA. SRS4, SRS5, and SRS6 along Shark River Slough; TS/Ph6, TS/Ph7 along Taylor River Slough, and TS/Ph8 in Joe Bay are part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program.

Root Biomass

I performed two separate field experiments to estimate root biomass in all six mangrove sites. Root cores were collected in December 2000 during the first experiment at the three Shark River sites and TS/Ph-6, and in May 2001 at TS/Ph-7 and TS/Ph-8. In each site, sampling points were established at the outside corners of two permanent vegetation plots, and the fifth sample located in between of the two plots. At TS/Ph-6 & 7, due to the physiognomy of the forest, scrub mangrove islands of similar size were selected as single sampling points and arranged around the plots in the same fashion as in the other sites. Root cores were collected at the edge of each mangrove island. In each site, two root cores (0-45 cm depth; shallow root zone) were collected as replicates at each sampling point, using a PVC coring device (10.2 cm diameter x 45 cm length). All root cores were stored separately in bags at 4°C and brought to the laboratory for further analyses. All root samples were processed separately and initially rinsed with water through 1-mm synthetic mesh screen to remove soil particles. Live roots were separated by hand picking those floating in fresh water, and sorted into diameter size classes of <2 mm, 2-5 mm, and >5 mm (fine, small, and coarse roots, respectively). Coarse roots included size classes between 5-20 mm; roots >20 mm in diameter were not included in this study. Each root sample was oven-dried at 60 °C to a constant mass, and weighed.

For the second experiment, root cores were collected in December 2002 at TS/Ph-7 and TS/Ph-8, and in May 2003 at the Shark River sites and TS/Ph-6. In contrast to the first experiment, root biomass was estimated at two depths, 0-45 cm (shallow root zone) and 45-90 cm (deeper root zone) in all sites by using the same PVC coring device as in the first experiment. In the Shark River sites, sampling points were established at the outside corners of two permanent vegetation plots. At each point, four cores (0-90 cm depth) were collected as

replicates and divided into 0-45 and 45-90 cm to estimate biomass at each of the root zones. At TS/Ph-6 & 7, mangrove islands of similar size were selected around the permanent plots and treated as single sampling points as in the first experiment. In TS/Ph-6, five mangrove islands were selected and cores (0-90 cm depth) were collected in two habitats (inland and edge) of each island. Duplicate cores from each habitat were divided into 0-45 and 45-90 cm. In TS/Ph-7, one mangrove island was selected in the upper part of each plot, and four cores were collected at the inland and edge habitats of each island; only two cores per habitat (inland and edge) were saved and divided into 0-45 and 45-90 cm to estimate root biomass. In TS/Ph-8, five sampling points were established around the two permanent plots in the same fashion as in the first experiment. In each point, four root cores (0-90 cm depth) were collected but only two cores were saved and divided into the two sampling depths. All samples were processed for root biomass as described above for the first experiment.

Root Productivity

I used the ingrowth core technique (Vogt et al. 1998) to estimate root productivity only in the second experiment at all sites. Ingrowth cores (10.2 cm diameter x 45 cm length) made of flexible synthetic mesh material and filled with pre-sieved sphagnum peat moss were installed in each of the cored holes formed during sampling of root biomass. Commercial sphagnum peat moss had similar characteristics to mangrove peat in my sites, including bulk density (0.15 vs. 0.21 g cm⁻³), organic matter content (AFDW: 97 vs. 75%), total C (470 vs. 330 mg g⁻¹), and total N (11 vs. 13 mg g⁻¹). Ingrowth cores were retrieved at one and three year intervals and the subsequent root growth within the ingrowth core was used to estimate annual root production at two depths (0-45 and 45-90 cm) during both time intervals. Cores were harvested during December 2003 (1-year interval) and February 2006 (3-year interval) at TS/Ph-7 and TS/Ph-8,

and during May 2004 (1-year interval) and February 2006 (3-year interval) at the Shark River sites and TS/Ph-6. During each time interval, two ingrowth cores (four in the case of TS/Ph-7) were retrieved as replicates from each depth at each sampling point in all sites. After each harvest, ingrowth cores were processed individually following the same protocol as in the root biomass section. Root turnover rate in the shallow root zone (0-45 cm depth) was calculated as root productivity divided by biomass (Eissenstat and Yanai 2002) of each root size class. Estimates of root turnover represent the average of root biomass cores and ingrowth cores for each sampling point within each site. Root longevity (turnover time) in the shallow root zone was calculated as the inverse of root turnover rate (yr^{-1}) for each root size class.

Root Nutrient Content

I determined nutrient content of root biomass samples (0-45 cm depth) for the first experiment. Four oven-dried root core samples were randomly selected from each site and considered as replicates; the size classes of each root core were combined for further nutrient analyses. It was not possible to determine nutrient concentration of each root size class due to small sample volumes. Total nitrogen (N) concentrations of root material were determined on two analytical replicates of each sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total phosphorus (P) was extracted on duplicate analytical replicates with 1 N HCL after combustion in a furnace at 550 °C (Aspila et al. 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas). Root nutrient data was expressed on a volume basis (mg cm^{-3}). The N:P atomic ratio of root tissue was used to determine site's nutrient condition (N or P-limited). An N:P atomic ratio <33 indicates N limitation, whereas N:P > 33 suggests P limitation (Koerselman and Meuleman 1996; Verhoeven et al. 1996).

Statistical Analyses

All statistical analyses were performed with PROC MIXED (SAS Institute, Cary, NC, USA). The variation in root biomass and productivity was not tested among size classes and estimates represent the sum of all size classes for each site. Root biomass was tested for differences among sites (first experiment) and sites and depth (second experiment) using a one- and two-way ANOVA, respectively. I used repeated measures ANOVA to test for differences in root productivity among sites, harvest, and depth (0-45 vs. 45-90 cm), with harvest as the repeated measure. Differences in root biomass and productivity were tested between mangrove island habitats (inland vs. edge) and sites (TS/Ph-6 & 7) with a two-way ANOVA. Variation in shallow fine root biomass and productivity was tested independently with a one-way ANOVA to determine differences among sites and regions (Shark River vs. Taylor River). Root turnover in the shallow root zone was tested for differences among sites and size classes using a two-way ANOVA. For TS/Ph-6 & 7, I only used data collected in the inland habitat of these mangrove islands to examine the variation in shallow fine root biomass, productivity and root turnover across all sites. This habitat represents more accurately patterns of root biomass accumulation and production as these mangrove islands grow in these two sites (see Fig. 2 on Ewe et al. 2007). Root nutrient content (total N and P) and N:P ratios of shallow root biomass samples were analyzed independently with one-way ANOVA to determine differences among sites. All effects were considered fixed. Sampling points were nested within each site, considered random effects, and treated as experimental units. The ANOVA design was unbalanced for most of the variables analyzed due to differences in the number of sampling points and total number of observations per point in each site. The Kenward-Roger procedure was used to adjust the degrees of freedom of the F test statistics when the design was unbalanced or when an unequal variance model was

significant (SAS Institute, Cary, NC, USA; Kenward and Roger 1997). Interaction effects were considered for all analyses. Pairwise comparisons were performed with Fisher's Least Significant Differences (LSD) when significant differences ($p < 0.05$) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. The assumption of homocedasticity was tested using the "null model" likelihood ratio test of the residual errors with a chi square distribution. All variables were log-transformed ($\ln(x + 1)$) prior to analysis to meet the ANOVA assumptions, except root turnover, root total N, and root N:P. Unless otherwise stated, data presented are means (± 1 SE) of untransformed data. Soil nutrient data (top 45 cm; Poret et al. 2007; Castañeda-Moya et al. unpubl. data) in all six FCE mangrove sites were used for regression analyses with shallow fine root biomass, productivity, and turnover, and root nutrient content.

RESULTS

Root Biomass

Shallow (0-45 cm depth) root biomass did not differ significantly (interaction site x experiment: $F_{5, 132} = 1.95$, $p = 0.1$) between experiments for any of the mangrove sites. Thus, root data were pooled together to obtain root estimates for the shallow root zone in each site. These data and the root data for the deeper (45-90 cm) root zone from the second experiment were used to estimate the variation in root biomass with depth at each of the mangrove sites.

Root biomass was significantly different among sites and depths, and there was a significant interaction between site and depth (Table 2.1). Shallow root biomass was greater in TS/Ph-8 ($3302 \pm 591 \text{ g m}^{-2}$) and SRS-5 ($3176 \pm 274 \text{ g m}^{-2}$) compared to SRS-6 ($1973 \pm 336 \text{ g m}^{-2}$; Fig. 2.2a). In the deeper root zone, TS/Ph-7 ($1778 \pm 575 \text{ g m}^{-2}$) had the highest root biomass and SRS-6 and TS/Ph-6 (560 ± 164 and $367 \pm 60 \text{ g m}^{-2}$, respectively) showed the lowest

estimates (Fig. 2.2a). Overall, mean root biomass was significantly higher in the shallow root zone ($2584 \pm 249 \text{ g m}^{-2}$) compared to the deeper root zone ($1008 \pm 205 \text{ g m}^{-2}$) at all sites, except at TS/Ph-7 where root biomass was not significantly different between the two root zones (Table 2.1; Fig. 2.2a).

Table 2.1 Statistical results of belowground root biomass, productivity, turnover and root nutrient content in mangrove forests of the Florida Coastal Everglades. Significance levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Source of variation	df	F	p
Root biomass			
Site	5, 24.7	6.4	***
Depth	1, 63.7	107.3	***
Site*Depth	5, 39	3.3	*
Fine root biomass			
Site	5, 99.6	2.7	*
Fine root productivity			
Site	5, 80	2.7	*
Root productivity			
Site	5, 17.9	1.5	ns
Harvest	1, 92	0.7	ns
Depth	1, 77.6	70.3	***
Site*Harvest	5, 91.9	2.2	ns
Site*Depth	5, 77.4	4.2	**
Harvest*Depth	1, 93.5	0.1	ns
Site*Harvest*Depth	5, 93.3	1.2	ns
Root turnover			
Site	5, 47.7	7.0	***
Size	2, 45.9	54.2	***
Site*Size	10, 45.9	4.4	***
Root nutrient content			
Total N (mg cm^{-3})	5, 18	6.4	**
Total P (mg cm^{-3})	5, 18	15.5	***
Atomic N:P	5, 18	94.2	***

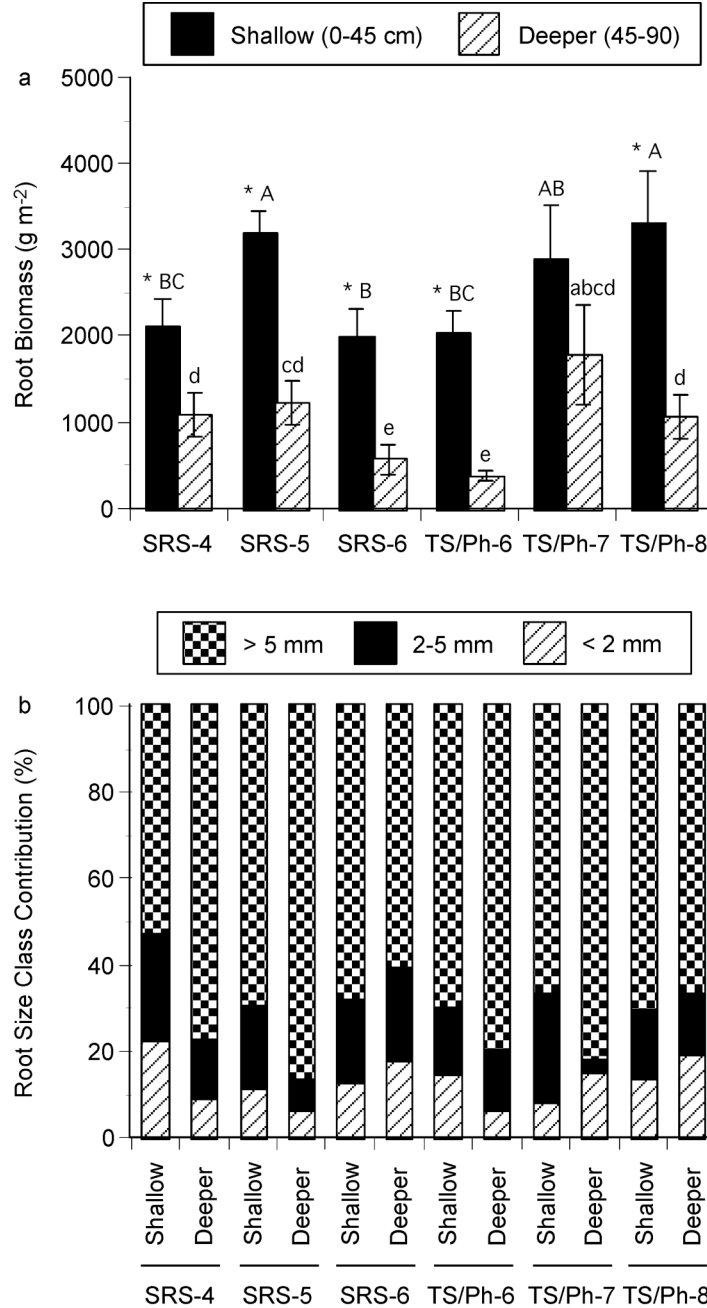


Fig. 2.2 Total root biomass in the shallow (0-45 cm) and deeper (45-90 cm) root zones (a) and root size class distribution with depth (b) in mangrove forests of the Florida Everglades. Asterisks indicate significant differences ($p < 0.05$) within each site. Means (± 1 SE) with different capital letters are significantly different ($p < 0.05$) among sites in the shallow root zone. Means (± 1 SE) with different small letters are significantly different ($p < 0.05$) among sites in the deeper root zone.

Total (0-90 cm) root biomass ranged from $2404 \pm 329 \text{ g m}^{-2}$ (TS/Ph-6) to $4673 \pm 401 \text{ g m}^{-2}$ (TS/Ph-7), with the highest contribution (62-85%) of roots in the shallow root zone at all sites. Estimates of total biomass followed the trend TS/Ph-7 > SRS-5 > TS/Ph-8 > SRS-4 > SRS-6 > TS/Ph-6, although there were no significant differences ($F_{1,35} = 0.32$, $p = 0.6$) in mean total biomass between the Taylor River region ($3811 \pm 710 \text{ g m}^{-2}$) and Shark River region ($3368 \pm 544 \text{ g m}^{-2}$). Most of the root biomass was distributed in the larger size class for both root zones at all sites (Fig. 2.2b). On average, the <2 mm and 2-5 mm size classes contributed 13 and 16% of the total live root biomass in each root zone at all sites, while the >5 mm size class accounted for 71% of the total biomass (Fig. 2.2b).

Total (0-90 cm) root biomass allocation also varied between the inland and edge habitats of mangrove islands at TS/Ph-6 and TS/Ph-7 (Table 2.2). Overall, the inland habitat ($4661 \pm 576 \text{ g m}^{-2}$) of both sites had the highest root biomass compared to the edge habitat ($2220 \pm 372 \text{ g m}^{-2}$). The inland habitat ($5975 \pm 1333 \text{ g m}^{-2}$) of TS/Ph-7 had the highest root biomass, while the edge habitat ($1059 \pm 203 \text{ g m}^{-2}$) of TS/Ph-6 had the lowest (Table 2.2). In general, total (0-90 cm) root biomass was significantly greater in the mangrove islands of TS/Ph-7 ($4677 \pm 868 \text{ g m}^{-2}$) compared to TS/Ph-6 ($2204 \pm 356 \text{ g m}^{-2}$; Table 2.2). There was no significant interaction between island habitats and sites indicating that the variation in root biomass between habitats is independent of site differences (Table 2.2).

Variation in shallow (top 45 cm of soils) fine (<2 mm) root biomass was also examined among sites, given that this root size class distribution accounts for most of nutrient uptake. Shallow fine root biomass varied significantly among mangrove sites and ranged from $253 \pm 38 \text{ g m}^{-2}$ (SRS-6) to $540 \pm 102 \text{ g m}^{-2}$ (TS/Ph-7; Table 2.1; Fig. 2.3). Along Shark River, fine root biomass allocation in the shallow root zone increased from the mouth of the estuary with

distance inland (Fig. 2.3). There were significant ($F_{1,105} = 5.1$, $p < 0.05$) differences in mean shallow fine root biomass between Shark River ($354 \pm 26 \text{ g m}^{-2}$) and Taylor River regions ($474 \pm 53 \text{ g m}^{-2}$; Fig. 2.3).

Table 2.2 Statistical results of root biomass and productivity (integrated to a depth of 90 cm) in the inland and edge habitats of mangrove islands at TS/Ph-6 and TS/Ph-7. Means (± 1 SE) followed by different letters within each column are significantly different (Fisher's LSD post hoc test). ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Site	Island Habitat	Biomass (g m^{-2})	Productivity ($\text{g m}^{-2} \text{ yr}^{-1}$)
TS/Ph-6	Inland	3348 (432) ^b	703 (150) ^a
	Edge	1059 (237) ^c	419 (30) ^b
TS/Ph-7	Inland	5975 (1412) ^a	491 (64) ^{ab}
	Edge	3379 (629) ^b	323 (18) ^b
ANOVA source:			
	Biomass	Productivity	
Site	$F_{1,24} = 16.2$ (***)	$F_{1,4.5} = 1.9$ (ns)	
Habitat	$F_{1,24} = 15.8$ (***)	$F_{1,27.9} = 9.2$ (*)	
Site*Habitat	$F_{1,24} = 0.1$ (ns)	$F_{1,27.9} = 0.6$ (ns)	

Root Productivity

Shallow and deeper root productivity estimates did not vary significantly among sites, and ranged from $260 \pm 40 \text{ g m}^{-2} \text{ yr}^{-1}$ (TS/Ph-7) to $468 \pm 78 \text{ g m}^{-2} \text{ yr}^{-1}$ (SRS-5) in the shallow root zone, and from $102 \pm 32 \text{ g m}^{-2} \text{ yr}^{-1}$ (SRS-6) to $210 \pm 32 \text{ g m}^{-2} \text{ yr}^{-1}$ (TS/Ph-8) in the deeper root zone (Table 2.1; Fig. 2.4a). There was no significant difference in root productivity among the six mangrove sites after either 1-yr ($284 \pm 23 \text{ g m}^{-2} \text{ yr}^{-1}$) or 3-yr harvest intervals ($231 \pm 15 \text{ g m}^{-2} \text{ yr}^{-1}$) due to high sample variability (Table 2.1). However, there was a significant interaction between site and depth effects, with higher root productivity in the shallow root zone ($341 \pm 22 \text{ g}$

$\text{m}^{-2} \text{yr}^{-1}$) compared to the deeper root zone ($166 \pm 11 \text{ g m}^{-2} \text{yr}^{-1}$) at all sites, except in TS/Ph-8 where root productivity estimates were not significantly different between the two root depths (Table 2.1; Fig. 2.4a).

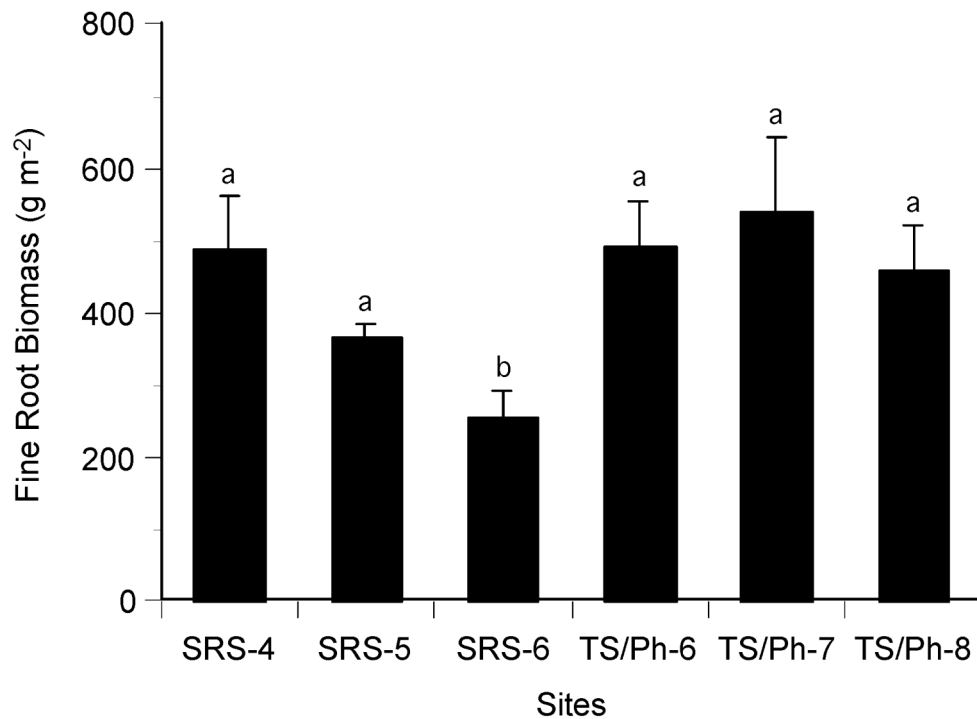


Fig. 2.3 Mean (± 1 SE) fine root biomass in the shallow (0-45 cm) root zone in mangrove forests of the Florida Everglades. Different letters indicate significant differences ($p < 0.05$) among sites.

Total (0-90 cm) root productivity did not differ significantly among sites, and ranged from $407 \pm 23 \text{ g m}^{-2} \text{yr}^{-1}$ (TS/Ph-7) to $643 \pm 93 \text{ g m}^{-2} \text{yr}^{-1}$ (SRS-5) with the highest root production (57-78%) in the shallow root zone compared to the deeper root zone at all sites. The production of roots by size classes differed significantly compared to root biomass, with fine roots contributing 21-50% of the total root productivity in each root zone at all sites (Fig. 2.4b).

On average, the small (2-5 mm) and coarse (>5 mm) roots accounted for 24 and 41% of the total root production in each root zone at all sites, respectively (Fig. 2.4b).

Total (0-90 cm) root productivity also varied between habitats (inland vs. edge) of mangrove islands at TS/Ph-6 and TS/Ph-7 (Table 2.2). Overall, total root productivity in the inland habitat ($597 \pm 106 \text{ g m}^{-2} \text{ yr}^{-1}$) was significantly higher compared to the edge habitat ($371 \pm 48 \text{ g m}^{-2} \text{ yr}^{-1}$) of mangrove islands (Table 2.2). The inland habitat ($703 \pm 150 \text{ g m}^{-2} \text{ yr}^{-1}$) of TS/Ph-6 had the highest root productivity and the edge habitat ($323 \pm 18 \text{ g m}^{-2} \text{ yr}^{-1}$) of TS/Ph-7 the lowest (Table 2.2). There were neither significant differences in total root productivity among sites nor a significant interaction between island habitats and sites (Table 2.2). The variation in shallow (0-45 cm depth) fine (<2 mm) root productivity was significant among mangrove sites, with the greatest root production in all Shark River sites (Table 2.1; Fig. 2.5). Mean shallow fine root production estimates were significantly higher in the Shark River region ($144 \pm 5 \text{ g m}^{-2} \text{ yr}^{-1}$) compared to the Taylor River region ($111 \pm 12 \text{ g m}^{-2} \text{ yr}^{-1}$; Fig. 2.5; $F_{1,84} = 4.6$, $p < 0.05$).

Root Turnover and Longevity

Root turnover in the shallow (0-45 cm) root zone differed significantly among sites and size class distribution (Table 2.1). Root turnover rates consistently decreased as the root size class distribution increased from <2 mm to >5 mm for all sites (Fig. 2.6). Fine root turnover rates ranged from $0.229 \pm 0.026 \text{ yr}^{-1}$ (TS/Ph-6) to $0.599 \pm 0.07 \text{ yr}^{-1}$ (SRS-6); from $0.065 \pm 0.012 \text{ yr}^{-1}$ (TS/Ph-7) to $0.243 \pm 0.054 \text{ yr}^{-1}$ (TS/Ph-6) for small roots, and from $0.040 \pm 0.011 \text{ yr}^{-1}$ (TS/Ph-7) to $0.152 \pm 0.023 \text{ yr}^{-1}$ (TS/Ph-6) for coarse roots (Fig. 2.6). There was a significant interaction between sites and root size classes (Table 2.1). Overall, mean turnover rates were higher at the

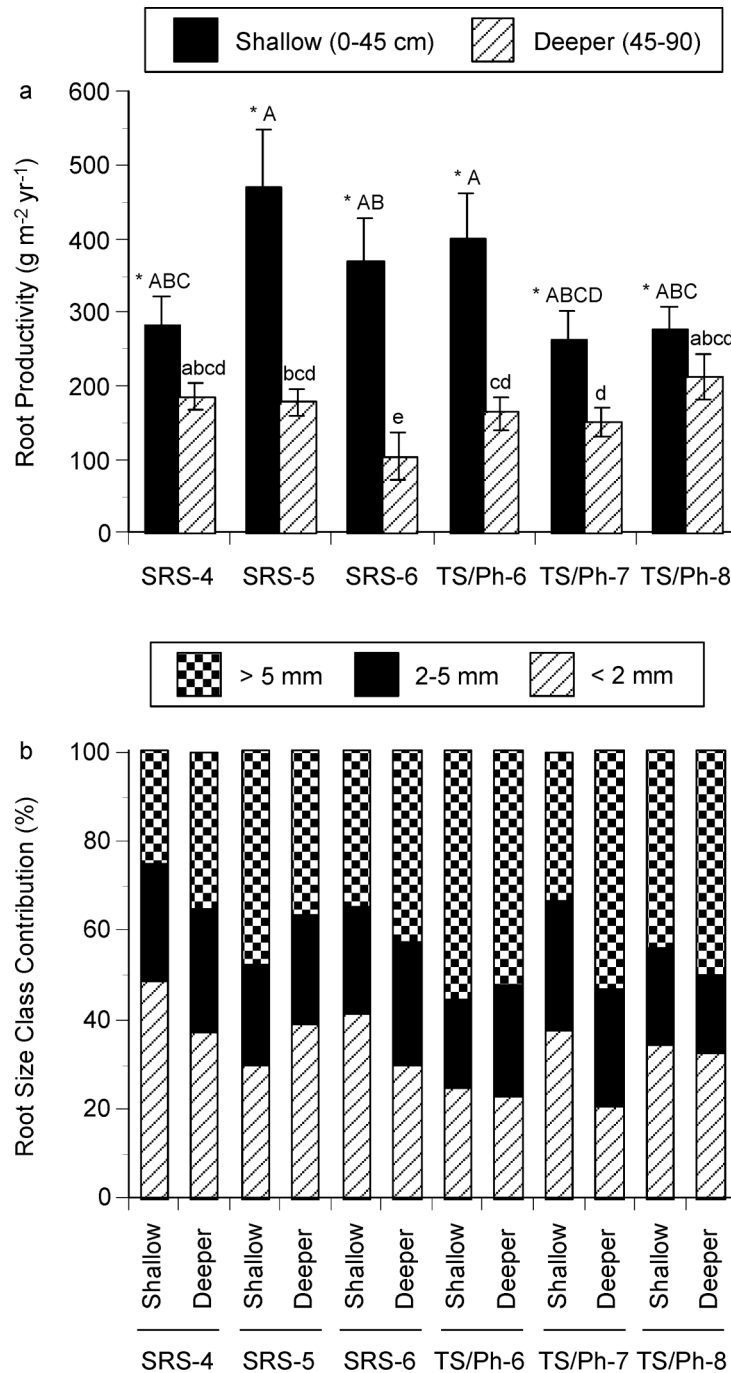


Fig. 2.4 Total root productivity in the shallow (0-45 cm) and deeper (45-90 cm) root zones (a) and root size class distribution with depth (b) in mangrove forests of the Everglades. Asterisks indicate significant differences ($p < 0.05$) within each site. Means (± 1 SE) with different capital letters are significantly different ($p < 0.05$) among sites in the shallow root zone. Means (± 1 SE) with different small letters are significantly different ($p < 0.05$) among sites in the deeper root zone.

Shark River sites compared to Taylor River sites for both the fine (0.427 ± 0.09 and $0.237 \pm 0.004 \text{ yr}^{-1}$) and small roots (0.178 ± 0.01 and $0.143 \pm 0.05 \text{ yr}^{-1}$). In contrast, mean turnover rates of coarse roots were fairly similar for both Shark and Taylor Rivers (0.090 ± 0.01 and $0.093 \pm 0.03 \text{ yr}^{-1}$, respectively). Root longevity estimates ranged from 1.7 to 4.4 yr for fine roots, from 4.1 to 15.4 yr for small roots, and from 6.6 to 24.8 yr for coarse roots at all sites (Table 2.3).

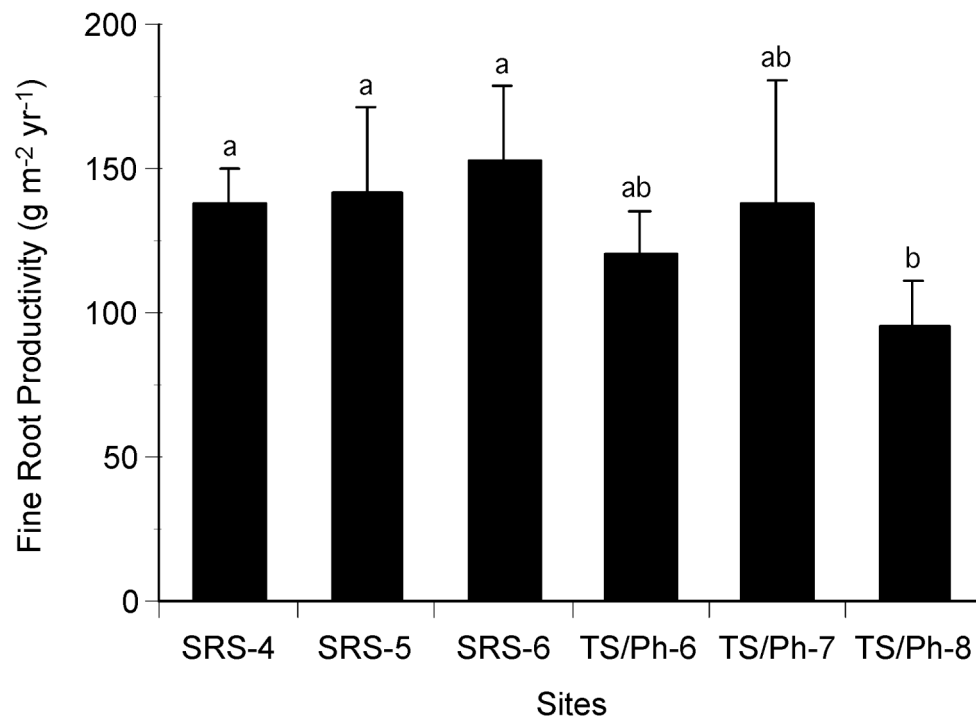


Fig. 2.5 Mean (± 1 SE) fine root productivity in the shallow (0-45 cm) root zone in mangrove forests of the Everglades. Different letters indicate significant differences ($p < 0.05$) among sites.

Root Nutrient Content

Root nutrient content of shallow root biomass differed significantly among sites (Table 2.3). Root N content was significantly higher at the Taylor River sites and SRS-6 compared to SRS-4 and SRS-5, and ranged from $0.016 \pm 0.001 \text{ mg cm}^{-3}$ (SRS-4) to $0.034 \pm 0.006 \text{ mg cm}^{-3}$ (TS/Ph-7; Table 2.3). Root P had the highest content at SRS-6 ($1.74 \pm 0.20 \text{ } \mu\text{g cm}^{-3}$) and differed

significantly from all other sites (Table 2.3). Along Shark River, root P content decreased significantly with distance inland from the mouth of the estuary (Table 2.3). The atomic N:P ratio of root tissue varied significantly from 33.3 ± 0.9 (SRS-6) to 125.6 ± 7.0 (TS/Ph-7) among sites, indicating P limitations at all sites, except at SRS-6 (Table 2.3).

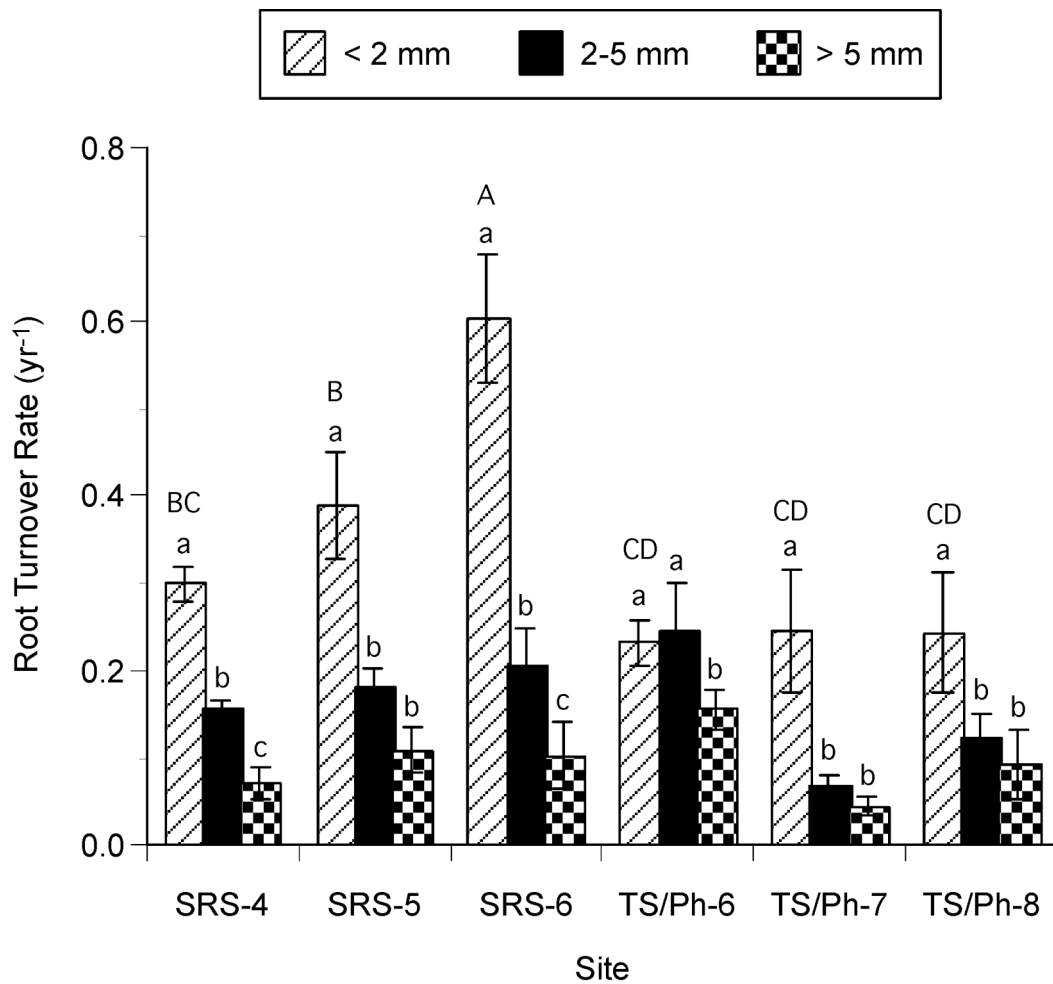


Fig. 2.6 Mean (± 1 SE) turnover rates (to a depth of 45 cm) of root size classes in mangrove forests of the Everglades. Different small letters indicate significant differences ($p < 0.05$) among root size classes within each site. Different capital letters indicate significant differences ($p < 0.05$) in fine root turnover among sites.

Table 2.3 Root longevity, root nutrient content, and root N:P atomic ratios in mangrove forests of the Florida Coastal Everglades. Means (± 1 SE) followed by different letters within each column are significantly different (Fisher's LSD post hoc test). Significant levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Sites	Root longevity (yr)			Root nutrient content		
	Fine (<2 mm)	Small (2-5 mm)	Coarse (>5 mm)	Total N (mg cm^{-3})	Total P ($\mu\text{g cm}^{-3}$)	Atomic N:P
SRS-4	3.4	6.5	15.0	0.016 ^c (0.001)	0.55 ^c (0.04)	63.1 ^d (1.2)
SRS-5	2.6	5.6	9.5	0.019 ^c (0.002)	0.80 ^b (0.07)	51.5 ^e (0.7)
SRS-6	1.7	4.9	10.1	0.026 ^{ab} (0.003)	1.74 ^a (0.20)	33.3 ^f (0.9)
TS/Ph-6	4.4	4.1	6.6	0.027 ^{ab} (0.002)	0.58 ^c (0.06)	102.8 ^b (4.3)
TS/Ph-7	4.1	15.4	24.8	0.034 ^a (0.006)	0.61 ^c (0.10)	125.6 ^a (7.0)
TS/Ph-8	4.2	8.3	11.3	0.029 ^a (0.001)	0.71 ^b (0.04)	89.5 ^c (2.3)

DISCUSSION

Landscape Patterns of Root Allocation

Patterns in root P content in my mangrove sites followed the observed soil P fertility gradient across FCE mangroves, indicating the strong association between substrate quality and P availability. Earlier studies have documented increases in root nutrient content with increasing nutrient availability in forest ecosystems, and thus its strong control on root substrate quality (Gordon and Jackson 2000; Hendricks et al. 2000). These observations are consistent with the observed decrease in root P content with increasing soil N:P ratios across FCE mangroves (Fig. 2.7), and suggest that root P used as a proxy of P availability is a strong indicator of soil fertility in my FCE mangrove sites. My results are in agreement with the observed gradient in foliar P and corresponding shifts in N:P ratios in seagrass communities from west to east of Florida Bay

(Fourqurean et al. 1992). This gradient in P availability has been suggested to control productivity and species composition of seagrass communities in this region (Herbert and Fourqurean 2009), as has been suggested for mangrove forests across FCE (Ewe et al. 2006). These results represent strong evidence concerning the interaction between resource gradients and ecosystem processes across the FCE landscape.

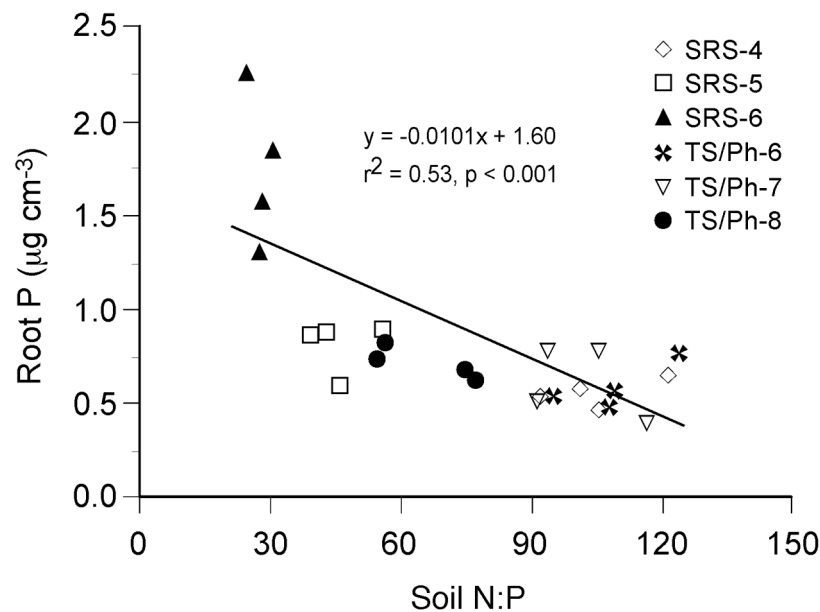


Fig. 2.7 Relationship between root P content and soil N:P ratios in mangrove forests of Everglades National Park. Standard parameters of the linear model are included.

There are large information gaps on belowground processes and how these processes respond to environmental gradients largely due to challenges in understanding root dynamics associated with limitations in sampling methodologies. There has been a recent focus on providing accurate estimates of root biomass and production by both indirect and direct methods (Clough 1992; Vogt et al. 1998; Clark et al. 2001; Bouillon et al. 2008). My results provide a comprehensive review of belowground biomass and productivity in mangroves worldwide and describe evidence of different belowground allocation patterns between riverine and scrub

mangroves and on factors controlling these biomass allocations along nutrient resource and hydroperiod gradients across the FCE landscape.

Total root biomass estimates presented in my study are variable across mangrove sites and within the range of values reported for other mangrove forests around the world (Table 2.4). However, special attention is needed in comparing global trends since different methodological approaches in estimating belowground mangrove biomass can cause varying results. Root estimates based on soil cores are similar across multiple sites, including my results, but are particularly lower relative to methods using soil pit, trench, and trench with root density model methods (Table 2.4). The most extreme estimates of root biomass have been reported for riverine mangrove forest in Panama (18,970 g m⁻²) using the soil pit method (Golley et al. 1975), for a *Bruguiera gymnorhiza* stand in Indonesia (19,610 g m⁻²) with the trench method, and for a *Rhizophora apiculata* forest in Thailand (50,950 g m⁻²) using the trench and root density model method (Komiyama et al. 1987). These methods allow larger size classes of roots to be included in sampling a defined area compared to soil cores that are restricted to core dimensions <10 cm in diameter, limiting the sampling of larger root size classes. The larger size class of roots and the more extensive sampling depth may explain higher biomass estimates in pit and trench techniques compared to more common estimates using soil cores (Table 2.4).

My total (0-90 cm) biomass estimates ranged from 2400 to 4700 g m⁻² and are similar to values reported for mangroves in Puerto Rico (Golley et al. 1962) and Gazi Bay, Kenya (Tamooch et al. 2008) using similar techniques and sampling depths (Table 2.4). My estimates for shallow root biomass (range: 1973 to 3300 g m⁻²; Fig 2.2a) are greater than values reported for mangrove forests in Cuba (Fiala and Hernandez 1993) and Micronesia (Gleason and Ewel

Table 2.4 Summary of belowground biomass and productivity of worldwide mangrove forests.

Location	Sampling method: Biomass	Sampling method: Productivity	Dominant species – Forest type	Belowground Biomass (g m ⁻²)	Belowground Productivity (g m ⁻² yr ⁻¹)	Reference
<u>Total (Fine: <2 mm)</u>						
Shark River (SRS-4), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ce – Riverine	3198 (587) ^a	465 (206) ^a	This study
Shark River (SRS-5), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ag – Riverine	4389 (442) ^a	643 (210) ^a	This study
Shark River (SRS-6), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ag – Riverine	2532 (353) ^a	469 (183) ^a	This study
Taylor River (TS/Ph-6), Florida (USA)	Soil cores	Ingrowth cores	Rm – Scrub	2404 (324) ^a	561 (137) ^a	This study
Taylor River (TS/Ph-7), Florida (USA)	Soil cores	Ingrowth cores	Rm – Scrub	4673 (508) ^a	407 (130) ^a	This study
Taylor River (TS/Ph-8), Florida (USA)	Soil cores	Ingrowth cores	Rm, Ce – Fringe	4358 (661) ^a	485 (164) ^a	This study
Utwe River, Micronesia	Soil cores	Ingrowth cores	Bg – Basin	720 ^b	(120) ^c	Gleason and Ewel 2002
Okat River, Micronesia	Soil cores	Ingrowth cores	Sa – Basin	870 ^b	(750) ^c	Gleason and Ewel 2002
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Fringe	952 (151) ^c	(460) ^c	Cormier 2003
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Interior	1191 (185) ^c	(91) ^c	Cormier 2003
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Riverine	1424 (183) ^c	(100) ^c	Cormier 2003
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Fringe	1368 (292) ^c	(63) ^c	Cormier 2003
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Interior	2640 (577) ^c	(119) ^c	Cormier 2003
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa – Riverine	449 (170) ^c	(95) ^c	Cormier 2003

Table 2.4 cont.

Location	Sampling method: Biomass	Sampling method: Productivity	Dominant species – Forest type	Belowground Biomass (g m ⁻²)	Belowground Productivity (g m ⁻² yr ⁻¹)	Reference
Rookery Bay and Naples Bay, Florida (USA)	Soil cores	Ingrowth cores	Rm – Fringe	15,395 ^c	(352) ^c	Giraldo 2005
Rookery and Naples Bays Florida (USA)	Soil cores	Ingrowth cores	Rm, Ag, Lr – Basin	6704 ^c	(314-378) ^c	Giraldo 2005
Rookery and Naples Bays Florida (USA)	Soil cores	Ingrowth cores	Rm – Scrub	6185 ^c	(307) ^c	Giraldo 2005
Windstar, Florida (USA)		Ingrowth cores	Lr, Ag, Rm – Basin		(140-150) ^c	McKee and Faulkner 2000
Henderson Creek, Florida (USA)		Ingrowth cores	Lr, Ag, Rm – Basin		(220-280) ^c	McKee and Faulkner 2000
Roatan Island, Honduras		Ingrowth cores	Rm – Fringe		265 (199) ^c	Cahoon et al. 2003
Roatan Island, Honduras		Ingrowth cores	Rm, Ag – Basin		302 (171) ^c	Cahoon et al. 2003
Twin Cays, Belize		Ingrowth cores	Rm – Fringe		525 (197) ^c	McKee et al. 2007
Twin Cays, Belize		Ingrowth cores	Rm – Transition		394 (189) ^c	McKee et al. 2007
Twin Cays, Belize		Ingrowth cores	Rm – Scrub		82 (43) ^c	McKee et al. 2007
Belize, Florida, Panama, Australia, New Zealand		Mass balance	Rm, Am, Ag – Fringe		337 ^e	Lovelock 2008
Belize, Florida Panama, Australia, New Zealand		Mass balance	Rm, Am, Ag – Scrub		476 ^e	Lovelock 2008
Mayaguez, Puerto Rico	Soil cores		Rm *	5000 (4000) ^d		Golley et al. 1962
Lane Cove River, Australia	Soil cores		Am *	14,730-16,030 ^b		Briggs 1977
Majana, Cuba	Soil cores		Rm – Fringe	1710 (818) ^c		Fiala and Hernandez 1993
Majana, Cuba	Soil cores		Ag – Basin	1080 (614) ^c		Fiala and Hernandez 1993
Brisbane River, Australia	Soil cores		Am *	10,900-12,700 ^b		Mackey 1993

Table 2.4 cont.

Location	Sampling method: Biomass	Sampling method: Productivity	Dominant species – Forest type	Belowground Biomass (g m ⁻²)	Belowground Productivity (g m ⁻² yr ⁻¹)	Reference
Hawkesbury River, Australia	Soil cores		Am *	4500-16,600 ^b		Saintilan 1997a
Hawkesbury River, Australia	Soil cores		Ac *	3500-10,600 ^b		Saintilan 1997a
Mary River, Australia	Soil cores		Am *	1500-6000 ^b		Saintilan 1997b
Mary River, Australia	Soil cores		Ac *	2500-8000 ^b		Saintilan 1997b
Western Australia	Soil cores		Am *	(1790) ^b		Alongi et al. 2000
Western Australia	Soil cores		Rs *	(5030) ^b		Alongi et al. 2000
Samana Bay, Dominican Republic	Soil cores		Rm, Lr *	6600 (790) ^c		Sherman et al. 2003
Gazi Bay, Kenya	Soil cores		Rmu *	2490 ^b		Kairo et al. 2008
Gazi Bay, Kenya	Soil cores		Am *	3910 ^d		Tamoooh et al. 2008
Gazi Bay, Kenya	Soil cores		Rmu *	3580 ^d		Tamoooh et al. 2008
Gazi Bay, Kenya	Soil cores		Sa *	4840 ^d		Tamoooh et al. 2008
Panama, Pacific coast	Soil pit		Rb *	18,970 ^b		Golley et al. 1975
Hatsaikhao, Thailand	Trench and root density model		Sa *	17,180 (10,370) ^d		Komiyama et al. 1987
Hatsaikhao, Thailand	Trench and root density model		Sa-Bg *	8480 (5630) ^d		Komiyama et al. 1987
Hatsaikhao, Thailand	Trench and root density model		Bg *	24,380 (1375) ^d		Komiyama et al. 1987
Hatsaikhao, Thailand	Trench and root density model		Ra *	50,950 (23,640) ^d		Komiyama et al. 1987
Thailand	Trench and root density model		Ct *	8750 ^d		Komiyama et al. 2000
Indonesia	Trench		Sa *	3850 ^b		Komiyama et al. 1988
Indonesia	Trench		Bg *	19,610 ^b		Komiyama et al. 1988
Indonesia	Trench		Ra *	11,080 ^b		Komiyama et al. 1988

Ag: *Avicennia germinans*; Am: *Avicennia marina*; Ac: *Aegiceras corniculatum*; Bg: *Bruguiera gymnorhiza*; Ce: *Conocarpus erectus*; Ct: *Ceriops tagal*; Lr: *Laguncularia racemosa*; Ra: *Rhizophora apiculata*; Rb: *Rhizophora brevistyla*; Rm: *Rhizophora mangle*; Rs: *Rhizophora stylosa*; Sa: *Sonneratia alba*.

Table 2.4 cont.

* Forest type was not reported

^a Root production or biomass estimates for size classes <2 to <20 mm in diameter (to a depth of 90 cm).

^b Root size class was not reported. Estimates for root biomass are reported for the top 30-60 cm of mangrove soils.

^c Root production or biomass estimates for size classes <2 to <20 mm in diameter (to a depth of 30-50 cm).

^d Root biomass estimates for size classes <40-50 mm in diameter (to a depth of 60 cm).

^e Root production (not direct estimates) was calculated by using the mass balance approach of Raich and Nadelhoffer (1989).

2002; Cormier 2003); but lower than values reported for mangroves in Florida (Giraldo 2005) and the Dominican Republic (Sherman et al. 2003; Table 2.4). These results present wide range of biomass estimates reported for mangrove locations around the world, even when similar sampling techniques and sampling depths are used. In addition, my estimates compared with studies using soil cores are problematic since root size class distribution is not defined in estimates of root biomass, particularly in the Old World (Table 2.4). The higher biomass values reported in these studies likely suggest that root size classes >20 mm were included, which dramatically increase biomass estimates compared to my values that are reported for size classes <20 mm in diameter.

My results reveal a significant decrease in total root biomass with soil depth at all sites, with most of the roots distributed (62-85%) in the shallow root zone compared to the deeper root zone. Similar patterns in the vertical distribution of root biomass have been reported for mangrove forests in Cuba (Fiala and Hernandez 1993) and Thailand (Komiyama et al. 2000; Tamooch et al. 2008). For instance, the highest root biomass (44-67%) was observed in the 0-20 cm soil depth in mangrove stands of Thailand compared to the lowest (4-20%) in the 40-60 cm soil depth (Tamooch et al. 2008). More roots in the upper soil layers reflects a physiological adaptation to facilitate the acquisition of water and nutrients from soil surface layers, as has been reported for terrestrial forests (Claus and George 2005). Increase hypoxia conditions with soil depth could also have a significant decrease in lateral root growth, root extension rates and root metabolic pathways of neotropical mangrove seedlings (McKee 1996; McKee and Mendelssohn 1987). Oxygen deficient sediments at deeper soil layers might constrain mangrove root growth and morphology if the supply of oxygen to the root system is less than that required for respiration (Gregory 1987). This affects the ability of mangrove roots to acquire nutrients.

Patterns in biomass allocation were also evident with root size distribution. The highest allocation (52-86%) in the coarse roots compared to fine and small root sizes in my mangrove sites is comparable to other studies in the Dominican Republic (Sherman et al. 2003) and Micronesia (Cormier 2003), where fine roots contributed <20% of the total, while coarse roots accounted for up to 88% of the total biomass. These results suggest that the higher standing biomass of coarse roots in my sites could be associated to the high amount of organic matter accumulation in mangrove soils due to slow decomposition of roots (Alongi et al. 2000; Middleton and McKee 2001; McKee et al. 2007; Poret et al. 2007). This, coupled to the lower turnover rates of coarse roots compared to fine roots could be significant for soil carbon storage of mangroves (Chmura et al. 2003).

In fact, root turnover rates significantly decreased with size class distribution in my mangrove sites reflecting differences in root longevity, which coincide with global patterns of root turnover rates in terrestrial ecosystems (Gill and Jackson 2000; King et al. 2002). My results showed that fine roots turn over faster and have the lowest longevity (2 to 4 yr) compared to small (4 to 15 yr) and coarse roots (7 to 25 yr; Table 2.3; Fig. 2.6). Fine roots play an important role in the acquisition of water and nutrients, and carbon flux; whereas coarse roots are more involved in storage and structural support (Eissenstat and Yanai 1997). Thus, fine roots have lower longevity due to their greater metabolic activity (i.e., respiration, high nutrient content) and greater energy required for their maintenance (Eissenstat and Yanai 1997; Norby and Jackson 2000). These observations suggest a cost-benefit tradeoff between root carbon allocation and energy expenditure for root construction and maintenance to maximize root efficiency (Eissenstat and Yanai 1997; Burton et al. 2000). My turnover rates of fine roots (0.23 to 0.60 yr⁻¹) are higher compared to those reported in mangrove forests of Micronesia (Cormier 2003) and

Florida (Giraldo 2005), and considerably lower (range: 0.1 to 0.5 yr⁻¹) compared to those of terrestrial forests (Burton et al. 2000; Gil and Jackson 2000). For small and coarse roots, my turnover and longevity rates are the first estimates for mangrove forests (Fig. 2.6; Table 2.3). These results clearly reflect different belowground allocation strategies among mangrove ecosystems in response to environmental gradients that could be important determinants for soil carbon storage in neotropical mangrove forests.

In contrast to root biomass, root productivity did not vary significantly among sites and harvest intervals due to high sample variability (Table 2.1). Similar results have been reported for mangrove forests in Micronesia, where root productivity did not vary among sites (Cormier 2003). My total (0-90 cm) root productivity estimates ranged from 407 to 643 g m⁻² yr⁻¹ and are higher compared to direct estimates reported for mangrove forests in Belize (McKee et al. 2007) and Honduras (Cahoon et al. 2003) and to indirect estimates reported for mangroves (scrub vs. tall forms) around tropical and subtropical latitudes (Lovelock 2008; Table 2.4). The significant decrease in root production with depth (57-78% root accumulation in the shallow root zone) is comparable to other studies in terrestrial forests (Tufekcioglu et al. 1999; Ostertag 2001; Ruess et al. 2003) and wetland ecosystems (Darby and Turner 2008b). For instance, 81% of fine root production was concentrated in the 0-20 cm soil depth in a boreal forest of Alaska (Ruess et al. 2003) compared to 64% in the 0-10 cm depth in a *S. alterniflora* Louisiana marsh (Darby and Turner 2008b). In addition, fine root productivity made a significant contribution (21-50%) to the total (0-90 cm) belowground allocation in my FCE mangrove sites (Fig. 2.4b). These results are in accordance with previous studies suggesting that carbon allocation to fine root production accounts for approximately one-third of the total annual carbon allocation belowground in forest ecosystems (Nadelhoffer and Raich 1992). The higher allocation (~70%) of root biomass to

coarse roots and the fact that fine root production is a significant component of total root productivity in my mangrove sites support the important role of belowground allocation in the soil carbon storage in mangrove forests (Chmura et al. 2003), as has been suggested for other forest and wetland ecosystems (Hendricks et al. 1993; Jackson et al. 1997; Khan et al. 2007; Darby and Turner 2008b).

My results provide evidence that patterns of belowground allocation respond to nutrient resource gradients across FCE mangroves. These generalizations have been demonstrated for leaf dynamics in several ecosystems and its often assumed that root dynamics will exhibit similar responses to those of leaves (Chapin 1980; Ostertag 2001). My total root biomass estimates increased with lower nutrient fertility across FCE mangrove sites, although some exceptions were evident. Along Shark River, SRS-4 and SRS-5 had higher total biomass compared to SRS-6 due to the P-limited conditions upstream of the estuary (Table 2.5). Along Taylor River, all sites significantly allocated higher total biomass similar to SRS-4 & 5, with the exception of TS/Ph-6 that had similar biomass allocation relative to SRS-6 (Table 2.4). Mangrove forests in TS/Ph-6 had the lowest forest development, productivity, and the highest nutrient limitation ($N:P = 109$) compared to all other FCE sites (Table 2.5). Based on most biomass allocation theory, the expectation is that root biomass allocation will increase with decreased nutrient resource availability. Yet, the mangrove peat overlying marl in this site is <0.5 m depth, restricting root accumulation to only this thin soil layer. In contrast, TS/Ph-7 & 8 have mangrove peat depths >1 m and between 2 (SRS-4) to 6.5 m (SRS-6) in the Shark River sites (Ewe et al. 2006). The shallower peat deposits in TS/Ph-6 relative to mangrove areas adjacent to the coast such as TS/Ph-7 & 8 could be associated to age differences (<50 years) in mangrove establishment

Table 2.5 Comparison of forest structure, aboveground net primary productivity (ANPP), hydroperiod (2001-2006), and soil nutrients (to a depth of 45 cm; 2000-2002) in Everglades mangrove forests. Values are the mean (\pm 1 SE).

Sites	Structure and productivity		Hydroperiod		Soil nutrients		
	Basal area (m ² ha ⁻¹)	ANPP (g m ⁻² yr ⁻¹)	Flooding duration (h yr ⁻¹)	Frequency of inundation (# tides yr ⁻¹)	Total N (mg cm ⁻³)	Total P (mg cm ⁻³)	Atomic N:P
SRS-4	19.6 ^a (3.5)	2066 ^c (48)	3965 (163)	217 (16)	2.3 (0.12)	0.05 (0.004)	105 (6.2)
SRS-5	20.7 ^a (4.0)	1173 ^c (65)	4716 (168)	165 (7)	2.4 (0.10)	0.12 (0.006)	46 (3.5)
SRS-6	39.7 ^a (5.0)	2208 ^c (88)	5592 (433)	395 (70)	2.5 (0.30)	0.20 (0.009)	28 (1.3)
TS/Ph-6	—	322 ^c	8566 (144)	12 (1)	1.7 (0.13)	0.03 (0.001)	109 (5.9)
TS/Ph-7	—	378 ^c	8653 (150)	6 (2)	2.5 (0.19)	0.06 (0.004)	102 (5.8)
TS/Ph-8	1.2 ^b (0.3)	340 ^c (30)	3541 (50)	48 (10)	2.4 (0.10)	0.10 (0.014)	66 (5.9)

^a Data from Chen and Twilley (1999b).

^b Data from Castañeda-Moya 2001-2004 (unpubl. data).

^c Data from Ewe et al. (2006). ANPP represents litterfall and wood production.

— Basal area was not calculated because mangrove tree heights <1.5 m.

and peat formation in this region. It has been demonstrated that mangrove forests in this southeastern region of the Everglades have encroached inland approximately 1.5 km during the past 50 yrs (Ross et al. 2000). Evidence of this encroachment of mangroves into freshwater wetlands has been observed in shifts of species composition from a *C. jamaicense*-dominated freshwater marsh to a marine and brackish *R. mangle*-dominated community. These changes in community composition result from gradual increase in sea level and reduction in freshwater drainage into this region (Ross et al. 2000). Thus, it appears that varying mangrove peat formation coupled to extreme nutrient limiting conditions in this southeastern region of the Everglades can also restrict root biomass allocation, particularly in scrub forests.

Trends in biomass allocation with nutrient availability were more evident for fine root dynamics. I found a significant negative relationship between fine root biomass and soil P density for all mangrove sites (Fig 2.8a). All Taylor River sites and SRS-4 had one of the lowest soil P density (range: 0.03 to 0.10 mg cm⁻³) and highest N:P ratios (range: 66 to 109), and allocated twice more fine root biomass compared to the fertile site SRS-6 (soil P = 0.20 mg cm⁻³; N:P = 28; Table 2.5; Fig. 2.3). In addition, fine root allocation increased with distance inland from the mouth of Shark River estuary, following the observed fertility gradient (Fig. 2.3; Chen and Twilley 1999a, b). These results suggest that soil P availability is a controlling factor on fine root biomass allocation in my FCE mangrove sites. My findings are consistent with those reported by Cormier (2003) along a soil fertility gradient in mangrove forests of Micronesia. The fringe and interior forests in Sapwalap River, Pohnpei had the greatest biomass allocation and the lowest soil fertility (N:P > 45-70) compared to the riverine site (N:P < 15; Table 2.4). Similar patterns in biomass allocation along natural fertility gradients have also been observed in montane forests of Hawaii (Ostertag 2001). In addition, a recent study in a Louisiana salt marsh

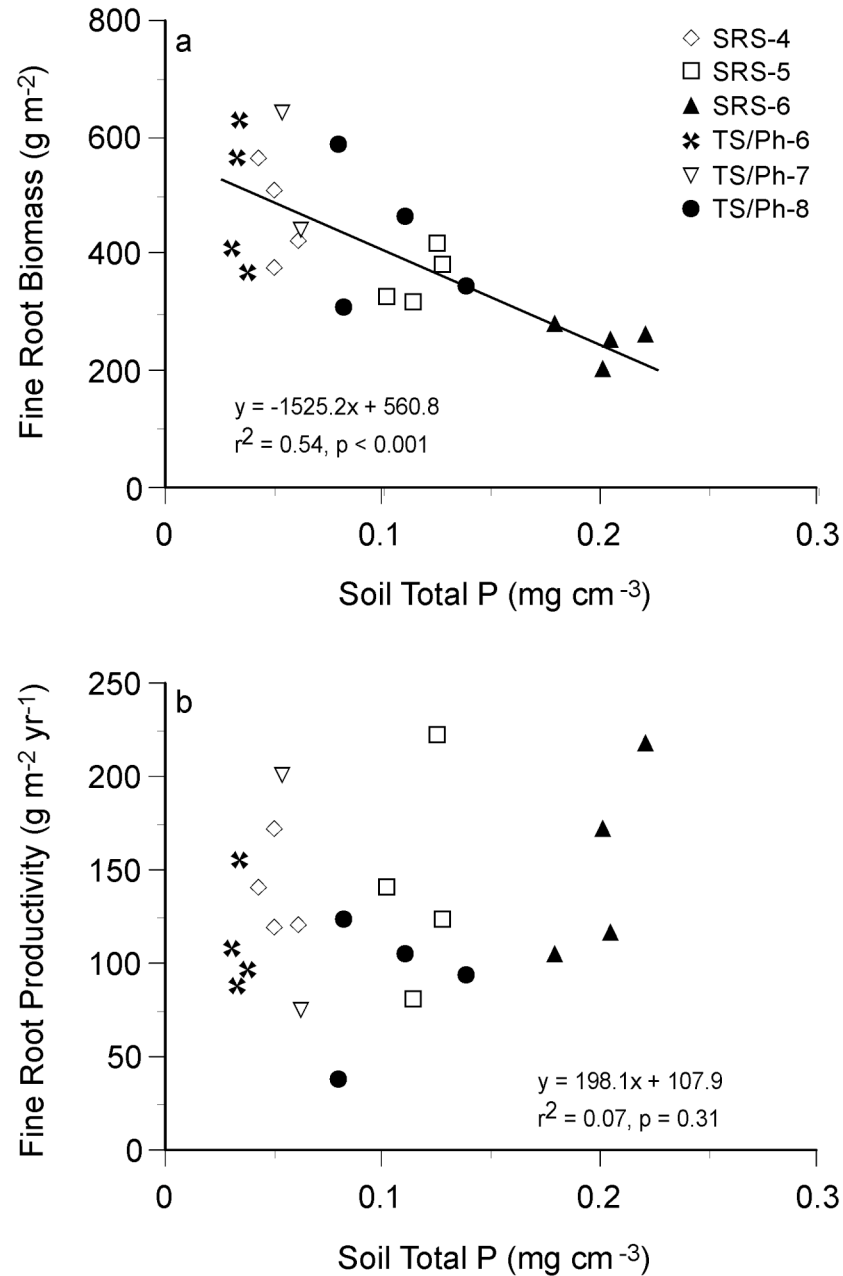


Fig. 2.8 Variation in shallow fine root biomass (a) and shallow fine root productivity (b) with soil P density in mangrove forests of Everglades National Park. Standard parameters of the linear regression models are included. The dotted line in the top panel indicates the model fitted line using all sites. The solid line in the top panel indicates the model fitted line using four sites (TS/Ph-6 & 7 were not included).

wetland indicated that belowground biomass of *Spartina alterniflora* decreased by 40-60% in response to P and P-Fe additions relative to control plots (Darby and Turner 2008a).

In contrast to fine root biomass, fine root productivity did not show any significant trend with increasing P density at all sites ($r^2 = 0.07$, $p=0.3$; Fig. 2.8b). Yet, fine root productivity was significantly higher in Shark River relative to Taylor River. There is evidence that increased nutrient availability leads to increases in fine root production in mangrove forests of Belize (McKee et al. 2007). Their results showed that P additions dramatically increased production rates of fine and coarse roots in interior and transition scrub mangroves compared to tall fringe mangroves that had no effect. Fine root production was 2 and 8 times greater in the fertilized plots of transition and interior scrub mangroves compared to control plots. In addition, fine root production in tall fringe mangroves was 5 times greater compared to the interior scrub forest under natural conditions (McKee et al. 2007), suggesting that growth is associated to a hydroperiod-mediated P subsidy.

This is consistent with my results as fine root productivity was 1.2 times greater in the Shark River sites compared to Taylor sites. The lower root production rates in these sites are probably associated to a combination of flooding and P limitation on root growth, particularly in TS/Ph-6 & 7 (McKee 2001; McKee et al. 2007). In contrast, Shark River sites are influenced by semidiurnal tides and moderate hydroperiods providing a subsidy of P and allowing less reducing conditions in mangrove soils (Table 2.5; Krauss et al. 2006). Although soil P fertility along Shark River increases from SRS-4 (0.05 mg cm^{-3}) to SRS-6 (0.20 mg cm^{-3} ; Table 2.5), fine root production rates at these three sites were not significantly different from one another. In fact, root decomposition rates at the Shark River sites were not significantly different from one another, but were significantly higher compared to Taylor River sites, except for TS/Ph-7,

indicating that soil P fertility and hydroperiod play a major role in root decomposition across FCE mangroves (Poret et al. 2007). Thus, it appears that the higher P availability in Shark River would promote greater annual turnover rates of fine roots that coincide with greater belowground carbon allocation associated with fine root production (Burton et al. 2000).

My results support the assumption that root turnover increases with nutrient availability since turnover rates of fine roots were 1.8 times greater at the Shark River sites compared to Taylor sites (Fig. 2.6). There is considerable evidence that fine root turnover increases with increasing nutrient availability in forest ecosystems (Aber et al. 1985; Nadelhoffer et al. 1985; Nadelhoffer 2000). Several studies have also showed that fine root turnover plays a major role in nutrient cycling and carbon input into the soil (Hendricks et al. 1993; Jackson et al. 1997), and that nutrient availability controls the timing and duration of root growth (Nadelhoffer et al. 1985). Indeed, my results show a significant decrease in fine root turnover with increasing N:P ratios across my mangrove sites, suggesting a strong coupling between P availability and carbon allocation to fine root production (Fig. 2.9). Similar results have been reported for mangrove forests in Micronesia, with the highest fine root turnover in the most fertile ($N:P < 15$) Pohnpei riverine site and the lowest rates at the nutrient limiting sites of fringe and interior mangroves with $N:P > 45$ (Cormier 2003).

The observed patterns in root allocation and turnover in my mangrove sites can also respond to changes in root nutrient content. The increase in longevity with root size class could be associated to a decrease in root nutrient content and respiration leading to shorter turnover rates, particularly at the Taylor River sites (Pregitzer et al. 1998). Coarse roots have a lower maintenance cost for respiration due to their greater longevity compared to fine roots, but are more expensive to build (Norby and Jackson 2000). Thus, the relative lower turnover and greater

longevity of fine roots in the Taylor River sites compared to Shark River could reflect a physiological adaptation of mangroves to nutrient loss in nutrient-poor environments (Nadelhoffer et al. 1985). This is particularly significant given the greater expenditure of energy in foraging for limiting nutrients (i.e., soil P) at these sites at the expenses of growth, which could add a physiological cost in maintaining root growth and higher turnover rates. In addition, lower fine root activity (i.e., respiration) at the Taylor sites would create a low carbon cost, permitting greater root longevity despite low nutrient gain per unit time (Eissenstat and Yanai 1997). In contrast, the higher root P content in the Shark River sites could result in a higher metabolic activity of fine roots leading to an increase in root production and turnover compared to Taylor sites. These observations supports the cost-benefit tradeoffs that mangroves need to cope in response to resource gradients to maximized root efficiency in terms of nutrients acquired per unit of carbon expended for root construction and maintenance (Burton et al. 2000).

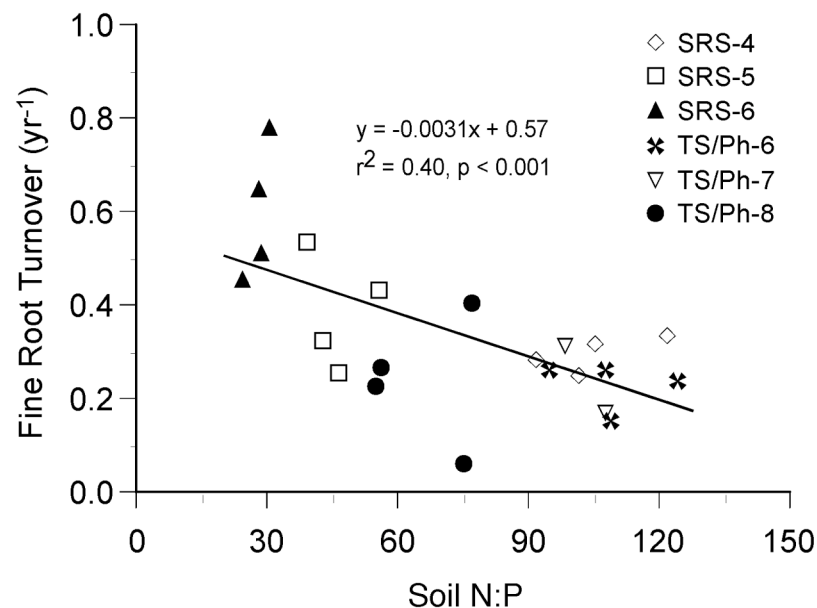


Fig. 2.9 Relationship between shallow fine root turnover and soil N:P ratios in mangrove forests of Everglades National Park. Standard parameters of the linear model are included.

Soil factors other than P availability, such as hydroperiod can also explain the variation in fine root dynamics across FCE mangroves. Shallow fine root biomass correlated negatively with frequency of inundation, suggesting that the higher frequency of inundation at the Shark River sites decreases root biomass allocation due to lower soil stress conditions (Fig. 2.10a). In fact,

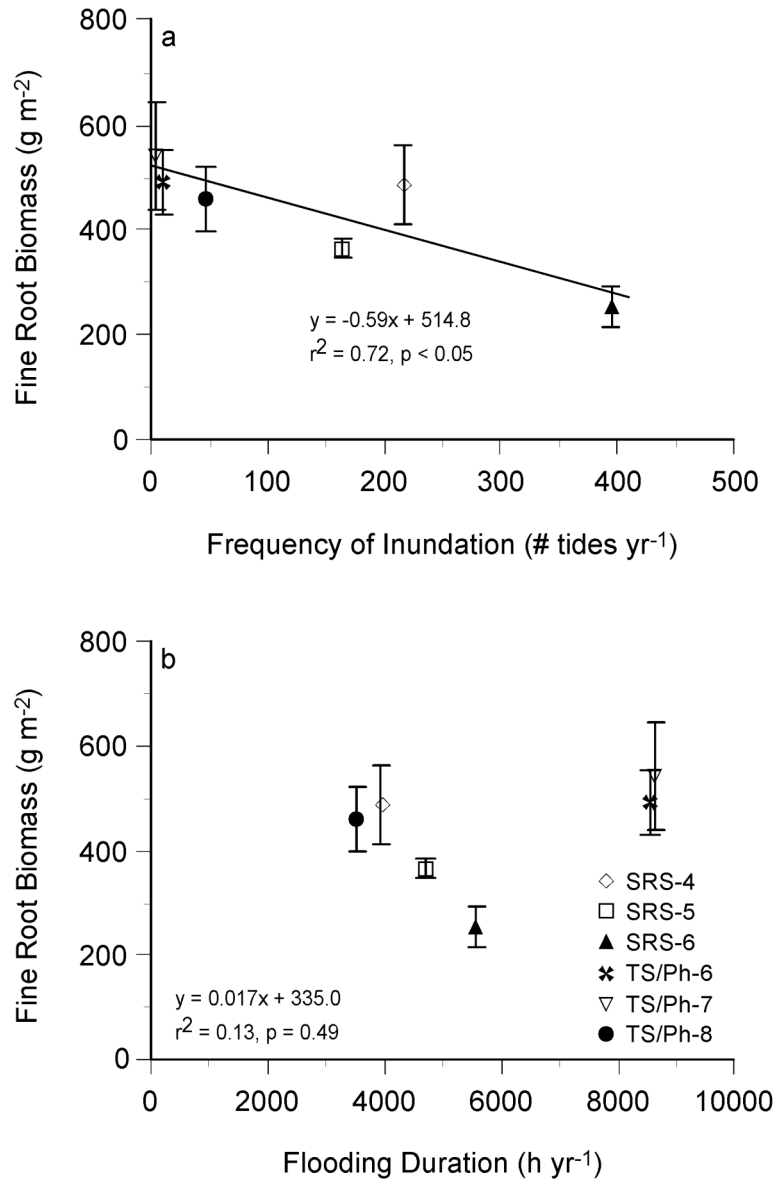


Fig. 2.10 Relationship between shallow fine root biomass and frequency of inundation (a) and flooding duration (b) in mangrove forests of Everglades National Park. Standard parameters of the linear regression model are included.

sulfide concentrations in the Taylor River sites (range: 0.86 to 1.6 mM) were significantly higher compared to those of Shark River sites (range: 0.01 to 0.14 mM; see Table 3.2; Mancera Pineda et al. 2009), supporting the regulatory effect of hydroperiod on root biomass allocation patterns (Krauss et al. 2006). Although fine root biomass was not correlated with flood duration (Fig. 2.10b), patterns in root biomass allocation can be associated to the competitive ability of mangrove species and their tolerance limit to flooding (Ball 1996; Cardona-Olarte et al. 2006; Krauss et al. 2006). For instance, *R. mangle* usually tends to occupy areas where more permanent flooding (50-75% of the year) occurs, while *L. racemosa* and *A. germinans* are generally restricted to flooding durations <50% of the year (Koch 1996; Cardona-Olarte et al. 2006). In addition, *R. mangle* out-competes *L. racemosa* and *A. germinans* under low nutrient availability, while *L. racemosa* dominates more fertile sites with moderate flooding (McKee 1995; Chen and Twilley 1998, 1999b; Krauss et al. 2006). My observations are consistent with these findings since *R. mangle* is the dominant species at TS/Ph-6 & 7. These two P-limited sites (N:P = 102 to 109) are characterized with permanent flooding ($\sim 8600 \text{ h yr}^{-1}$) and a negligible tidal frequency (6-12 tides yr^{-1}) relative to Shark River sites, with moderate flooding (range: 4000 to 5600 h yr^{-1}) and a significant tidal frequency (165-395 tides yr^{-1} ; Table 2.5). The lower P fertility and permanent flooding conditions at TS/Ph-6 & 7 compared to Shark River sites could explain why *R. mangle* is the dominant species in this region of southeastern Everglades (Koch 1997). In contrast, the higher tidal influence and moderate flooding conditions in Shark River sites allow the co-existence of all three-mangrove species, with dominance of *L. racemosa* in the most fertile site of SRS-6 and *R. mangle* in the P-limited sites of SRS-4 & 5. Thus, it appears that the lack of correlation between fine root biomass and flood duration is not surprising, since the competitive ability of mangrove species and the morphological adaptations they have developed

to cope with soil stress conditions such as flooding and low nutrient availability determine different biomass allocation and species distribution patterns (Krauss et al. 2006).

Moreover, few studies have documented the effect of hydroperiod on changes in biomass allocation in mangroves, with permanent flood hydroperiods restricting mangrove growth and moderate flood durations maximizing growth and productivity (Cardona-Olarte et al. 2006; Krauss et al. 2006). Greenhouse studies have documented significant shifts in biomass allocation between root and shoots in neotropical mangrove seedlings under different hydroperiod conditions (Krauss et al. 2006). Their results indicate that *L. racemosa* seedlings allocated more biomass to aboveground components relative to roots under intermittent and flooded conditions, in contrast to *A. germinans* seedlings that tended to distribute more biomass to roots with greater flood duration (Krauss et al. 2006). Similarly, significantly less above- and belowground biomass allocation was observed in other forested wetlands under permanently flooded conditions compared to moderate flooding (Megonigal and Day 1992; Day and Megonigal 1993). For instance, saplings of *Taxodium distichum* allocated less roots (28% of total dry mass) in the permanent flooding treatments compared to 46% allocation in the intermittently flooded treatment (Megonigal and Day 1992). These findings support my assumption that soil factors other than P availability, such as hydroperiod can exert a positive effect on root biomass allocation to reduce the negative effects of high sulfide concentrations and more anaerobic conditions in the soil due to low frequency of inundation and permanently flooded conditions.

My results support the existing theory that plants invest carbon and energy into above- and belowground structures proportionately to resource supply to improve the acquisition of the limiting resource (Grime 1977; Chapin 1980; Tilman 1985; Bazzaz 1997). In addition to nutrient resources, hydroperiod gradients (i.e., frequency of inundation) were significant in controlling

biomass allocation patterns in FCE mangroves by minimizing stress from regulators (Krauss et al. 2006). My findings have also tested the assumption that variation in resources and hydroperiod can explain varying root allocation patterns in FCE mangrove sites, as has been suggested for the landscape vegetation patterns of mangrove forests in this coastal region (Twilley and Rivera-Monroy 2005, 2009). Mangrove forests at SRS-6 allocated the lowest root biomass and exhibited the highest forest development and productivity compared to upstream sites of this estuary and scrub mangroves at TS/Ph-7 & 8 that are all P-limited (Table 2.5). Contrary to my expectations, TS/Ph-6 did not follow this general model of biomass allocation in response to resource gradients likely due to age differences in mangrove peat formation and permanently flooded conditions. However, fine root dynamics in this site responded to nutrient resource and hydroperiod gradients. In addition, the Shark River sites exhibited higher fine root productivity rates compared to Taylor River sites suggesting that the extreme P-limited conditions together with a lack of tidal influence and flooded hydroperiods in these sites constrain root production and turnover.

My results provide evidence that stress conditions coupled to site-specific life history traits of mangrove species along both Shark River and Taylor River regions, which are predictably related to habitat stability and productivity, determine the degree of plasticity in belowground allocation across the FCE landscape (Schlichting 1986). Thus, it is intuitive to assume that mangroves in the Taylor River region tend to produce roots with greater longevity and low morphological plasticity as a mechanism of nutrient conservation, while mangroves at the more fertile region of Shark River should produce short-lived roots with rapid potential rates of nutrient uptake and rapid growth rates (Eissenstat and Yanai 1997). These tradeoffs suggest the strong link between belowground processes and the phenotypic plasticity of mangrove roots

in response to nutrient resource and hydroperiod gradients across the FCE landscape. This is particularly significant given that fine root production and accumulation is the primary process controlling soil formation in scrub mangrove forests of Belize, explaining 42% of the variation in elevation change (McKee et al. 2007). Thus, this feedback of mangrove root dynamics in this P-limited carbonate ecosystem of south Florida could have tremendous implications as to how soil formation and accretion serve as adaptations of mangroves in the Caribbean region to future impacts of sea-level rise.

Simulation Models of Root Allocation

Model simulations of nutrient biogeochemistry (NUMAN) emphasized the significance of root production in controlling soil formation in mangrove forests along Shark River estuary (Chen and Twilley 1999a). Yet, many of these simulation results were based on assumptions due to the lack of direct measurements in belowground processes at that time. Root biomass and production estimates in the NUMAN model indicate that values are highly overestimated compared to actual field observations (Tables 2.6 and 2.7). Simulated results showed that root biomass allocation in the shallow (0-45 cm) and deeper (45-90) root zones were consistently higher in SRS-6 compared to sites upstream (SRS-4 & 5) the estuary (Table 2.6). In contrast, field observations had an opposite trend with higher root biomass allocated in upstream sites compared to SRS-6 for both root zones (Table 2.6). In addition, simulated total root biomass was on average ~2 and 6 times higher in upstream sites and SRS-6 compared to field estimates, respectively (Table 2.6). Simulated fine and coarse root production for both shallow and deeper root zones showed the same trend as simulated root biomass along the estuary; whereas actual root production estimates from this study showed no significant differences in productivity among Shark River sites (Table 2.7). Simulated total root production was 1.9 and 5 times greater

in upstream sites and SRS-6 compared to field observations, respectively (Table 2.7). The larger distribution of roots in the shallow root zone compared to the deeper root zone for both root biomass and productivity was the only consistent pattern between simulated results and field observations (Tables 2.6 and 2.7).

These observations suggest that simulation results of root allocation were highly overestimated compared to actual field observations due to assumptions for parameters in the model based on general literature values (Chen and Twilley 1999a). They assumed an average ratio of belowground:aboveground biomass of 0.74 calculated for mangrove forests in Puerto Rico and Panama (Golley et al. 1962; Golley et al. 1975). This fixed ratio was used to calculate root biomass using actual aboveground biomass values calculated for the Shark River sites (Chen and Twilley 1999b). They also assumed roots were distributed to a depth of 150 cm at all sites using a root biomass attenuation factor with depth that is accurate. However, the surface biomass estimates that were used to generate biomass with depth based on this root attenuation coefficient overestimated total biomass per unit area.

This lack of agreement between simulation results and field observations due to model assumptions demonstrates the potential error in overestimating root biomass for FCE mangroves when using literature values from another region, and indicate the high variability in community structure across neotropical mangrove regions. These results support the significance of direct measurements on belowground processes to adequately calibrate, validate, and test these biomass allocation models for FCE mangroves. Model simulations have been a useful tool for understanding mangrove forest dynamics (Chen and Twilley 1998; Berger et al. 2008) and for developing management plans for mangrove rehabilitation and restoration in neotropical mangroves including south Florida (Chen and Twilley 1998; Twilley and Rivera-Monroy 2005)

Table 2.6 Comparison of model (NUMAN) simulations and field estimates (this study) of root biomass in mangrove forests of the Florida Coastal Everglades.

Root zone	Root biomass (g m ⁻²)	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
(Chen and Twilley 1999a)							
Shallow (0-45 cm)	Model simulations	4800	7721	15,442			
Deeper (45-90 cm)	Model simulations	756	1216	2433			
Total (0-90 cm)	Model simulations	5556	8937	17,875			
Actual data from this study							
Shallow (0-45 cm)	Model simulations	5934	6606	9234	759	759	271
	Field estimates	2121	3176	1973	2037	2895	3302
Deeper (45-90 cm)	Model simulations	935	1041	1455	120	120	43
	Field estimates	1078	1213	559	367	1778	1056
Total (0-90 cm)	Model simulations	6869	7647	10,689	879	879	314
	Field estimates	3199	4389	2532	2404	4673	4358

Table 2.7 Comparison of model (NUMAN) simulations (Chen and Twilley 1999a) and field estimates (this study) of root productivity in mangrove forests of the Florida Coastal Everglades.

Root zone	Root productivity (g m ⁻²)	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
Fine (<2 mm)							
Shallow (0-45 cm)	Model simulations	480	772	1544			
	Field estimates	137	141	152	100	98	95
Deeper (45-90 cm)	Model simulations	76	122	243			
	Field estimates	69	69	31	37	31	69
Total (0-90 cm)	Model simulations	556	894	1787			
	Field estimates	206	210	183	137	129	164
Small (2-5 mm) + Coarse (> 5 mm)							
Shallow (0-45 cm)	Model simulations	204	328	656			
	Field estimates	144	327	215	300	161	179
Deeper (45-90 cm)	Model simulations	32	52	103			
	Field estimates	115	107	72	124	117	142
Total (0-90 cm)	Model simulations	236	380	760			
	Field estimates	259	433	286	424	278	321
Total (<2 to 20 mm)							
Shallow (0-45 cm)	Model simulations	684	1100	2200			
	Field estimates	281	468	367	400	260	275
Deeper (45-90 cm)	Model simulations	108	173	347			
	Field estimates	184	175	102	161	147	210
Total (0-90 cm)	Model simulations	792	1274	2547			
	Field estimates	465	643	469	561	407	485

and Colombia (Twilley et al. 1999). Their integration with empirical data can provide valuable insights to adequately simulate complex biogeochemical processes in FCE mangroves, particularly when environmental gradients are a common feature across the coastal landscape controlling patterns in biomass and productivity of south Florida mangroves (Ewe et al. 2006). Therefore, future research will be aimed to re-calibrate the NUMAN model with actual data of root biomass and productivity from my study and root decomposition results (Poret et al. 2007) to simulate and forecast short- and long-term patterns in belowground allocation of mangroves in the Caribbean region in response to current changes in sea level.

SUMMARY

Landscape gradients in resources, regulators and hydroperiod across distinct coastal basins of FCE allowed me to test the hypothesis that root dynamics respond to resource gradients by allocating biomass and net primary productivity to facilitate nutrient acquisition but also minimizing stress from regulators and hydroperiod in flooded soil conditions.

Mangrove forests at SRS-6 allocated the lowest root biomass and showed the highest rates of root turnover compared to sites (SRS-4 & 5) upstream of Shark River and Taylor River sites that have strong P-limited conditions. Root biomass and production significantly decreased with soil depth at all sites, indicating that the higher distribution of roots in the shallow root zone (0-45 cm) may reflect a physiological adaptation of mangroves to facilitate the acquisition of water and nutrients from soil surface layers.

The significant increase in fine root biomass with decreasing frequency of inundation reflects an adaptation of scrub mangroves in Taylor River to reduce the negative effects of high sulfide concentrations and more anaerobic conditions in the soil due to low frequency of inundation and permanently flooded conditions. In addition, the Shark River sites exhibited

higher fine root productivity rates compared to Taylor River sites suggesting that the extreme P-limited conditions together with a lack of tidal influence and flooded hydroperiods in these sites constrain root production and turnover.

Root turnover rates consistently decreased as the root size class distribution increased, indicating differences in root longevity. Mangroves in the Taylor River region tend to produce roots with greater longevity and low morphological plasticity as a mechanism of nutrient conservation, while mangroves at the more fertile region of Shark River should produce short-lived roots with rapid potential rates of nutrient uptake and rapid growth rates. These tradeoffs suggest the strong link between belowground processes and the morphological and physiological plasticity of mangrove roots in response to environmental gradients.

Simulation models of root allocation were highly overestimated compared to actual field observations due to model assumptions, demonstrating the potential error in overestimating root biomass for FCE mangroves when using literature values from another region. This lack of agreement between simulation results and field observations results support the significance of direct measurements on belowground processes to adequately calibrate, validate, and test these biomass allocation models for FCE mangroves.

REFERENCES

- Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, C.A. McClaugherty, and J. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* 66: 317-321.
- Alongi, D.M., B.F. Clough, P. Dixon, and F. Tirendi. 2003. Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees* 17: 51-60.
- Alongi, D.M., F. Tirendi, and B.F. Clough. 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. *Aquatic Botany* 68: 97-122.

- Aspila, K.I., H. Agemian, and S.Y. Chau. 1976. A semi-automated method for the determination of inorganic, organic and total phosphate in sediments. *Analyst* 101: 187-197.
- Ball, M.C. 1996. Comparative ecophysiology of mangrove forests and tropical lowland moist rainforest. In *Tropical Forest Plant Ecophysiology*, eds. S.S. Mulkey, R.L. Chazdon, and A.P. Smith, 461-496. New York, NY.: Chapman and Hall.
- Bazzaz, F.A. 1997. Allocation of resources in plants: State of the science and critical questions. In *Plant resource allocation*, eds. F. A. Bazzaz and J. Grace, 1-37. San Diego, California: Academic Press.
- Berger, U., V. Rivera-Monroy, T.W. Doyle, F. Dahdouh-Guebas, N.C. Duke, M. Fontalvo-Herazo, H. Hildenbrandt, N. Koedam, U. Mehlig, C. Piou, and R.R. Twilley. 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests. *Aquatic Botany* 89: 260-274.
- Bloom, A.J., F.S.I. Chapin, and H.A. Mooney. 1985. Resource limitation in plants - an economic analogy. *Annual Review of Ecology and Systematics* 16: 363-392.
- Bouillon, S., A.V. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N.C. Duke, E. Kristensen, S.Y. Lee, C. Marchand, J.J. Middleburg, V. Rivera-Monroy, T.J.I. Smith, and R.R. Twilley. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles* 22: GB2013, doi:2010.1029/2007GB003052.
- Briggs, S.V. 1977. Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology* 2: 369-373.
- Burton, A.J., K.S. Pregitzer, and R.L. Hendrick. 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. *Oecologia* 125: 389-399.
- Cahoon, D.R., P. Hensel, J. Rybczyk, K.L. McKee, E. Proffitt, and B.C. Perez. 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology* 91: 1093-1105.
- Cardona-Olarte, P., R.R. Twilley, K.W. Krauss, and V.H. Rivera-Monroy. 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. *Hydrobiologia* 569: 325-341.
- Castañeda-Moya, E., V.H. Rivera-Monroy, and R.R. Twilley. 2006. Mangrove zonation in the dry life zone of the Gulf of Fonseca, Honduras. *Estuaries and Coasts* 29: 751-764.
- Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, K. Zhang, S.E. Davis, III., and M. Ross. 2010. Sediment and nutrient deposition associated with Hurricane Wilma in mangroves of the Florida Coastal Everglades. *Estuaries and Coasts* 33: 45-58.

- Chambers, R.M., and K.A. Pederson. 2006. Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands. *Hydrobiologia* 569: 63-70.
- Chapin, F.S.I. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233-260.
- Chapin, F.S.I., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* 37: 49-57.
- Chapin, F.S.I., P.M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *The American Naturalist* 127: 48-58.
- Chen, R., and R.R. Twilley. 1998. A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. *Journal of Ecology* 86: 1-12.
- Chen, R., and R.R. Twilley. 1999a. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44: 93-118.
- Chen, R., and R.R. Twilley. 1999b. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955-970.
- Childers, D.L. 2006. A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569: 531-544.
- Chmura, G.L., S.C. Anisfeld, D.R. Cahoon, and J.C. Lynch. 2003. Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles* 17: 1111, doi:1110.1029/2002GB001917.
- Clark, D.A., S. Brown, D.W. Kicklighter, J.Q. Chambers, J.R. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: Concepts and field methods. *Ecological Applications* 11: 356-370.
- Claus, A., and E. George. 2005. Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequence. *Canadian Journal of Forest Research* 35: 1617-1625.
- Clough, B.F. 1992. Primary productivity and growth of mangrove forests. In *Tropical Mangrove Ecosystems*, eds. A. I. Robertson and D. M. Alongi, 225-249. Washington, DC.: American Geophysical Union.
- Comley, B.W.T., and K.A. McGuinness. 2005. Above- and below-ground biomass, and allometry, of four common northern Australian mangroves. *Australian Journal of Botany* 53: 431-436.

- Cormier, N. 2003. Belowground productivity in mangrove forests of Pohnpei and Kosrae, Federal States of Micronesia. M.S. Thesis. University of Louisiana at Lafayette, Lafayette, LA.
- Darby, F.A., and R.E. Turner. 2008a. Below- and aboveground biomass of *Spartina alterniflora*: Response to nutrient addition in a Louisiana salt marsh. *Estuaries and Coasts* 31: 326-334.
- Darby, F.A., and R.E. Turner. 2008b. Below- and aboveground *Spartina alterniflora* production in a Louisiana salt marsh. *Estuaries and Coasts* 31: 223-231.
- Davis, S.E., D.L. Childers, J.W. Day, Jr., D.T. Rudnick, and F. Sklar. 2001. Nutrient dynamics in vegetated and unvegetated areas of a southern Everglades mangrove creek. *Estuarine, Coastal and Shelf Science* 52: 753-765.
- Davis, S.E.I., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W.J. Day, C.D. Huttel, C.J. Madden, E. Reyes, D. Rudnick, and F. Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida Gulf coast estuary. *Journal of Coastal Research* 20: 1198-1208.
- Day, F.P., and J.P. Megonigal. 1993. The relationship between variable hydroperiod, production, allocation, and belowground organic turnover in forested wetlands. *Wetlands* 13: 115-121.
- Delgado, P., P.F. Hensel, J.A. Jimenez, and J.W. Day, Jr. 2001. The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. *Aquatic Botany* 71: 157-178.
- Eissenstat, D.M., C.E. Wells, R.D. Yanai, and J.L. Whitbeck. 2000. Building roots in a changing environment: Implications for root longevity. *New Phytologist* 147: 33-42.
- Eissenstat, D.M., and R.D. Yanai. 1997. The ecology of root lifespan. *Advances in Ecological Research* 27: 1-60.
- Eissenstat, D.M., and R.D. Yanai. 2002. Root life span, efficiency, and turnover. In *Plant Roots: The hidden half*, eds. Y. Waisel, Y. Eshel, and U. Kafkafi, 221-238. New York: Marcel Dekker.
- Ellison, A.M. 2002. Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees* 16: 181-194.
- Ewe, S.M.L., L. da S.L. Sternberg, and D.L. Childers. 2007. Seasonal plant water uptake patterns in the saline southeast Everglades ecotone. *Oecologia* 152: 607-616.
- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, D. Iwaniec, V. Rivera-Monroy, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP)

- along tow freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569: 459-474.
- Feller, I.C., C.E. Lovelock, and K.L. McKee. 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems* 10: 347-359.
- Feller, I.C., K.L. McKee, D.F. Whigham, and J.P. O'Neill. 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145-175.
- Feller, I.C., D.F. Whigham, K.L. McKee, and C.E. Lovelock. 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia* 134: 405-414.
- Fiala, K., and L. Hernandez. 1993. Root biomass of a mangrove forest in southwestern Cuba (Majana). *Ekologia (Bratislava)* 12: 15-30.
- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.
- Gill, R.A., and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147: 13-31.
- Giraldo, B. 2005. Belowground productivity of mangrove forests in southwest Florida. Dissertation. Louisiana State University, Baton Rouge, LA.
- Gleason, S.M., and K.C. Ewel. 2002. Organic matter dynamics on the forest floor of a Micronesian mangrove forest: An investigation of species composition shifts. *Biotropica* 34: 190-198.
- Gleeson, S.K., and D. Tilman. 1992. Plant allocation and the multiple limitation hypothesis. *The American Naturalist* 139: 1322-1343.
- Golley, F., H.T. Odum, and R.F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9-19.
- Golley, F.B., J.T. McGinnis, R.G. Clements, G.I. Child, and M.J. Duever. 1975. Mineral cycling in a tropical moist forest ecosystem, Athens, GA.: University of Georgia Press.
- Gordon, W.S., and R.B. Jackson. 2000. Nutrient concentrations in fine roots. *Ecology* 81: 275-280.

- Gregory, P.J. 1987. Development and growth of root systems in plant communities. In Root development and function, eds. P. J. Gregory and D. A. Rose, 147-166. Cambridge: Cambridge University Press.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169-1194.
- Haynes, B.E., and S.T. Gower. 1995. Belowground carbon allocation in control and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* 15: 317-325.
- Hendricks, J.J., J.D. Aber, K.J. Nadelhoffer, and R.D. Hallett. 2000. Nitrogen controls on fine root substrate quality in temperate forest ecosystems. *Ecosystems* 3: 57-69.
- Hendricks, J.J., K.J. Nadelhoffer, and J.D. Aber. 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology and Evolution* 8: 174-178.
- Herbert, D.A., and J.W. Fourqurean. 2009. Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinum* in Florida Bay. *Estuaries and Coasts* 32: 188-201.
- Jackson, R.B., H.A. Mooney, and E.D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* 94: 7362-7366.
- Kenward, M., and J. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983-997.
- Khan, M.N.I., R. Suwa, and A. Hagihara. 2007. Carbon and nitrogen pools in a mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil-vegetation system. *Wetlands Ecology and Management* 15: 141-153.
- King, J.S., T.J. Albaugh, H.L. Allen, M. Buford, B.R. Strain, and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytologist* 154: 389-398.
- Koch, M.S. 1996. Resource availability and abiotic effects on *Rhizophora mangle* L. (Red Mangrove) development in South Florida. Ph.D. Dissertation. University of Miami, Coral Gables, Florida.
- Koerselman, W., and A.F.M. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33:
- Komiyama, A., S. Havanond, W. Srisawatt, Y. Mochida, K. Fujimoto, T. Ohnishi, S. Ishihara, and T. Miyagi. 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) forest. *Forest Ecology and Management* 139: 127-134.

- Komiyama, A., H. Moriya, H. Suhardjono, T. Toma, and K. Ogino. 1988. Forest as an ecosystem, its structure and function. In *Biological Systems of Mangroves*, eds. K. Ogino and M. Chihara, 85-151. Ehime: Ehime University.
- Komiyama, A., K. Ogino, S. Aksornkoae, and S. Sabhasri. 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. *Journal of Tropical Ecology* 3: 97-108.
- Krauss, K.W., T.W. Doyle, R.R. Twilley, V. Rivera-Monroy, and J.K. Sullivan. 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia* 569: 311-324.
- Lodge, T.E. 2005. *The Everglades Handbook: Understanding the Ecosystem*, 2nd edition. Boca Raton, Florida: CRC Press.
- Lovelock, C.E. 2008. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 11: 342-354.
- Lovelock, C.E., M.C. Ball, B. Choat, B.M.J. Engelbrecht, N.M. Holbrook, and I.C. Feller. 2006. Linking physiological processes with mangrove forest structure: Phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant, Cell and Environment* 29: 793-802.
- Lovelock, C.E., I.C. Feller, K.L. McKee, B.M. Engelbrecht, and M.C. Ball. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology* 18: 25-33.
- Lugo, A.E. 1990. Fringe wetlands. In *Ecosystems of the World 15, Forested Wetlands*, eds. A. E. Lugo, M. Brinson, and S. Brown, 143-169. Amsterdam: Elsevier.
- Lugo, A.E., and S.C. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5: 39-64.
- Mackey, A.P. 1993. Biomass of the mangrove *Avicennia marina* (Forsk.) Vierh. near Brisbane, south-eastern Queensland. *Australian Journal of Marine and Freshwater Research* 44: 721-725.
- Majdi, H., and P. Kangas. 1997. Demography of fine roots in response to nutrient applications in a Norway spruce stand in south-western Sweden. *Ecoscience* 4: 199-205.
- Mancera Pineda, J.E., R.R. Twilley, and V.H. Rivera-Monroy. 2009. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic discrimination in mangroves in Florida Coastal Everglades as a function of environmental stress. *Contributions in Marine Science* 38: 109-129.
- McKee, K.L. 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. *Oecologia* 101: 448-460.

- McKee, K.L. 1996. Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. *Tree Physiology* 16: 883-889.
- McKee, K.L. 2001. Root proliferation in decaying roots and old root channels: a nutrient conservation mechanism in oligotrophic mangrove forests? *Journal of Ecology* 89:
- McKee, K.L., D.R. Cahoon, and I.C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545-556.
- McKee, K.L., and P. Faulkner. 2000. Restoration of biogeochemical function in mangrove forests. *Restoration Ecology* 8: 247-259.
- McKee, K.L., and I.A. Mendelssohn. 1987. Root metabolism in the black mangrove (*Avicennia germinans* (L.) L): response to hypoxia. *Environmental and Experimental Botany* 27: 147-156.
- Megonigal, J.P., and F.P. Day. 1992. Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. *Ecology* 73: 1182-1193.
- Middleton, B.A., and K.L. McKee. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *Journal of Ecology* 89: 818-828.
- Murphy, P.G., and A.E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67-88.
- Nadelhoffer, K.J. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* 147: 131-139.
- Nadelhoffer, K.J., J.D. Aber, and J.M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: A new hypothesis. *Ecology* 66: 1377-1390.
- Nadelhoffer, K.J., and J.W. Raich. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* 73: 1139-1147.
- Naidoo, G. 2009. Differential effects of nitrogen and phosphorus enrichment on growth of dwarf *Avicennia marina* mangroves. *Aquatic Botany* 90: 184-190.
- Norby, R.J., and R.B. Jackson. 2000. Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist* 147: 3-12.
- Ostertag, R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* 82: 485-499.

- Poret, N., R.R. Twilley, V.H. Rivera-Monroy, and C. Coronado-Molina. 2007. Belowground decomposition of mangrove roots in Florida Coastal Everglades. *Estuaries and Coasts* 30: 1-6.
- Pregitzer, K.S., M.J. Laskowski, A.J. Burton, V.C. Lessard, and D.R. Zak. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* 18: 665-670.
- Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric CO₂, soil nitrogen and turnover of fine roots. *New Phytologist* 129: 579-585.
- Raich, J.W., and K.J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70: 1346-1354.
- Ruess, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Sveinbjornsson, M.F. Allen, and G.E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73: 643-662.
- Saenger, P. 1982. Morphological, anatomical and reproductive adaptations of Australian mangroves. In *Mangrove ecosystems in Australia: Structure, function and management*, eds. B. F. Clough, Canberra, Australia: Australian National University Press.
- Saintilan, N. 1997a. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research* 48: 147-152.
- Saintilan, N. 1997b. Above- and below-ground biomass of mangroves in a sub-tropical estuary. *Marine and Freshwater Research* 48: 601-604.
- Sanford, R.L.J., and E. Cuevas. 1996. Root growth and rhizosphere interactions in tropical forests. In *Tropical forest plant ecophysiology*, eds. S. S. Mulkey, R. L. Chazdon, and A. P. Smith, 268-300. New York, NY.: Chapman and Hall.
- Santantonio, D., R.K. Hermann, and W.S. Overton. 1977. Root biomass studies in forest ecosystems. *Pedobiologia* 17: 1-31.
- Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17: 667-693.
- Sherman, R.E., T.J. Fahey, and P. Martinez. 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems* 6: 384-398.
- Simard, M., K. Zhang, V.H. Rivera-Monroy, M.S. Ross, P.L. Ruiz, E. Castañeda-Moya, R.R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in

- Everglades National Park with SRTM elevation data. *Photogrammetric Engineering and Remote Sensing* 72: 299-311.
- Sutula, M. 1999. Processes controlling nutrient transport in the southeastern Everglades wetlands. Ph.D. Dissertation. Louisiana State University, Baton Rouge.
- Tamooch, F., M. Huxham, M. Karachi, M. Mencuccini, J.G. Kairo, and B. Kirui. 2008. Below-ground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya. *Forest Ecology and Management* 256: 1290-1297.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist* 125: 827-852.
- Tufekcioglu, A., J.W. Raich, T.M. Isenhardt, and R.C. Schultz. 1999. Fine root dynamics, coarse root biomass, root distribution, and soil respiration in a multispecies riparian buffer in central Iowa, USA. *Agroforestry Systems* 44: 163-174.
- Turner, R.E., E.M. Swenson, C.S. Milan, J.M. Lee, and T.A. Oswald. 2004. Below-ground biomass in healthy and impaired salt marshes. *Ecological Research* 19: 29-35.
- Twilley, R.R., A.E. Lugo, and C. Patterson-Zucca. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology* 67: 670-683.
- Twilley, R.R., and V.H. Rivera-Monroy. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research* 40: 79-93.
- Twilley, R.R., and V.H. Rivera-Monroy. 2009. Ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. In *Coastal Wetlands: An integrated ecosystem approach*, eds. G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and M. M. Brinson, 641-683. Elsevier B.V.
- Twilley, R.R., V.H. Rivera-Monroy, R. Chen, and L. Botero. 1999. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. *Marine Pollution Bulletin* 37: 404-419.
- Verhoeven, J.T.A., W. Koerselman, and A.F.M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology and Evolution* 11: 494-497.
- Vogt, K.A., D.J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil* 200: 71-89.

- Vogt, K.A., D.J. Vogt, A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant and Soil* 187: 159-219.
- Wood, T.E., D. Lawrence, and D.A. Clark. 2006. Determinants of leaf litter nutrient cycling in a tropical rain forest: Soil fertility versus topography. *Ecosystems* 9: 700-710.

*** CHAPTER 3**
SEDIMENT AND NUTRIENT DEPOSITION ASSOCIATED WITH HURRICANE
WILMA IN MANGROVES OF THE FLORIDA COASTAL EVERGLADES

INTRODUCTION

Hurricanes are large-scale pulsing events that shape community structure and function of tropical and subtropical forest ecosystems (Michener et al. 1997; Lugo 2000, 2008). Hurricane effects often include widespread changes in the physical environment of the forest, vegetation structure, species composition, succession, nutrient cycling, and animal population dynamics (Lodge and McDowell 1991; Lugo 2008). Mangrove forests are particularly more susceptible to physical changes in forest structure because of their position in the intertidal zone, usually experiencing the brunt of tropical storms (Sherman et al. 2001; Piou et al. 2006). Hurricane effects on mangrove forests depend on several factors such as the position of the forest relative to hurricane track, physical characteristics of a storm (i.e., intensity, radius to maximum wind speed, velocity), and the degree of protection offered by topographic features (Krauss et al. 2005; Piou et al. 2006; Zhang et al. 2008).

Despite their low floristic complexity relative to tropical rainforests, Neotropical mangrove forests are highly resilient to natural disturbances such as tropical storms or hurricanes. These forested wetlands have developed key life history traits that allow trajectories in ecosystem structure and function at decadal time scales depending on the frequency and intensity of hurricane disturbances (Smith et al. 1994; Alongi 2008). Such resilient traits include large nutrient reserves (belowground biomass, soil and litter), rapid nutrient turnover rates (litter immobilization, efficient microbial-plant interactions), high rates of water-use and nutrient use

* Previously published by *Estuaries and Coasts* 2010, 33(1): 45-58, and used by permission of Springer Science + Business Media (Appendix A).

efficiency, and a unique and simple tree architecture that, for some mangrove species, includes resprouting from epicormic shoots (Alongi 2008). Hurricane events also trigger processes that help to maintain soil vertical accretion through large-scale sediment deposition and redistribution by storm surge (Cahoon 2006; Day et al. 2007; Turner et al. 2007). Yet, few studies have documented the positive role of hurricane deposition in controlling soil vertical accretion in coastal wetlands (Cahoon et al. 1995; Nyman et al. 1995; Turner et al. 2007; Whelan et al. 2009), or have focused on the potential influence of these disturbance processes in maintaining mangrove soil elevation relative to sea level.

Hurricanes can also play an important role in the nutrient biogeochemistry of mangroves in zones of high disturbance frequency, which influences patterns in vegetation structure and community composition. Allochthonous mineral input has been recognized as a key process in controlling soil formation in mangrove wetlands (Chen and Twilley 1999a). Mineral inputs (i.e., Ca-bound P) during storm events to the mouth of Shark River estuary from the Gulf of Mexico, rather than upland inputs of nutrients, are hypothesized to control patterns of mangrove forest structure and productivity in the southwestern Everglades (Chen and Twilley 1999a, b). These allochthonous mineral inputs enhance P concentrations and lower N:P ratios in mangroves at the mouth of Shark River estuary, where soil properties are strongly associated with higher biomass (150-200 Mg ha⁻¹) and tree height (18-20 m) in contrast to upstream sites of this estuary and other regions of southeastern Florida (biomass < 50 Mg ha⁻¹; tree height < 5m; Ewe et al. 2006; Simard et al. 2006). Simulation models of soil organic matter content and bulk density along Shark River estuary demonstrated that field observations could only be calibrated by varying allochthonous inputs of mineral matter during storm events at the mouth of the estuary (Chen and Twilley 1999a). There was some documentation of this phenomenon from Hurricane Irene

(1999) when sediment deposits were measured as sources of carbonate-bound P to the Taylor River mangrove ecotone of south Florida (Davis et al. 2004).

South Florida is characterized by a high recurrence of tropical storms and hurricanes as other mangrove areas in the Caribbean-Gulf of Mexico region, and thus it is an excellent region to test storm effects on the structure and function of mangrove forests (Duever et al. 1994; Smith et al. 1994; Krauss et al. 2005). It is estimated that south Florida has been struck by 40 hurricanes between 1871 and 2003, with an average frequency of about once per three years (Lodge 2005). Moreover, the frequency of direct hits by major storms (category 3-5) in south Florida is approximately once every 20 years (Gentry 1974). Hurricane Wilma, a Category 3 storm, made landfall on the southwestern coast of Florida between Everglades City and Cape Romano on October 24, 2005 (Fig. 3.1a; Zhang et al. 2008). Maximum sustained winds over the Florida Coastal Everglades (FCE) were estimated to be near 105 km hr^{-1} when it made landfall (Pasch et al. 2006). The eye of the hurricane had a diameter of 89-105 km and a wind speed of 43 and 46 m s^{-1} at Broad Creek and Shark River, respectively (Fig. 3.1a; Zhang et al. 2008). For a time, hurricane Wilma was the strongest Atlantic tropical storm on record with a minimum central pressure at the time of peak intensity of 882 mb (Pasch et al. 2006). The large-scale physical damage to mangrove forest structure included defoliation, tree snapping, uprooting, depending on the distance from and compass position relative to the eye-wall.

The proximity of Wilma's landfall relative to our long-term mangrove study sites in FCE provided an excellent opportunity to evaluate the role of these pulsing events on soil nutrient biogeochemistry, forest community structure, and net primary productivity. In this study, we report on the quantity of sediment deposition and changes in soil nutrient pools in our mangrove sites to evaluate whether pulsing events such as Hurricane Wilma are significant to soil nutrient

inventories and vertical accretion by addressing the following questions: (1) What are the sediment characteristics, distribution and thickness of the sediments deposited by Hurricane Wilma in FCE mangrove sites? (2) What are relative inputs of total N and P from hurricane deposits to the nutrient pools accumulated in mangrove soils? (3) What are the fractions of inorganic and organic P in storm deposits, and how do these pools differ from those already present in mangrove soils? (4) What is the role of hurricane sediment deposition in maintaining landscape patterns of soil fertility and vertical accretion of mangroves in FCE? We report on the short-term effect of a hurricane disturbance on spatial patterns of sediment deposition and surface nutrient pools to understand how these processes may influence longer term mangrove forest dynamics as has been hypothesized for FCE.

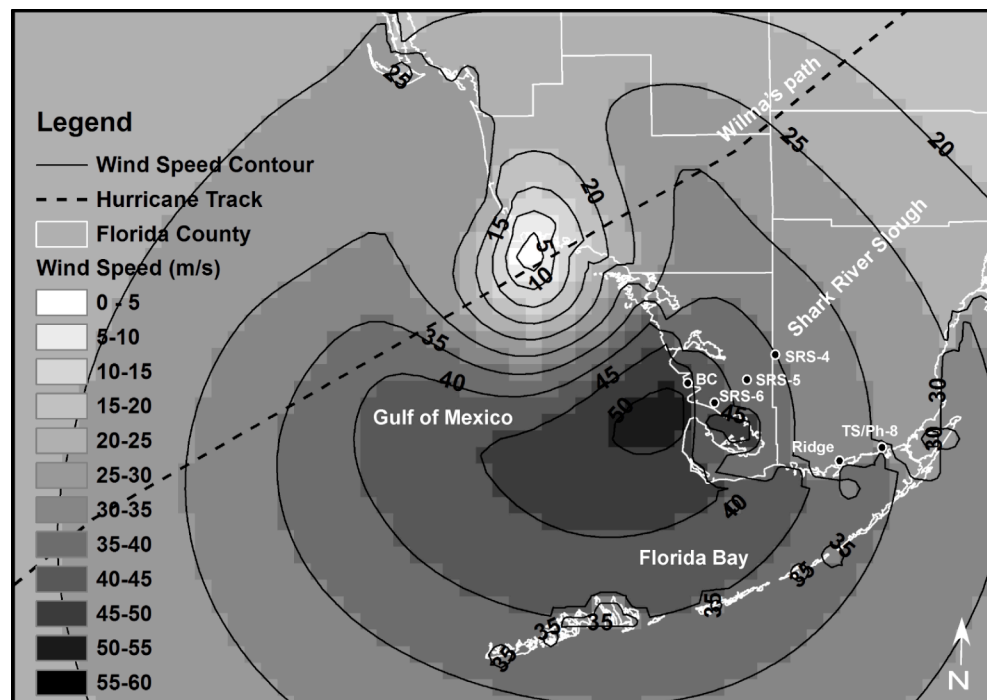


Fig. 3.1a Hurricane Wilma's track and wind fields during its passage across south Florida, U.S.A. The wind field was created using observations at 10:30 UTC on October 24, 2005. The wind speed represents maximum 1-min sustained surface wind 10 m above the ground/ocean surface. The wind field and track data were obtained from the Hurricane Research Division and the National Hurricane Center of NOAA, respectively.

MATERIALS AND METHODS

Study Sites

This study was conducted in mangrove forests of Everglades National Park (ENP), which occupy an estimated total area of 144,447 ha (Fig. 3.1b; Simard et al. 2006). This area represents approximately two-thirds of all mangrove cover in south Florida and is the largest mangrove area in the continental USA (Lodge 2005). Mangrove forests form a continuous band that extends along a freshwater-estuarine gradient from the southernmost freshwater marshes of the Everglades and Big Cypress Swamp to the open waters of Florida Bay and the Gulf of Mexico (Wanless et al. 1994).

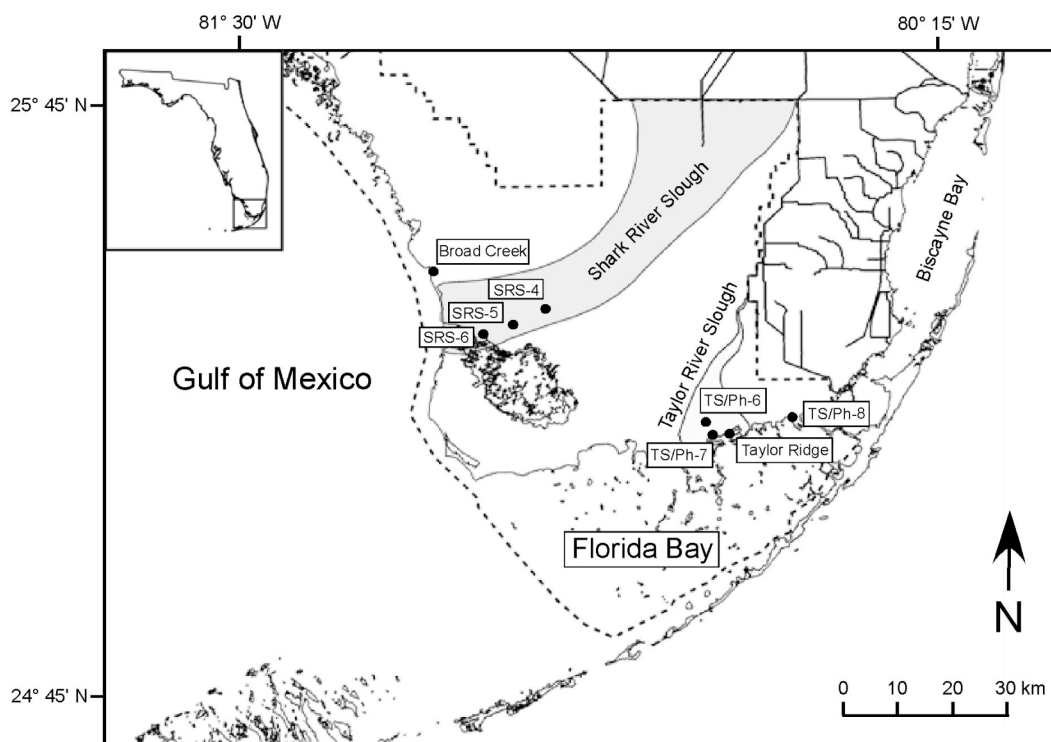


Fig. 3.1b Location of the study sites in the Everglades National Park (ENP), south Florida, USA. SRS-4, SRS-5, and SRS-6 along Shark River Slough; TS/Ph-6, TS/Ph-7 along Taylor River Slough, and TS/Ph-8 in Joe Bay are part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program. The Taylor Ridge site was located ~1 km east of the Taylor River mouth. The inset shows the location of ENP in southern Florida, U.S.A.

Mangrove forests in south Florida are distributed along the coastal margin where the limestone platform is covered with a thick layer (0.5-6.5 m) of wetland peat deposits (Wanless et al. 1994; Ewe et al. 2006). In 2000, mangrove sites were established along the Shark River and Taylor River estuaries as part of the FCE Long Term Ecological Research (LTER) program (Childers 2006; <http://fcelter.fiu.edu/>). Mangrove forests along Shark River are characterized as riverine mangroves consisting of *Rhizophora mangle* (L.), *Avicennia germinans* (L.), and *Laguncularia racemosa* (Gaertn). *Conocarpus erectus* L. is restricted to upstream locations (SRS-4) of Shark River. Shark River sites are located approximately 4.1 km (SRS-6), 9.9 km (SRS-5), and 18.2 km (SRS-4) from the mouth of Shark River estuary (Fig. 3.1b). Lower Shark River sites (SRS-5 & 6) are tide-dominated, while SRS-4 is influenced by runoff although a tidal influence is observed, particularly in the dry season (Chen and Twilley 1999b). A similar riverine mangrove site was established 2 km upstream from the mouth of Broad Creek (BC), approximately 11 km northwest of Shark River (Fig. 3.1b; Zhang et al. 2008). Tides in the Everglades are semi-diurnal with mean tidal amplitude of 1.1 m in the southwestern region and from negligible to 0.5 m in the southeastern region and Florida Bay (Wanless et al. 1994).

Along the southeastern edge of the Florida peninsula along Florida Bay, mangrove zones are dominated by *R. mangle* scrub forest (tree heights ≤ 1.5 m) with clusters of *C. erectus*. A 1 km wide depositional berm (Buttonwood Ridge; ~ 0.5 m in height) that stretches roughly 60 km across the southern tip of Florida isolates these scrub forests (e.g., TS/Ph-6 & 7) from the direct influence of Florida Bay (Davis et al. 2004). Forests on the Buttonwood Ridge are dominated by *C. erectus* and *A. germinans*, while *R. mangle* borders it. Taylor River is one of several small mangrove channels that cuts through the Buttonwood Ridge and serves as a surface water link between the southern Everglades and Florida Bay (see description in Davis et al. 2001). The

study site in the Buttonwood Ridge was established approximately 1 km east of the Taylor River mouth site (TS/Ph-7; Fig. 3.1b). Another site, TS/Ph-8, was located near Snook Creek, a tributary of Joe Bay (Fig. 3.1b), which is not bounded by Buttonwood Ridge. This site supports a mixed community of sawgrass (*Cladium jamaicense*) and mangroves, with mangrove tree heights of about 3-4 m. *Rhizophora mangle* dominates the fringe areas and tidal creeks, whereas *C. erectus* is found in the interior parts (Ewe et al. 2006). Mangrove waterways of this southeastern Everglades region are non-tidal systems in contrast to Shark River and Broad Creek, and water flow is determined by the interactions of seasonal precipitation, upland runoff, and wind (Sutula 1999; Davis et al. 2001).

We compared storm deposits in all six of the long-term FCE mangrove plots and those along new transects established for this post-hurricane study. Comparisons among mangrove transect and plots of southwest (Shark River and Broad Creek) and southeast (Taylor River, Taylor Ridge, and Joe Bay) Florida allow us to test if there are gradients in storm-related nutrient inputs to the mangroves of FCE. In addition, two of the FCE mangrove plots (TS/Ph-6 & 7) along Taylor River are isolated from Florida Bay by the Buttonwood Ridge, compared to Joe Bay (TS/Ph-8) that is hydrologically coupled to Florida Bay. It has been suggested that this ridge prevents storm deposits from fertilizing mangroves and thus limiting mangrove structure. Finally, location of plots inland from the mouths of Shark and Taylor Rivers allow us to test how far inland storm deposits can impact the nutrient inventory of mangrove soils. These results are specific to the conditions of Hurricane Wilma, but present one observation to test these ideas as to how nutrient redistribution during storm events may impact mangrove patterns in this oligotrophic coastal ecosystem (Childers 2006).

Hydrology and Storm Surge

Water levels were measured in some of the FCE-LTER mangrove locations affected by Hurricane Wilma (SRS-4, 5 & 6 as well as TS/Ph-8). Ultrasonic water level recorders (model 220, Infinities USA, Inc., Port Orange, Florida) were installed in the interior of each mangrove site about 50-80 m from shore. Water level recorders were placed on top of a PVC pipe (1.5 m above the soil surface) that was placed approximately 1 m below the soil surface. Water levels relative to soil surface were recorded at 1 h intervals.

Sediment Core Collection and Analyses

We measured the physico-chemical properties, distribution, and thickness of storm sediments from duplicate sediment cores collected at sampling points along transects at Broad Creek (December 2005), at SRS-6 (December 2005), and Taylor Ridge (October 2006). All soil-sediment cores were collected with a piston corer (2.5 cm diameter x 15 cm length), sectioned into two layers, storm deposits (of variable depths) and surface mangrove soils (top 10 cm), and the depth of each layer was registered. The storm layer was easily distinguished from the mangrove soil layer because of its gray color, fine sand texture, and organic-free deposits. Samples were temporarily stored in plastic bags at 4 °C and brought to the laboratory for further analyses.

Transects were positioned perpendicular from the mangrove shoreline (i.e., 0 m from water) to the interior of the mangrove forest at each site, and transect lengths varied depending on soil elevation and mangrove cover at each site. The SRS-6 transect is across an island (700 m wide) surrounded by numerous channels as part of original classification of vegetation. For the purposes of this study, we divided the transect into two sections, SRS-6E (250 m in length) and SRS-6W (350 m in length) to characterize storm sediment deposition with distance inland from

shoreline on both sides of the island. The Buttonwood Ridge transect was 150 m in length and established from the shoreline with Florida Bay to the interior of Taylor Ridge. Soil-sediment cores were also collected from two permanent vegetation plots at SRS-6 ($n = 8$) in December 2005 and at TS/Ph-8 ($n = 4$) in October 2006. Vegetation plots were located 50 m (SRS-6) and 30 m (TS/Ph-8) from the shoreline of Shark River estuary and Joe Bay, respectively. The plots of SRS-6 were located approximately 100 m north of the 700 m long transect (east-west direction).

Surface soil and storm layers of cores were oven-dried at 60 °C to a constant weight and weighed to determine bulk density. Core samples were ground with a Wiley Mill to pass through a 250- μm -mesh screen. Organic matter content is defined as percent of ash-free dry weight (AFDW %), determined by combusting samples in a furnace for 2 h at 550 °C (Davies 1974). Data were expressed on a volume basis (mg cm^{-3}) using bulk density values. Total nitrogen (N) was determined on two analytical replicates of each core sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total phosphorus (P) was extracted on duplicate core samples with 1 N HCL after combustion in a furnace at 550 °C (Aspila et al. 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas).

We used a sequential fractionation scheme (Hedley et al. 1982) to determine inorganic and organic pools of P in soil and sediment core samples. First, labile inorganic P (labile P_i) that is directly exchangeable with soil solution was measured with anion-exchange resin strips (2 x 6 cm) in bicarbonate form and subsequently extracted with 0.5 M HCL (Lajtha et al. 1999). Second, labile and plant-available P sorbed onto soil surfaces (labile sorbed- P_i) was extracted with 0.5 M NaHCO_3 . Next, an extraction with NaOH 0.1 M released Fe and Al-bound inorganic P (Fe/Al-bound P_i). Then, occluded Fe and Al-bound inorganic P was extracted by

ultrasonification (for 20 min in a bath sonicator) with fresh NaOH 0.1 M. Finally, Ca-bound inorganic P (Ca-bound P_i) was extracted with 1 M HCL. All extractions were equilibrated for a period of 18 h by continuous shaking on a mechanical shaker at 180 rpm. Subsamples of the NaHCO_3 and NaOH extracts were digested using an alkaline persulfate digestion procedure to determine total P in the extract. Organic P in each extract was calculated as total P less inorganic P in the extract (Lajtha et al. 1999). Residual P was determined as the difference between total P extracted with the Aspila et al. (1976) method and the sum of all extracted forms of P. After each step, extracts were centrifuged and the supernatants were analyzed colorimetrically for soluble reactive phosphate (assumed to be inorganic PO_4^{-3}) using a segmented flow analysis Flow Solution IV autoanalyzer.

Statistical Analyses

All statistical analyses were performed with PROC MIXED (SAS Institute, Cary, NC, USA). Data collected within the plots of SRS-6 and TS/Ph-8 were analyzed separately with a two-way ANOVA to test for differences in organic matter content, bulk density, and nutrient concentrations (total N and P) among sites and layers. For the transect data, we used a randomized block ANOVA design to test for differences in deposition depth, bulk density, organic matter content, and total N and P among sites, distance along transects, and layer (soil vs. sediment). Differences among inorganic and organic pools of P were tested independently within each layer using the same randomized block ANOVA design. All effects were considered fixed. Distance was nested within each site and was treated as a block. Prior to analysis, the actual sampling distance along each transect was normalized on a scale of 0 to 1 to facilitate further ANOVA comparisons among main effects. The ANOVA design was unbalanced for each variable due to differences in the number of sampling points and total number of observations

recorded along each transect. The Kenward-Roger procedure was used to adjust the degrees of freedom of the F test statistics when an unequal variance model was significant (SAS Institute, Cary, NC, USA; Kenward and Roger 1997). Interaction effects were considered for all analyses. Pairwise comparisons were performed with Tukey's HSD test when significant differences ($p < 0.05$) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. The assumption of homocedasticity was tested using the "null model" likelihood ratio test of the residual errors with a chi square distribution. All variables were log-transformed ($\ln(x + 1)$) prior to analysis to meet the ANOVA assumptions, except total N, total P, bulk density, and deposition depth. Unless otherwise stated, data presented are means (± 1 SE) of untransformed data.

RESULTS

Hydrology and Storm Surge

Water levels from Shark River estuary responded to a distinct storm surge on October 24, 2005 (Fig. 3.2). Storm surge within the forest (relative to soil surface) was higher at the mouth of Shark River (SRS-6 and SRS-5) and decreased upstream (SRS-4, 18.2 km from the mouth). The estimated water level in SRS-6 was approximately 3-4 m above soil level, based on field observations (see dotted line on Fig. 3.2). The water level recorder is positioned 1.5 m above the soil surface, preventing any actual measurements above that depth. Water marks on tree trunks of mangroves and hurricane sediment deposition observed in equipment positioned on platforms above soil level (~3-4 m) in the interior part of the forest (100 m inland), suggest the estimated maximum water level reached during the storm surge. Water levels in SRS-5 and SRS-4 peaked at 1.04 and 0.46 m above the soil surface, respectively. In Shark River, water levels peaked at the downstream sites in the morning compared to late afternoon at upstream site. At TS/Ph-8, peak

water level was about 0.86 m above the soil surface in the morning. Overall, the storm surge in our mangrove sites lasted approximately 7-8 h, based on data recorded by the instruments (Fig. 3.2).

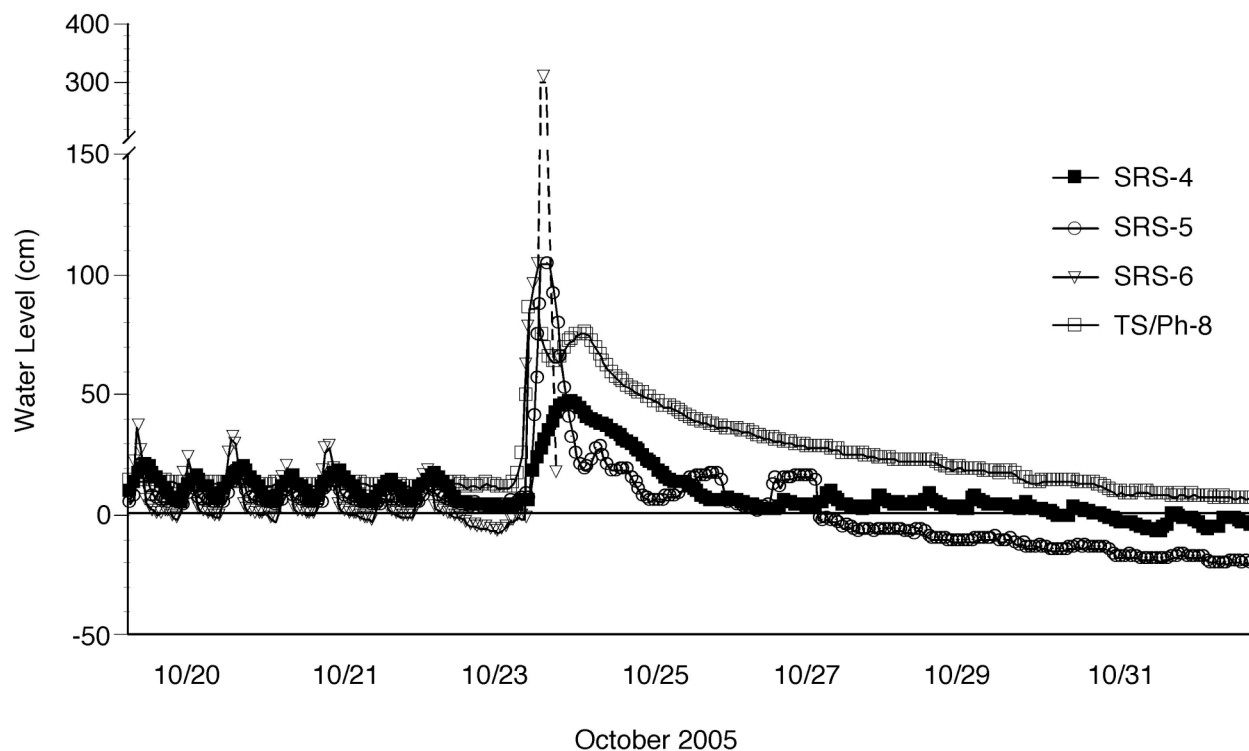


Fig. 3.2 Water levels in mangrove forests of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program during the passage of Hurricane Wilma on October 24, 2005. The zero mark is relative to the soil surface in each site. All water level data are not referenced to the North American Vertical Datum of 1988 (NAVD88). The dotted line indicates the maximum water level observed in SRS-6 based on field observations.

Soil and Sediment Properties

There was a different pattern of sediment deposition among the long-term mangrove plots compared to transects established to measure post-hurricane effects (Table 3.1). The most inland plot of Shark River Slough, SRS-4 (18.2 km from the mouth of Shark River), had no observed sediment deposits, compared to a slight film of deposits in SRS-5 that was not measurable using

our coring technique (<0.5 cm). This is in contrast to significant deposits measured in both plots and transects of SRS-6 and along the transect of Broad Creek, both in close proximity to the Gulf of Mexico. In southeastern FCE, the inland plots of Taylor River, TS/Ph-6 and TS/Ph-7 had no observable storm deposits, compared to measurable deposits in TS/Ph-8 plots and the Taylor Ridge transect near Taylor River (Table 3.1).

Table 3.1 Bulk density and organic matter content of storm sediments and surface soils (top 10 cm) measured in transects and plots of mangrove forests in the Florida Coastal Everglades (FCE) after the passage of Hurricane Wilma. Means (± 1 SE) followed by different small letters within each row are significantly different for each variable (Tukey HSD post hoc test: $p < 0.05$). Means (± 1 SE) followed by different capital letters within each column are significantly different (Tukey HSD post hoc test: $p < 0.05$).

Site	Bulk Density (mg cm^{-3})		Organic Matter (mg cm^{-3})	
	Storm sediments	Surface soils	Storm sediments	Surface soils
Transects				
Broad Creek	489.9 (46.9) ^{a, B}	180.5 (17.5) ^{b, B}	60.0 (1.9) ^{b, B}	104.1 (6.9) ^{a, B}
SRS-6E	642.9 (112.2) ^{a, AB}	156.9 (15.1) ^{b, B}	68.9 (9.6) ^{b, B}	109.9 (8.1) ^{a, AB}
SRS-6W	716.5 (108.6) ^{a, AB}	153.1 (10.3) ^{b, B}	77.6 (12.7) ^{b, B}	111.7 (6.0) ^{a, AB}
Taylor Ridge	748.8 (44.1) ^{b, A}	974.1 (28.7) ^{a, A}	131.8 (4.9) ^{a, A}	147.3 (8.5) ^{a, A}
Plots ^c				
SRS-4 ^d				
SRS-5 ^e				
SRS-6	686.5 (33.3) ^{a, A}	203.7 (7.0) ^{b, A}	69.0 (3.7) ^{b, A}	123.8 (6.8) ^{a, A}
TS/Ph-6 ^d				
TS/Ph-7 ^d				
TS/Ph-8	371.5 (45.9) ^{a, B}	194.1 (15.2) ^{b, A}	80.7 (11.7) ^{a, A}	62.4 (8.9) ^{a, B}

^c Statistical results using only plot data.

^d Storm sediments were not observed in these plots and therefore sampling was not performed.

^e Storm sediments not sufficient amount (< 0.5 cm) to sample.

There was a significant decrease in thickness of storm sediment with distance inland from shore along each of four transects (Table 3.2; Fig. 3.3). Sediment deposition averaged 2.5 cm within the first 250 m from shore at Broad Creek (BC) transect and decreased to 1.0 cm from 450 to 700 m inland. In SRS-6E, deposition averaged 2.5 cm within the first 100 m and

decreased to 1.0 cm at 250 m inland. At SRS-6W, sediment deposition decreased from 1.3 to 0.5 cm along the 350 m transect. Along the Taylor Ridge transect, deposition was highly variable and averaged 2.2 cm during first 40 m from shore and decreased to 1.0 cm at the end of the transect (Fig. 3.3). In TS/Ph-8, deposition on the permanent plots was 4.5 ± 0.5 cm ($n = 4$), while in the SRS-6 plots deposition averaged 2.3 ± 0.1 cm ($n = 8$).

Bulk density was significantly different between sediment and soil layers (Tables 3.1, 3.2), with higher bulk density in the storm sediment layer (650.4 ± 30.9 mg cm⁻³) compared to surface soil layer (top 10 cm of soil = 366.2 ± 11.8 mg cm⁻³). There was a significant interaction between sites and layers (Tables 3.1, 3.2). All sites had higher bulk densities in the storm sediments (range from 489.9 ± 46.9 to 716.5 ± 108.6 mg cm⁻³) than in surface soils (range from 153.1 ± 10.3 to 180.5 ± 17.5 mg cm⁻³), except on Taylor Ridge, where both storm sediments and surface soils had high bulk density values (Table 3.1). In plots of TS/Ph-8 and SRS-6, bulk density of storm sediment deposits was 2 and 3 times that of mangrove soils, respectively (interaction site x layer: $F_{1,20} = 26.8$, $p < 0.001$; Table 3.1).

Organic matter content was significantly lower in storm sediments (84.5 ± 7.2 mg cm⁻³) compared to surface soils (top 10 cm = 118.3 ± 7.3 mg cm⁻³; Tables 3.1, 3.2). There was a significant interaction between sites and layers (Table 3.1, 3.2). All sites had higher organic matter content in soil surface (top 10 cm) compared to storm sediment deposits, except in Taylor Ridge, where organic matter content was not significantly different between the two layers (Table 3.1). In general, organic matter content in surface soils ranged from 61.6 ± 0.5 mg cm⁻³ (TS/Ph-8) to 147.3 ± 8.5 mg cm⁻³ (Taylor Ridge), and from 60.0 ± 1.9 mg cm⁻³ (BC) to 131.8 ± 4.9 mg cm⁻³ (Taylor Ridge) in storm sediment deposits (Table 3.2).

Table 3.2 Statistical results of physico-chemical properties measured in storm sediments and surface soils (top 10 cm) along transects in mangrove forests of the Florida Coastal Everglades (FCE) after the passage of Hurricane Wilma. Significant levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant. – = not determined.

Variables	Site			Distance (Site)			Layer (sediment vs. soil)			Site x Layer		
	df ^a	F	p	df ^a	F	p	df ^a	F	p	df ^a	F	p
Deposition Depth (cm)	3, 20	12.5	***	23, 20	10.3	***	–	–	–	–	–	–
Bulk Density (mg cm ⁻³)	3, 21.6	125.9	***	25, 18.2	1.1	ns	1, 22.4	73.2	***	3, 21.6	43.8	***
Organic Matter (mg cm ⁻³)	3, 72	31.6	***	25, 72	1.0	ns	1, 72	38.7	***	3, 72	4.1	**
Total N (mg cm ⁻³)	3, 72	12.3	***	25, 72	1.9	*	1, 72	20.3	***	3, 72	2.2	ns
Total P (mg cm ⁻³)	3, 72	17.6	***	25, 72	1.5	ns	1, 72	30.9	***	3, 72	21.1	***

^a The degrees of freedom (df) of the denominator were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

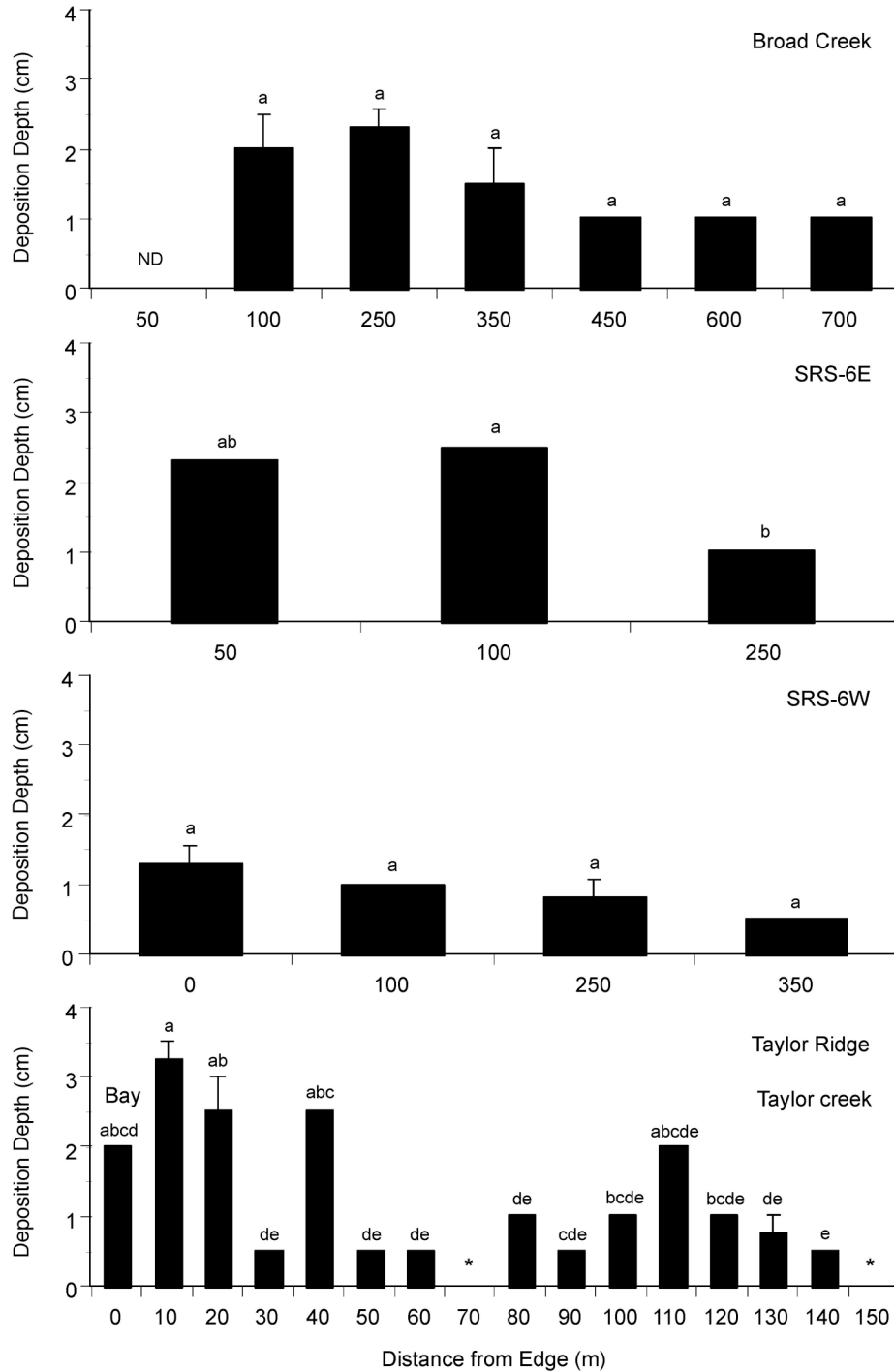


Fig. 3.3 Depth of storm sediment deposits at four mangrove sites in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005. Different letters indicate significant differences ($p < 0.05$) among sampling points along each transect. ND indicates samples were not collected. Asterisks indicate no storm deposition.

Total N concentrations were significantly lower in storm sediments ($2.7 \pm 0.1 \text{ mg cm}^{-3}$) than in the soil surface ($3.2 \pm 0.2 \text{ mg cm}^{-3}$; Table 3.2), and there was no significant interaction between sites and layers (Table 4.2; Fig. 4.4a). In general, N concentrations in the storm deposits ranged from 1.9 ± 0.3 (BC) to $3.2 \pm 0.1 \text{ mg cm}^{-3}$ (Taylor Ridge), compared to 2.8 ± 0.1 (SRS-6W) to $3.4 \pm 0.2 \text{ mg cm}^{-3}$ (Taylor Ridge) in the soil surface layer (Fig. 3.4a). Results in the plots of SRS-6 and TS/Ph-8 were different, with higher total N in storm deposits of TS/Ph-8 ($2.4 \pm 0.4 \text{ mg cm}^{-3}$) compared to soil surface ($1.9 \pm 0.3 \text{ mg cm}^{-3}$), although this difference was not significant; whereas SRS-6 followed the same pattern as results for the transects in the southwest, with lower total N in sediment deposits compared to soils (interaction site x layer: $F_{1,20} = 14.0$, $p = 0.0013$; Fig. 3.4a).

Mean total P concentrations were significantly different among sites and layers (Table 3.2, Fig. 3.4b). In contrast to N, total P was significantly higher in storm deposits ($0.36 \pm 0.02 \text{ mg cm}^{-3}$) compared to the soil surface ($0.22 \pm 0.02 \text{ mg cm}^{-3}$). There was a significant interaction between sites and layers (Table 3.1; Fig. 3.4b). Sites SRS-6W, SRS-6E, and BC had significantly higher P concentrations in storm deposit sediments (range from 0.38 to 0.51 mg cm^{-3}) compared to soil surface (range from 0.16 to 0.29 mg cm^{-3} ; Fig. 3.4b). Same trend was observed for the plots of SRS-6 with a higher total P density in storm sediments compared to soils, whereas TS/Ph-8 had significantly lower total P density in sediment deposits, similar to that of soil surface (interaction site x layer: $F_{1,20} = 6.4$, $p = 0.0196$; Fig. 3.4b). Total P density in SRS-6 sediment deposits was significantly seven times higher than in TS/Ph-8 (Fig. 3.4b). In contrast, an opposite trend was observed in Taylor Ridge with lower values in storm sediments ($0.10 \pm 0.01 \text{ mg cm}^{-3}$; Fig. 3.4b) than in soil surface ($0.22 \pm 0.02 \text{ mg cm}^{-3}$).

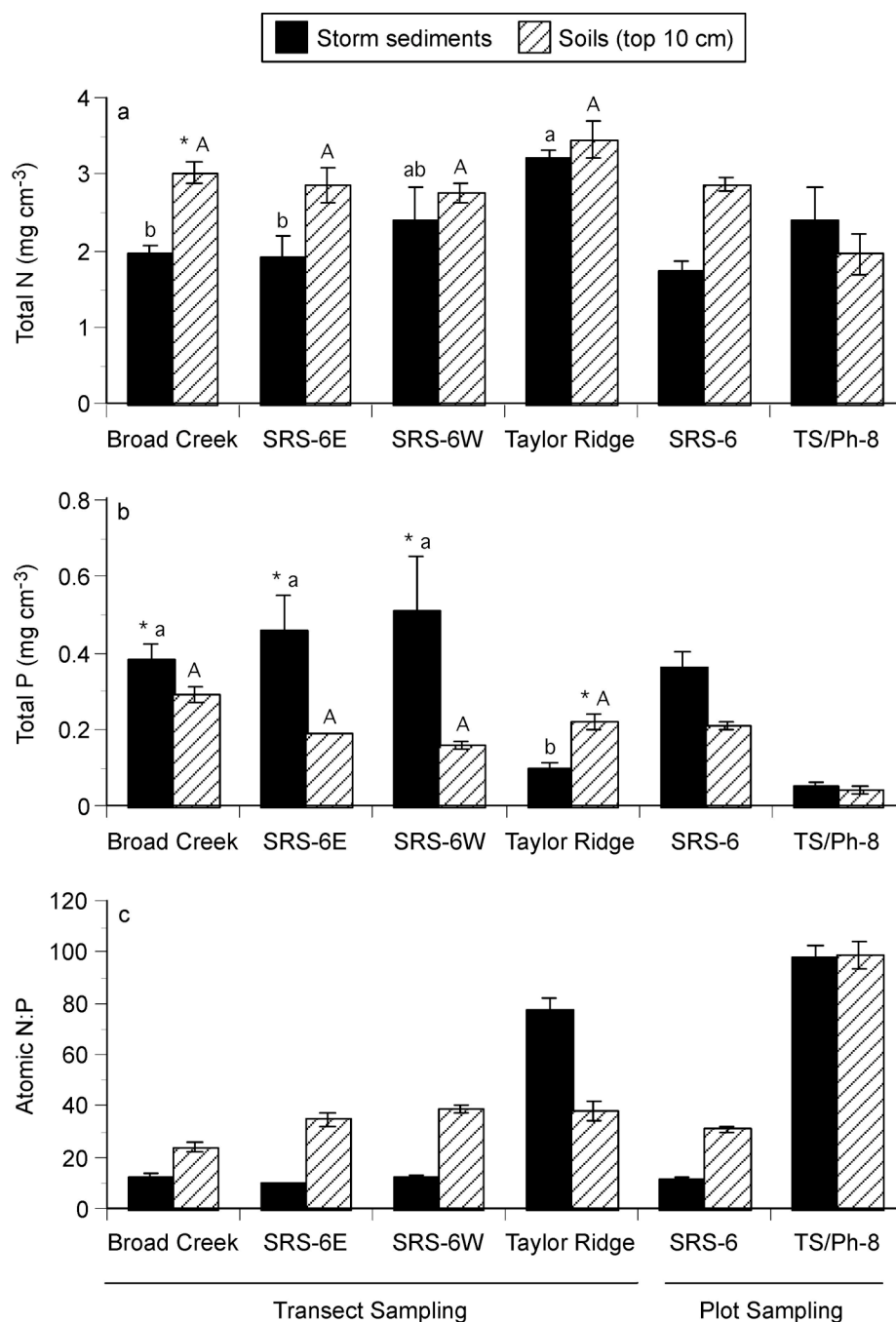


Fig. 3.4 Mean (± 1 SE) total nitrogen (a) and total phosphorus (b) concentrations, and atomic N:P ratios (c) in storm sediments and surface soils (top 10 cm) at sites sampled in transects and long-term plots in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005. Asterisks indicate significant differences ($p < 0.05$) within each site. Different small letters indicate significant differences ($p < 0.05$) among sites in the storm sediment layer for each sampling technique (transects vs. plots). Different capital letters indicate significant differences ($p < 0.05$) among sites in the surface soil layer for each sampling technique (transects vs. plots).

Ca-bound P_i was significantly the largest bioavailable fraction of P in storm deposits at all sites ranging from 0.029 ± 0.003 (Taylor Ridge) to $0.130 \pm 0.03 \text{ mg cm}^{-3}$ (SRS-6W; Table 3.3), and accounted for up to 25-29% of total P (Fig. 3.5). The amount of labile P_i fraction was the second largest fraction of storm sediment deposits in all sites, with the highest concentrations in SRS-6E ($0.050 \pm 0.01 \text{ mg cm}^{-3}$) and lowest in Taylor Ridge ($0.027 \pm 0.003 \text{ mg cm}^{-3}$; Table 3.3); the contribution of this fraction comprised 11-23% of total P (Fig. 3.5). Concentrations of the Fe/Al-bound P_i fraction of storm deposits were also significantly different among sites, with BC, SRS-6E, and SRS-6W showing the highest concentrations of P relative to Taylor Ridge. Mean P concentrations of this fraction ranged from $0.002 \pm 0.0002 \text{ mg cm}^{-3}$ to $0.011 \pm 0.001 \text{ mg cm}^{-3}$. The organic P fractions (extractions of NaHCO_3 and NaOH) of storm sediments had the lowest concentrations of P in all sites compared to the other fractions, with concentrations ranging from 0.001 ± 0.0002 to $0.007 \pm 0.002 \text{ mg cm}^{-3}$ (Table 3.3). No significant differences were observed in the NaOH organic P fraction among sites (Table 3.3). The relative contribution of the Fe/Al-bound and the organic P fractions was <4% in all sites (Fig. 3.5). The amount of residual P of storm sediments did vary significantly among sites and was the largest fraction overall (Fig. 3.5; Table 3.3). At TS/Ph-8, the Ca-bound and labile inorganic P fractions had the lowest P concentrations (0.012 ± 0.003 and $0.013 \pm 0.002 \text{ mg cm}^{-3}$, respectively) of all storm sediment P fractions (Table 3.3).

The P fractions in mangrove soils showed a similar trend among sites as storm deposits, although concentrations and relative contributions (<15% of total P) were lower (Table 3.3; Fig. 3.5). In general, the Ca-bound P_i and labile P_i concentrations were significantly higher in soils at all sites, however, the amount of the NaOH organic P fraction in SRS-6E, SRS-6W, and BC was also a significant pool of total P (Table 3.3). The Ca-bound P fraction had the highest

Table 3.3 Phosphorus (P) fractions in storm sediments and surface soils (top 10 cm) in mangrove forests of the Florida Coastal Everglades (FCE) after the passage of Hurricane Wilma. Means (± 1 SE) followed by different small letters across each row are significantly different (Tukey HSD post hoc test). Means (± 1 SE) followed by different capital letters within each column are significantly different (Tukey HSD post hoc test). ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Site	Soil P Fractions (mg cm^{-3})					
	Ca-bound P_i	Labile P_i	Fe/Al-bound P_i	$\text{NaHCO}_3 P_o$	$\text{NaOH } P_o$	Residual P
Storm sediments						
Broad Creek	0.105 (0.015) ^{a, A}	0.042 (0.003) ^{b, AB}	0.011 (0.001) ^{c, A}	0.007 (0.002) ^{cd, A}	0.007 (0.005) ^{ce, A}	0.211 (0.044) ^{a, A}
SRS-6E	0.129 (0.015) ^{a, A}	0.050 (0.008) ^{b, A}	0.008 (0.001) ^{ce, A}	0.003 (0.000) ^{de, AB}	0.001 (0.001) ^{be, A}	0.261 (0.072) ^{a, A}
SRS-6W	0.130 (0.026) ^{a, A}	0.056 (0.011) ^{b, AB}	0.007 (0.001) ^{c, A}	0.003 (0.001) ^{d, B}	0.003 (0.001) ^{de, A}	0.310 (0.105) ^{a, A}
Taylor Ridge	0.029 (0.003) ^{a, B}	0.027 (0.003) ^{a, B}	0.002 (0.0002) ^{b, B}	0.003 (0.001) ^{bc, B}	0.004 (0.001) ^{bd, A}	0.051 (0.016) ^{a, B}
TS/Ph-8 ^h	0.012 (0.003)	0.013 (0.002)	0.002 (0.0002)	0.001 (0.0002)	0.002 (0.0004)	0.017 (0.001)
Surface soils						
Broad Creek	0.025 (0.006) ^{b, AB}	0.018 (0.003) ^{bc, A}	0.010 (0.0016) ^{cd, A}	0.002 (0.0008) ^{e, B}	0.016 (0.0036) ^{bd, A}	0.220 (0.013) ^{a, A}
SRS-6E	0.014 (0.007) ^{b, BC}	0.014 (0.001) ^{bc, A}	0.005 (0.0003) ^{e, AB}	0.001 (0.0002) ^{f, B}	0.017 (0.0013) ^{bd, A}	0.135 (0.010) ^{a, A}
SRS-6W	0.009 (0.003) ^{b, C}	0.014(0.002) ^{bc, A}	0.004 (0.0007) ^{e, B}	0.001 (0.0001) ^{f, B}	0.013 (0.0019) ^{d, A}	0.123 (0.008) ^{a, A}
Taylor Ridge	0.040 (0.006) ^{b, A}	0.017 (0.004) ^{c, A}	0.002 (0.0003) ^{df, C}	0.006 (0.0018) ^{e, A}	0.002 (0.0006) ^{bf, B}	0.156 (0.021) ^{a, A}
TS/Ph-8 ^h	0.007 (0.001)	0.009 (0.001)	0.003 (0.0006)	0.002 (0.0006)	0.001 (0.0002)	0.026 (0.008)
ANOVA source ^g :	Storm sediments		Surface soils			
Site	$F_{3, 5.2} = 21.7$ (**)		$F_{3, 172} = 22.9$ (***)			
Distance (site)	$F_{18, 61.2} = 2.2$ (*)		$F_{18, 172} = 4.1$ (***)			
P Fraction	$F_{5, 12.6} = 321.0$ (***)		$F_{5, 172} = 401.0$ (***)			
Site x P Fraction	$F_{15, 24.6} = 6.6$ (***)		$F_{15, 172} = 20.9$ (***)			

^g Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed.

^h Not included in any of the statistical analysis.

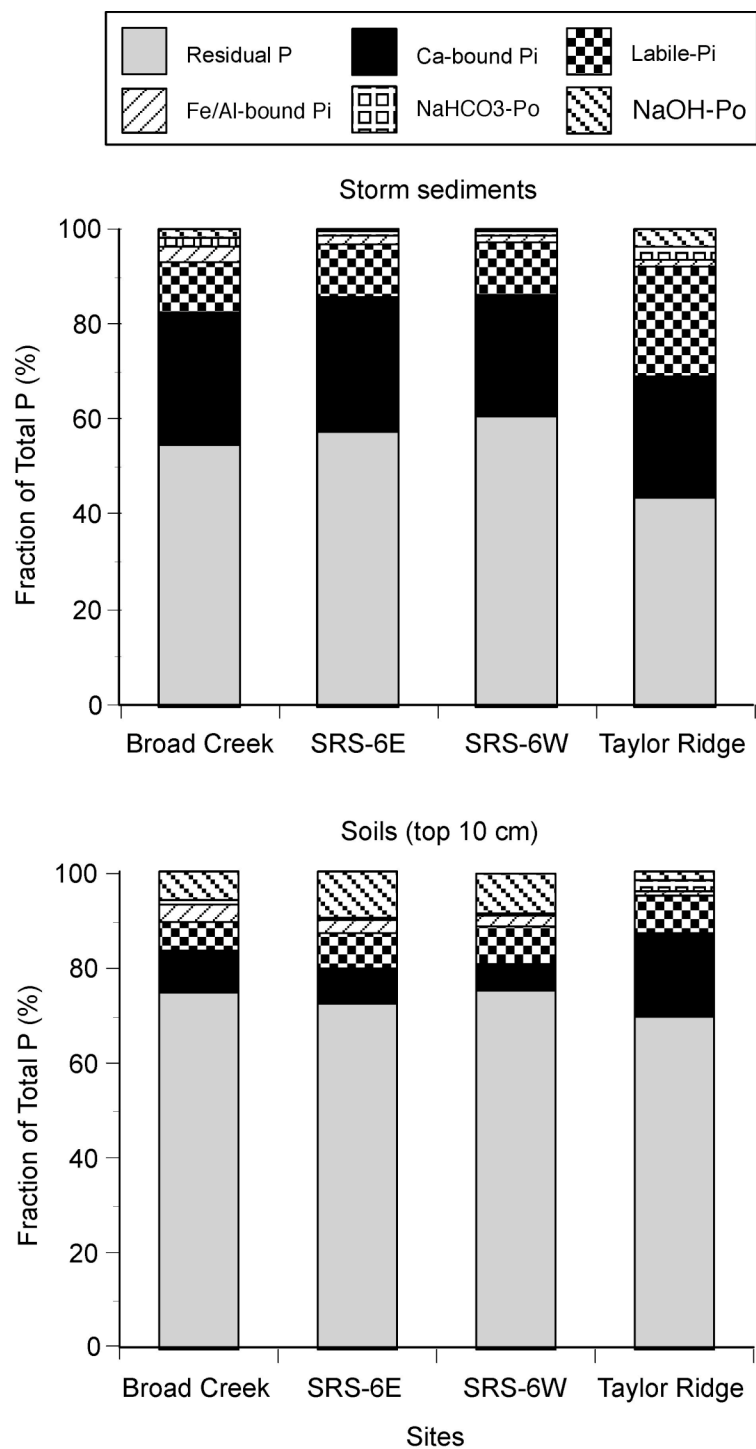


Fig. 3.5 Contribution of P fractions to the total P pool in storm sediments and surface soils (top 10 cm) at four mangrove sites in the Florida Coastal Everglades after the passage of Hurricane Wilma on October 24, 2005.

concentration in Taylor Ridge soils ($0.040 \pm 0.01 \text{ mg cm}^{-3}$) and the lowest in SRS-6W ($0.009 \pm 0.003 \text{ mg cm}^{-3}$). There were no significant differences in the labile inorganic fraction among sites, with values ranging from 0.014 to 0.018 mg cm^{-3} (Table 3.3). The Fe/Al-bound P_i and NaHCO_3 P_o fractions represented the smallest soil pools at all sites ranging from 0.001 to 0.010 mg cm^{-3} (Table 3.3). The amount of residual P in soils did not vary significantly among sites and was consistently the largest soil P fraction (Fig. 3.5, Table 3.3). In TS/Ph-8, the Ca-bound and labile inorganic P fractions had the lowest P concentrations (0.007 ± 0.001 and $0.009 \pm 0.001 \text{ mg cm}^{-3}$, respectively) of all soil P fractions (Table 3.3).

DISCUSSION

Storm Surge and Soil Vertical Accretion

The passage of Hurricane Wilma through FCE had significant effects on local hydrology, sediment deposition, and nutrient biogeochemistry of mangrove soils. The storm surge within mangroves was ~ 3 m at the mouth of Shark River estuary and decreased to 0.50 m at the upper mangrove sites about 18 km from the mouth of the estuary. This pattern is consistent with water levels >4 m in mangrove sites adjacent to the Gulf of Mexico coast compared to water levels of about 0.5-1.0 m in upstream locations during the passage of Hurricanes Andrew and Wilma across several locations on southwestern ENP (Risi et al. 1995; Smith et al. 2009). Similarly, in the Florida Bay area, Davis et al. (2004) documented a flood surge depth from about 0.2 to 0.5 m across the Taylor Ridge area, east of Taylor River from Hurricane Irene in 1999.

Large amounts of sediment from the coastal shelf were redistributed and deposited across mangrove forests of FCE associated with the storm surge. We observed maximal deposition in mangrove areas adjacent to the mouth of Shark River and found no storm deposits from Wilma in areas 18.2 km (SRS-4) from the Gulf of Mexico. Patterns in sediment deposited by Hurricane

Wilma were relatively similar to those observed following Hurricane Andrew, ranging from 1-10 and 0-20 cm in mangrove forests between Lostman's River (~12 km northwest of Broad Creek) and Shark River (Smith et al. 1994; Risi et al. 1995). Sediment deposition during Andrew extended up to 10-15 km inland across mangrove wetlands, becoming thinner with distance from the Gulf of Mexico, with no deposition in the upstream bays such as the Tarpon Bay area (near our SRS-4 site). A separate survey following Wilma measured maximal sediment deposition (<10 cm) in mangrove areas adjacent to the coast (2-5 km) between Lostman's River and areas south of Shark River (Smith et al. 2009). Deposits gradually decreased upstream of tidal rivers, with no deposition in mangrove forests located approximately 15.5 km from the Gulf of Mexico. All of these studies, including our survey, found that sediment deposition varied spatially within each mangrove site, with higher deposition in areas adjacent to the shore in the fringe mangrove zone, and lower deposition in the interior forest.

In the Florida Bay area, Davis et al. (2004) also found a similar pattern of sediment deposition (5 cm) in the Taylor Ridge area as a result of Hurricane Irene in October 1999. Yet, the deposition associated with this relatively weak category 1 storm was confined to a 60 m zone in the center of Taylor Ridge, while our results show deposition from Wilma was maximal in the shore fringe of Taylor Ridge (Fig. 3.3). The overall variability in sediment deposition along Taylor Ridge could be attributed to the geomorphology of the coast, the local microtopography, the accumulation of sediments in depressions as the surge receded, and the direction and strength of the storm surge as it struck the area (Davis et al. 2004).

Sediment deposited by Hurricane Wilma represents a significant adjustment in soil elevation of mangroves compared to vertical accretion rates estimated with radioisotope methods. This impact of hurricane Wilma on mangrove forests within FCE is localized within 10

km upstream of the Gulf of Mexico in areas that do not have geomorphic features that act as barriers to storm surge effects. This allochthonous sediment input along with autochthonous processes (belowground root growth) occurring in the soil profile result in vertical accretion (Cahoon and Lynch 1997). Accretion is often measured using techniques such as soil marker horizons (feldspar; Cahoon et al. 1996) or radionuclides (^{137}Cs , ^{210}Pb ; Callaway et al. 1996) that integrate accretion and erosion processes on longer time scales than single depositional events. Sediment deposition estimated in SRS-6 and TS/Ph-8 plots resulting from Hurricane Wilma was 8 and 17 times greater than the annual vertical accretion rate (0.30 ± 0.03 and $0.27 \pm 0.03 \text{ cm yr}^{-1}$, respectively) based on ^{137}Cs data (Castañeda-Moya unpubl. data). If compared to higher estimates of vertical accretion based on ^{210}Pb (Chen and Twilley 1999a; 0.89 cm yr^{-1}), sediment deposition is three times the long-term accretion rate. The lower accretion rates are similar to those reported for fringe and riverine mangrove forests in the Gulf of Mexico region ($0.16\text{-}0.24 \text{ cm yr}^{-1}$) using ^{137}Cs and ^{210}Pb radionuclides (Lynch et al. 1989); and also comparable with those reported for other coastal wetlands after hurricane events (Cahoon et al. 1995; Nyman et al. 1995; Turner et al. 2007). For instance, storm-associated sediments from Hurricane Andrew were 4-11 times greater than the long-term (30 years; ^{137}Cs techniques) annual rate in Louisiana coastal marshes (Cahoon et al. 1995; Nyman et al. 1995), generating about 2-6 cm of deposition from this hurricane event. It is evident that in both mangroves and salt marshes, hurricanes can deliver significant short-term changes to elevation of coastal wetlands.

Storm surge sediments are particularly important in the carbonate environmental setting of south Florida where the terrestrial sediment supply is low or absent, resulting in root production as one of the primary soil-building mechanisms in mangrove wetlands (Parkinson et al. 1994; Chen and Twilley 1999a). Although our results showed a relative gain in soil elevation

of FCE mangrove forests after the passage of Hurricane Wilma, other soil processes linked to hydrological conditions in this region, including sediment erosion and compaction (Cahoon et al. 2003), soil shrinking and swelling (Whelan et al. 2005), and shallow subsidence (Cahoon et al. 1995; Cahoon and Lynch 1997), need to be considered as potential factors controlling soil elevation changes in mangroves. For instance, Wilma increased soil elevation 4.3 cm in SRS-6, and within one year after the storm there was a decrease in elevation to 3.3 cm due to erosion (0.9 cm) and compaction from shallow subsidence (0.1 cm; Whelan et al. 2009). Thus, long-term effects of hurricane sediment deposits due to sediment volume changes may be limited compared to other factors (e.g. groundwater).

Soil Nutrient Inputs

Sediment deposition from Hurricane Wilma made significant contributions to the nutrient pools of mangrove soils at specific locations along FCE. Bulk sediment inputs from Broad Creek to Taylor Ridge ranged from 500 to 700 mg cm⁻³, compared to <400 mg cm⁻³ in Joe Bay on the eastern edge of FCE. Wilma approached into south Florida from the west-southwest and had a greater impact from Shark River to Taylor Ridge compared to the eastern edge of FCE. Over the study area, maximum sustained wind speeds for Hurricane Wilma reached 45-50 m s⁻¹ in the Shark River and Broad Creek areas at landfall compared to weaker winds (30-35 m s⁻¹) in the Joe Bay area (Fig. 3.1a). These conditions determined the magnitude of storm-surge-related sediment deposition patterns between the western and eastern Everglades. Inputs of organic matter and total N followed these patterns of bulk density gradients, with the exception of higher nitrogen input to Joe Bay mangroves relative to sediment deposition. Total N concentrations of sediment deposited during this hurricane event accounted for 7% (SRS-6W), 8% (SRS-6E), 9% (BC), 12% (Taylor Ridge), and 14% (SRS-6) of the total N pool in the top 10 cm of mangrove soils, except

in TS/Ph-8 where the contribution was 56%. In contrast, the contribution of total P from this hurricane event was significantly higher ranging from 20% (BC), 23% (SRS-6W), 30% (SRS-6E), 39% (SRS-6) to 54% (TS/Ph-8), with the exception of Taylor Ridge that only had 7% of the soil total P deposited during this one single event.

The gradient in total P input across mangrove zones located near shore from west (Broad Creek: 0.81 ± 0.09 mg P g⁻¹ dry mass) to east (TS/Ph-8: 0.14 ± 0.03 mg P g⁻¹ dry mass) direction across FCE is proportionally higher than the magnitude of sediment deposition. This is also evident when comparing the N:P ratios of sediment input across this west to east gradient (Fig. 3.4c). To the west near Broad Creek and mouth of Shark River, N:P ratios of sediment input range from 9.6 to 12.3, indicating an enrichment of total P in the bulk sediments deposited (Fig. 3.4c). Along Taylor Ridge, the N:P ratio dramatically increases to 77 and at TS/Ph-8 the ratio is near 98, similar to the ratio of soils in mangroves of that area (Fig. 3.4c). This gradient of lower P deposition in mangroves along the eastern region of Florida Bay is similar to that found in seagrass communities across this coastal landscape (Fourqurean et al. 1992). There is a strong gradient in P content and corresponding shift in N:P ratios in seagrass communities from west to east of Florida Bay. Foliar P concentrations of *Thalassia testudinum*, used as a proxy for P availability decreases from northwest (2.0 mg P g⁻¹ dry mass) to the east (0.5 mg P g⁻¹ dry mass) of the bay, while foliar N:P ratios increase from 20 to 80 along the same gradient (Fourqurean et al. 1992). This P gradient has been suggested to control productivity and species composition of seagrass communities in this region (Herbert and Fourqurean 2009). Our survey suggests that this P gradient from west to east may also result in a gradient of P input associated with sediment deposition during storm events in this region, contributing to gradients in mangrove productivity (Ewe et al. 2006).

Resource gradients in P density also exist in mangrove soils from shoreline to more inland locations that regulate mangrove productivity (Chen and Twilley 1999b). For example, mangroves along Shark River estuary have concentrations of Ca-bound P (top 20 cm of mangrove soils) that are 40-fold higher at the mouth of Shark River than in SRS-4, 18.2 km from the mouth. It has been assumed that marine sediment inputs as represented by this Ca-bound P fraction from the Gulf of Mexico during hurricane events are the source of P that controls and supports optimum mangrove forest development near the mouth of Shark River estuary (Chen and Twilley 1999a, b). Our results reveal that the Ca-bound P portion of storm deposits was the most significant fraction contributing 25-29% to the total P pool. Moreover, the lower residual P (44-46%) of storm deposits compared to surface soils (70-75%; Fig. 3.5) reflects the contribution of mineral sediments during this hurricane event. These patterns of Ca-bound portion of TP in storm sediment deposits associated with the passage of Wilma, along with the significant total load of P compared to soil nutrient inventories support this assumption.

In addition, mangrove forests along Taylor River inland of the Buttonwood Ridge are isolated from P deposited during these storm events (Davis et al. 2004). It has been hypothesized that this reduction in P loading during hurricanes due to this geomorphic feature results in P-limited scrub mangrove forests in this region of FCE (Koch 1997; Ewe et al. 2006). This geomorphic feature, along with the gradient in reduced P concentration to the east of Florida Bay, resulted in less P loading to mangroves in this region of FCE during Hurricane Wilma. Each hurricane that hits the region has a different direction, angle of approach, strength, size, etc., and therefore has a unique effect on storm surge-related sediment deposition and nutrient input to mangrove soils. Yet, it is apparent from this hurricane and evidence from previous storm

events that these loadings and concentration gradients of P in the region of Buttonwood Ridge have a profound effect on sediment and nutrient distribution in mangrove soils.

Allochthonous mineral inputs through sedimentation can significantly contribute to the long-term P storage and soil fertility condition in wetlands (Reddy and DeLaune 2008). Input of nutrients from Hurricane Wilma – in a single pulsing event – is an important contribution to soil fertility of mangrove forests in near shore mangroves in western regions of FCE. In areas that do not receive this pulse of P including more inland regions of the western FCE, mangroves inland of Buttonwood Ridge, and those farther east of Florida Bay, have lower accumulation of total P in soils. These features of the landscape control storm surge distribution (distance inland and geomorphic features) and nutrient gradients (west to east gradients of Florida Bay) and therefore establish the oligotrophic condition of this ecosystem (Noe et al. 2001). The contrasting landscape scale patterns of P-limited conditions from west to east, and from shore to inland locations associated with mangrove biomass (Simard et al. 2006) and productivity (Ewe et al. 2006) are evidently influenced by hurricane events that distribute sediment and nutrients. This additional input of nutrients with storm deposits can explain why total P is three times higher in western Shark River estuary than in Taylor River Slough (Chambers and Pederson 2006).

Landscape vegetation patterns of mangrove forests in the FCE represent the interplay of gradients in resources, regulators, and hydroperiod (Twilley and Rivera-Monroy 2005). Hurricane disturbances not only play an important role in inducing changes to vegetation, but also by distributing nutrients at fine spatial and temporal scales that can influence mangrove forest regeneration (Lugo 2008). This is particularly true in a carbonate based coastal setting where patterns of P accumulation in mangrove soils result in strong gradients in mangrove forest structure and productivity in the Everglades. In addition, hurricane deposits are relatively more

stable and consolidated than organic peat deposits, further contributing to soil volume and hence elevation. Allochthonous mineral inputs during hurricane events have also been associated with the long-term vertical accretion and stability of mangrove forests of the Everglades landscape (Chen and Twilley 1999a). For both salt marshes and mangroves, such pulsed events may be particularly important to how coastal wetlands have adapted to the impact of sea-level rise (Gilman et al. 2007; McKee et al. 2007) and increased frequency and intensity of hurricanes over the past half century (Webster et al. 2005). This feedback of hurricane disturbance on sediment deposition, accretion and nutrient deposition in this P-limited carbonate ecosystem may have important implications as to how soil formation and accretion serve as adaptations of mangroves to future impacts of sea-level rise.

SUMMARY

The passage of Hurricane Wilma across Shark River estuary in 2005 allowed us to quantify sediment deposition and nutrient inputs in FCE mangrove forests associated with this storm event, and to evaluate whether these pulsing events are sufficient to regulate nutrient biogeochemistry in mangrove forests of south Florida. Our results support the assumption of Chen and Twilley (1999b) since sediment deposition and associated P inputs along the estuarine gradient of Shark River were confined to mangrove areas near the mouth (SRS-6), with no deposition in areas upstream the estuary (SRS-4). In addition, sediment deposition was no observable in mangrove areas of Taylor River (TS/Ph-6 & 7), largely as result of the Buttonwood Ridge formation, where most of the sediment was deposited.

Bulk density, organic matter content, and inorganic and organic P pools of storm sediments differed from surface (0-10 cm) mangrove soils at each site. Total P inputs from storm-derived sediments were equivalent to twice the average surface soil nutrient P density

(0.19 mg cm⁻³); whereas, total N inputs contributed 0.8 times the average soil nutrient N density (2.8 mg cm⁻³). The Ca-bound P fraction of storm deposits was the most significant fraction contributing 25-29% of the total P pool.

There was a strong gradient in total P deposition to mangrove soils from west to east direction across FCE associated with this storm event. N:P ratios of sediment input increased from west (Broad Creek = 9.6; Shark River=12.3) to east (TS/Ph-8 = 98) indicating and enrichment of total P in the bulk sediments deposited by the storm.

Vertical accretion resulting from this hurricane event – in a single pulsing event – was one order of magnitude greater compared to the annual vertical accretion rate averaged over the past 50 years, suggesting the significant contribution of allochthonous mineral inputs during hurricane events to soil volume and elevation of FCE mangroves.

The observed gradient in total P deposition across FCE, with lower P loading in mangroves along the eastern region of Florida Bay suggest the significance of these pulses in P fertility during hurricanes to gradients in mangrove productivity.

REFERENCES

- Alongi, D.M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science* 76: 1-13.
- Aspila, K.I., H. Agemian, and S.Y. Chau. 1976. A semi-automated method for the determination of inorganic, organic and total phosphate in sediments. *Analyst* 101: 187-197.
- Cahoon, D.R. 2006. A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29: 889-898.
- Cahoon, D.R., P. Hensel, J. Rybczyk, K.L. McKee, E. Proffitt, and B.C. Perez. 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology* 91: 1093-1105.
- Cahoon, D.R., and J.C. Lynch. 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. *Mangroves and Salt Marshes* 1: 173-186.

- Cahoon, D.R., J.C. Lynch, and R.M. Knaus. 1996. Improved cryogenic coring device for sampling wetland soils. *Journal of Sedimentary Research* 66: 1025-1027.
- Cahoon, D.R., D.J. Reed, J.W.J. Day, G.D. Steyer, R.M. Boumans, J.C. Lynch, D. McNally, and N. Latif. 1995. The influence of Hurricane Andrew on sediment distribution in Louisiana coastal marshes. *Journal of Coastal Research* 21: 280-294.
- Callaway, J.C., J.A. Nyman, and R.D. DeLaune. 1996. Sediment accretion in coastal wetlands: A review and simulation model of processes. *Current Topics in Wetland Biogeochemistry* 2: 2-23.
- Chambers, R.M., and K.A. Pederson. 2006. Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands. *Hydrobiologia* 569: 63-70.
- Chen, R., and R.R. Twilley. 1999a. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44: 93-118.
- Chen, R., and R.R. Twilley. 1999b. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955-970.
- Childers, D.L. 2006. A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569: 531-544.
- Davies, B.E. 1974. Loss-on-ignition as an estimate of soil organic matter. *Soil Science Society of American Proceedings* 38: 150-151.
- Davis, S.E., D.L. Childers, J.W. Day, Jr., D.T. Rudnick, and F. Sklar. 2001. Nutrient dynamics in vegetated and unvegetated areas of a southern Everglades mangrove creek. *Estuarine, Coastal and Shelf Science* 52: 753-765.
- Davis, S.E.I., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W.J. Day, C.D. Huttie, C.J. Madden, E. Reyes, D. Rudnick, and F. Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida Gulf coast estuary. *Journal of Coastal Research* 20: 1198-1208.
- Day, J.W.J., D.F. Boesch, E.J. Clairain, G.P. Kemp, S.B. Laska, W.J. Mitsch, K. Orth, H. Mashriqui, D.J. Reed, L. Shabman, C.A. Simenstad, B.J. Streever, R.R. Twilley, C.C. Watson, J.T. Wells, and D.F. Whigham. 2007. Restoration of the Mississippi Delta: Lessons from Hurricanes Katrina and Rita. *Science* 315: 1679-1684.
- Duever, M.J., J.F. Meeder, L.C. Meeder, and J.M. McCollom. 1994. The climate of South Florida and its role in shaping the Everglades ecosystem. In *Everglades: The Ecosystem and Its Restoration*, eds. S. M. Davis and J. C. Ogden, 225-248. Delray Beach, Florida: St. Lucie Press.

- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, D. Iwaniec, V. Rivera-Monroy, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along tow freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569: 459-474.
- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.
- Gentry, R.C. 1974. Hurricanes in south Florida. I. In *Environments of South Florida: Present and Past*, eds. P. J. Gleason, Miami, Florida: Miami Geologic Society.
- Gilman, E., J. Ellison, and R. Coleman. 2007. Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. *Environmental Monitoring and Assessment* 124: 105-130.
- Hedley, M.J., J.W.B. Stewart, and B.S. Chauhan. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Science Society of American Journal* 46: 970-976.
- Herbert, D.A., and J.W. Fourqurean. 2009. Phosphorus availability and salinity control productivity and demography of the seagrass *Thalassia testudinum* in Florida Bay. *Estuaries and Coasts* 32: 188-201.
- Kenward, M., and J. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983-997.
- Koch, M.S. 1997. *Rhizophora mangle* L. seedling development into sapling stage across resource and stress gradients in subtropical Florida. *Biotropica* 29: 427-439.
- Krauss, K.W., T.W. Doyle, R.R. Twilley, and T.J.I. Smith. 2005. Woody debris in the mangrove forests of south Florida. *Biotropica* 37: 9-15.
- Lajtha, K., C.T. Driscoll, W.M. Jarrel, and E.T. Elliot. 1999. Soil phosphorus characterization and total element analysis. In *Standard soil methods for Long-Term Ecological Research*, eds. G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, 115-142. New York, NY: Oxford University Press, Inc.
- Lynch, J.C., J.R. Meriwether, B.A. McKee, F. Vera-Herrera, and R.R. Twilley. 1989. Recent accretion in mangrove ecosystems based on ¹³⁷Cs and ²¹⁰Pb. *Estuaries* 12:284-299.
- Lodge, D.J., and W.H. McDowell. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica* 23: 373-378.
- Lodge, T.E. 2005. *The Everglades Handbook: Understanding the Ecosystem*, 2nd edition. Boca Raton, Florida: CRC Press.

- Lugo, A.E. 2000. Effects and outcomes of Caribbean hurricanes in a climatic change scenario. *The Science of the Total Environment* 262: 243-251.
- Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology* 33: 368-398.
- McKee, K.L., D.R. Cahoon, and I.C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545-556.
- Michener, W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climatic change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770-801.
- Noe, G.B., D.L. Childers, and R.D. Jones. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: why is the Everglades so unique? *Ecosystems* 4: 603-624.
- Nyman, J.A., C.R. Crozier, and R.D. DeLaune. 1995. Roles and patterns of hurricane sedimentation in an estuarine marsh landscape. *Estuarine, Coastal and Shelf Science* 40: 665-679.
- Parkinson, R.W., R.D. DeLaune, and J.R. White. 1994. Holocene sea-level rise and the fate of mangrove forests in the Wider Caribbean region. *Journal of Coastal Research* 10: 1077-1086.
- Pasch, R.J., E.S. Blake, H.D. Cobb, and D.P. Roberts. 2006. Tropical cyclone report Hurricane Wilma. . National Weather Service. National Hurricane Center, <http://www.nhc.noaa.gov>, Miami, Florida.
- Piou, C., I.C. Feller, U. Berger, and F. Chi. 2006. Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. *Biotropica* 38: 365-374.
- Reddy, K.R., and R.D. DeLaune. 2008. *Biogeochemistry of wetlands: science and applications*, Boca Raton, Florida: CRC Press.
- Risi, J.A., H.R. Wanless, L.P. Tedesco, and S. Gelsanliter. 1995. Catastrophic sedimentation from Hurricane Andrew along the southwest Florida coast. *Journal of Coastal Research* 21: 83-102.
- Sherman, R.E., T.J. Fahey, and P. Martinez. 2001. Hurricane impacts on a mangrove forest in the Dominican Republic: Damage patterns and early recovery. *Biotropica* 33: 393-408.
- Simard, M., K. Zhang, V. Rivera-Monroy, M.S. Ross, P.L. Ruiz, E. Castañeda-Moya, R.R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. *Photogrammetric Engineering and Remote Sensing* 72: 299-311.

- Smith, T.J.I., G.H. Anderson, K. Balentine, G. Tiling, G.A. Ward, and K.R.T. Whelan. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: Sediment deposition, storm surges and vegetation. *Wetlands* 29: 24-34.
- Smith, T.J.I., M.B. Robblee, H.R. Wanless, and T.W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44: 256-262.
- Sutula, M. 1999. Processes controlling nutrient transport in the southeastern Everglades wetlands. Ph.D. Dissertation. Louisiana State University, Baton Rouge.
- Turner, R.E., E.M. Swenson, C.S. Milan, and J.M. Lee. 2007. Hurricane signals in salt marsh sediments: Inorganic sources and soil volume. *Limnology and Oceanography* 52: 1231-1238.
- Twilley, R.R., and V. Rivera-Monroy. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research* 40: 79-93.
- Wanless, H.R., R.W. Parkinson, and L.P. Tedesco. 1994. Sea level control on stability of Everglades wetlands. In *Everglades. The ecosystem and its restoration* eds. S. M. Davis and J. C. Ogden, 199-223. Delray Beach, Florida: St. Lucie Press.
- Webster, P.J., G.J. Holland, J.A. Curry, and H.R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309: 1844-1846.
- Whelan, K.R.T., T.J.I. Smith, G.H. Anderson, and M.L. Ouellette. 2009. Hurricane Wilma's impact on overall soil elevation and zones within the soil profile in a mangrove forest. *Wetlands* 29: 16-23.
- Whelan, K.R.T., T.J.I. Smith, D.R. Cahoon, J.C. Lynch, and G.H. Anderson. 2005. Groundwater control of mangrove surface elevation: shrink and swell varies with soil depth. *Estuaries* 28: 833-843.
- Zhang, K., M. Simard, M.S. Ross, V. Rivera-Monroy, P. Houle, P.L. Ruiz, R.R. Twilley, and K.R.T. Whelan. 2008. Airborne laser scanning quantification of disturbances from hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA. *Sensors* 8: 2262-2292.

CHAPTER 4

PATTERNS OF COMMUNITY STRUCTURE AND TOTAL NET PRIMARY PRODUCTIVITY OF MANGROVE FORESTS IN THE FLORIDA COASTAL EVERGLADES, USA

INTRODUCTION

Primary productivity represents the major input of carbon and biological energy into world's ecosystems and can be considered as an integrative measurement of ecosystem functioning (McNaughton et al. 1989; Sala and Austin 2000). Mangrove forests thriving along tropical and subtropical coastlines are among the most productive marine ecosystems in the world, ranking second in importance in terms of net primary productivity (NPP) only to coral reefs (Duarte and Cebrian 1996). Mangrove forests produce organic carbon well in excess of the ecosystem requirements and are considered important sites for carbon burial (~10%) and carbon export (~40%) to adjacent coastal waters, suggesting their significant contribution to carbon biogeochemistry in the coastal zone (Twilley et al. 1992; Duarte and Cebrian 1996; Jennerjahn and Ittekkot 2002; Bouillon et al. 2008). Global estimates indicate that mangrove coverage is approximately 160,000 km², and although it represents <1% of the earth's total surface, they play an important ecological and socioeconomical role within the coastal zone (Ewe et al. 1998; FAO 2003). Mangrove ecosystems have been widely recognized for providing a variety of goods and services to humans (e.g., commercial fisheries, nursery grounds for fish and crustaceans), preserving ecosystem integrity and regional biodiversity (Ewel et al. 1998; Nagelkerken et al. 2008; Walters et al. 2008), contributing to coastline protection (Field 1995), acting as a buffer against tsunamis (Alongi 2008), and for playing an important role in the global coastal carbon budget (Twilley et al. 1992; Jennerjahn and Ittekkot 2002; Chmura et al. 2003; Duarte et al. 2005; Bouillon et al. 2008; Kristensen et al. 2008).

It has been suggested that the community structure and productivity of mangroves represent the outcome and interactions of several factors that operates at distinct global, regional, and local scales (Twilley 1995). Climate and the variability in regional geophysical processes within a coastal landform control the basic patterns in mangrove forest structure and productivity and determine in large part the network in energy flow and material cycling (Thom 1982, Twilley 1995). Local variations in topography and hydrology within a coastal landform influence the distribution of soil resources and abiotic regulators along with hydroperiod gradients resulting in the development of distinct ecological types of mangroves such as riverine, fringe, basin, scrub, and overwash (Lugo and Snedaker 1974). The interaction and degree of these environmental gradients including regulators, resources, and hydroperiod define a constraint envelope for determining the structure and productivity of mangrove wetlands within a coastal setting (Twilley and Rivera-Monroy 2005). This multigradient model has been experimentally tested using greenhouse experiments and patterns across natural gradients in oligotrophic systems manipulated with nutrient fertilizers.

The importance of these environmental gradients, resources, regulators and hydroperiod, in controlling vegetation patterns and productivity of mangrove ecosystems is well documented in the literature (Lugo and Snedaker 1974; Boto and Wellington 1984; McKee 1993; Chen and Twilley 1999b; Feller et al. 2003a, b; Krauss et al. 2006). Salinity and nutrient availability have been recognized as one of the main factors in controlling mangrove forest structure and productivity (Lugo and Snedaker 1974; Cintron et al. 1978; Chen and Twilley 1999b; Feller et al. 2003a, b; Castañeda-Moya et al. 2006). For instance, studies have demonstrated a significant decrease in aboveground net primary productivity (NPP_A) with increasing salinity along the intertidal zone in mangrove forests of Guadalupe and Martinique (Imbert et al. 2000), Florida

(McKee and Faulkner 2000), and the Dominican Republic (Sherman et al. 2003). These studies suggest that hypersaline conditions in the soil can impose a higher metabolic cost and carbon assimilation capacity of mangroves resulting in reductions of productivity and biomass allocation (Sobrado and Ball 1999; Naidoo 2006). Mangrove species also respond to low nutrient availability with morphological and physiological plasticity (Feller et al. 2003a, b; Lovelock et al. 2004). Long-term fertilization experiments of *Rhizophora mangle* in Belize (Feller et al. 2003a; Lovelock et al. 2006), Florida (Koch and Snedaker 1997) and Panama (Lovelock et al. 2004) have suggested that these scrub forests respond positively to P additions increasing NPP_A and shifting resource allocation from roots to shoots.

Moreover, patterns in above- and belowground productivity and biomass allocation in mangroves also respond to changes in hydroperiod (Twilley et al. 1986). Flooded hydroperiods can restrict mangrove growth and shift biomass allocation between root and shoots of neotropical mangrove seedlings (Cardona-Olarte et al. 2006; Krauss et al. 2006), while moderate hydroperiods can maximize growth and productivity (Twilley et al. 1986; Krauss et al. 2006). A recent study in mangrove forests of Belize has also indicated that root production decreases from tall fringe to scrub interior mangroves in response to permanent flooding, and parallels the aboveground productivity gradient (McKee et al. 2007). These studies support the multigradient model that contrasting patterns in productivity and biomass allocation respond to the interaction and degree of resources, regulators, and hydroperiod along the intertidal zone (Twilley and Rivera-Monroy 2005).

In the neotropics, most studies of NPP in mangrove forests have primarily focused on NPP_A and the factors controlling local and landscape vegetation patterns. Although numerous studies have measured mangrove litterfall as a proxy for describing productivity and testing

hypothesis about NPP_A under different environmental settings and latitudinal gradients (Lugo and Snedaker 1974; Pool et al. 1975; Twilley et al. 1986; Saenger and Snedaker 1993; Twilley et al. 1997; Arreola-Lizarraga et al. 2004), there are only few studies that have concurrently estimated aboveground wood production (Day et al. 1987, 1996; see Bouillon et al. 2008 for a recent review). Moreover, there are large information gaps on root biomass, productivity, and turnover and how these processes respond to environmental gradients largely due to challenges to understanding root dynamics due to limitations in sampling methodologies (Clough 1992; Clark et al. 2001; Bouillon et al. 2008). Few estimates of root biomass indicate that neotropical mangroves allocate a large proportion (40-60%) of their total biomass to belowground (Golley et al. 1962; Golley et al. 1975; Fiala and Hernandez 1993; Sherman et al. 2003; Giraldo 2005). Direct estimates of root production and turnover are also scarce (McKee and Faulkner 2000; Cahoon et al. 2003; Giraldo 2005; McKee et al. 2007), and thus there is no clear pattern of carbon allocation within belowground biomass in response to environmental gradients, reducing the accuracy to quantify total NPP (NPP_T) of mangrove forests.

Understanding the allocation of carbon to above- and belowground biomass and productivity is significant for the global carbon budget of mangrove ecosystems (Bouillon et al. 2008). Recent estimates for mangrove forests indicate that litterfall (NPP_L), wood (NPP_W), and root production (NPP_B) account for ~31, 31, and 38% of the global NPP_T , respectively (Bouillon et al. 2008). These estimates underscore the significant contribution of NPP_W and NPP_B to NPP_T of mangrove forests worldwide, and indicate the need for studies that encompass both the NPP_A ($NPP_L + NPP_W$) and NPP_B to accurately estimate NPP_T and the proportion of carbon allocated to above- and belowground production ($NPP_B:NPP_A$ ratio) of mangrove forests. Moreover, these estimates will contribute to a better understanding of the landscape patterns of NPP and carbon

allocation of mangrove forests in different environmental settings across environmental gradients.

The Florida Coastal Everglades (FCE) is characterized as an oligotrophic P-limited wetland system (Noe et al. 2001; Davis 1994), where the limiting nutrient along the coastal margin is supplied by the Gulf of Mexico, rather than the upper watershed (Chen and Twilley 1999a, b; Childers et al. 2006). There are also strong environmental gradients as a common feature of the coastal landscape of FCE (Fourqurean et al. 1992; Koch 1997; Chen and Twilley 1999b; Childers et al. 2006; Ewe et al. 2006). Mangrove forests are one of the most conspicuous vegetation communities across this coastal landscape (Lodge 2005) distributed within two major drainage basins, Shark River Slough (western region) and Taylor River Slough (eastern region) across a carbonate environmental setting (Wanless et al. 1994). This ecosystem is ideal to test hypotheses that allocation patterns of biomass and NPP of mangroves respond to the interaction of environmental gradients resulting in distinct mangrove types at the same latitudinal gradient across the Everglades. Riverine mangrove forests along Shark River exhibit a productivity gradient associated with decreasing P availability as distance inland increases from the mouth of the estuary (Chen and Twilley 1999b; Ewe et al. 2006). Deposition of allochthonous mineral inputs (i.e., Ca bound-P) during storm events at the mouth of estuaries and decreased input to more inland mangroves has been suggested to regulate the structure and productivity of mangrove forests in southwestern Everglades (Chen and Twilley 1999b; Castañeda-Moya et al. 2010). These allochthonous mineral inputs enhance P concentrations and lower N:P ratios in mangroves areas adjacent to the mouth of Shark River estuary, where soil properties are correlated with higher aboveground biomass (120-150 Mg ha⁻¹) and tree height (18-20 m) in contrast to upstream areas of this estuary and the southeastern region of Florida (biomass <50

Mg ha⁻¹; tree height < 5 m; Ewe et al. 2006; Simard et al. 2006). Scrub mangrove forests along Taylor River (e.g., TS/Ph-6 & 7) receive less inorganic sediment during storm events due to a geological berm called the “Buttonwood Ridge”. This depositional feature (~1 km wide, ~0.5 m in height) that stretches approximately 60 km across the southern tip of Florida has been hypothesized to isolate these mangroves from storm deposits of P from Florida Bay (Davis et al. 2004). Mangroves to the east of Taylor River (e.g., TS/Ph-8, Joe Bay) do receive these storm deposits during storm events, but they are low in P content compared to mangroves in the southwestern region, including the mouth of Broad Creek and Shark River estuaries (Castañeda-Moya et al. 2010).

In this study, I present a comprehensive long-term (2001-2004) analysis of community structure, above- and belowground biomass and NPP_T, and soil properties and hydroperiod of mangrove forests across the FCE landscape. This is one of the first studies that includes both above- and belowground estimates of NPP_T for neotropical mangrove forests. My objective is to evaluate the long-term spatial and temporal patterns of community structure, above- and belowground biomass and NPP_T of mangroves in Shark River and Taylor River Sloughs. I also characterize the long-term spatial and temporal variation in mangrove soil properties and hydroperiod along these two estuaries, and evaluate what are the relative factors controlling rates of biomass and NPP_T between these two watersheds. I test the hypothesis that the allocation of belowground biomass and NPP_B relative to aboveground allocations is greater in the Taylor River region compared to the Shark River region, describing mangrove vegetation strategies associated with P limitation and flooded hydroperiods (Mancera Pineda et al. 2009). I address the following questions: (1) What is the community structure and NPP_A rates of mangrove forests across the P-limited conditions of the Florida Coastal Everglades? (2) What is the seasonal and

inter-annual variation in rates of NPP_A across mangrove sites? (3) What is the NPP_T in the Shark River and Taylor River regions, and what is the relative contribution of NPP_B to NPP_T across these regions? (4) What is the production ratio of belowground biomass to aboveground biomass across mangrove sites? (5) What is the spatial and temporal variation in soil properties, and what are the relative soil factors controlling rates of biomass and NPP_T across FCE mangrove sites? This information of how mangrove biomass and NPP_T are allocated between above- and belowground in response to environmental stress across the FCE landscape (Mancera Pineda et al. 2009) will improve our understanding of carbon dynamics (storage, production and allocation) and will be critical to the accurate development of carbon budgets in neotropical mangrove forests.

MATERIALS AND METHODS

Experimental Design

In 2000, three mangrove sites were established each along Shark River (SRS-4, SRS-5, and SRS-6) and Taylor River (TS/Ph-6, TS/Ph-7, and TS/Ph-8) estuaries as part of the FCE Long Term Ecological Research (LTER) program (Fig. 4.1; Childers 2006; <http://fcelter.fiu.edu/>). In each site, two 20 x 20 m permanent vegetation plots (20-m apart) were established approximately between 30-50 m from the shoreline to monitor forest structural attributes and soil biogeochemical properties. In addition, at the Shark River sites two transects ranging from 100 to 200 m in length depending on the mangrove forest extension at each site were established perpendicular to the mangrove shoreline in 2002 to evaluate the spatial distribution, species composition and growth of mangrove species. At TS/Ph-8, transects were not established due to the fringe mangrove zone was too narrow (<50 m).

Hydroperiod

Continuous water level recorders allowed me to measure flood duration and frequency in all six FCE-LTER mangrove sites from 2001 to 2005. Ultrasonic water level recorders (model 220, Infinities USA, Inc., Port Orange, Florida) were installed in the interior of each mangrove site about 50-80 m inland from shore. Water level recorders were placed on top of a PVC pipe that was exposed 1.5 m above the soil surface and buried approximately 1 m below the soil surface (2.5 m length total). Water levels relative to soil surface were recorded at 1 h intervals. Results of water level patterns are presented only to represent a selected dry and wet season during 2002 (2003 for TS/Ph-7) for all sites, due to similarity in water levels among seasons during 2001-2005. Flooding duration and frequency data were analyzed for the entire period of data collection.

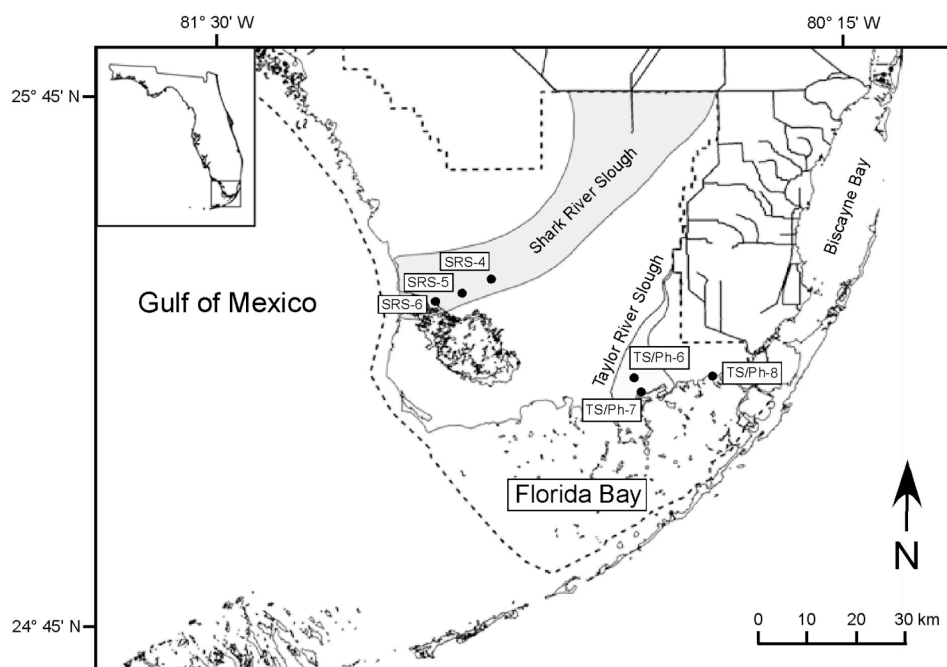


Fig. 4.1 Location of the study sites in the Everglades National Park (ENP), south Florida, USA. SRS-4, SRS-5, and SRS-6 along Shark River Slough; TS/Ph-6 and TS/Ph-7 along Taylor River Slough, and TS/Ph-8 in Joe Bay are part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program.

Soil Properties

Pore water parameters were monitored in all six FCE mangrove sites. Within each site, four repeated sampling stations were randomly established in each plot to measure porewater salinity, temperature (°C), porewater nutrients and sulfide concentrations, and soil redox potential (Eh). Porewater samples were collected at 30 cm depth (McKee et al. 1988) during the dry (May) and wet (October) seasons from 2001 to 2004 in all sampling stations. One porewater aliquot was assayed for temperature and salinity using a portable YSI salinity-conductivity-temperature meter (model 30, YSI Incorporated, Yellow Springs, Ohio). A second sample was added to an equal volume of antioxidant buffer in the field and transported to the laboratory within 12 h to be analyzed for sulfide concentrations with a silver/sulfide electrode (model 9616BN, Orion Research, Beverly, MA). A third porewater sample was filtered using a GF/F filter and stored frozen until assayed for ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), soluble reactive phosphorus (SRP) using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas). Nitrate concentrations were only measured in 2004 due to analytical problems with the analysis during previous years. Soil Eh (0, 10, 45 cm depth) was measured by duplicate in situ using a multi-depth platinum probe (Hargis and Twilley 1994).

Soil nutrient concentrations (total C, N, and P), bulk density and organic matter content were analyzed in all six FCE mangrove sites. Soil cores were collected once at each site in May 2001 and January 2002. Duplicate soil cores were randomly collected from each plot using a PVC suction-coring device (15 cm diameter x 45 cm length; Meriwether et al. 1996). Soil cores were gently extruded, divided into 2-cm intervals and stored on ice in plastic bags for further analyses. Soil samples were oven-dried at 60 °C to a constant weight and weighed to estimate

soil bulk density. Subsamples of soil cores were ground with a Wiley Mill to pass through a 250- μm mesh screen. Organic matter content is defined as percent of ash-free dry weight (AFDW %) determined by combusting samples in a furnace for 2 h at 550 °C (Davies 1974). Data was expressed on a volume basis using bulk density values. Total carbon (C) and nitrogen (N) concentrations were determined on two analytical replicates of each soil sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total P was extracted on duplicate soil samples with 1 N HCL after combustion in a furnace at 550 °C (Aspila et al. 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas).

Forest Structure, Aboveground Biomass and Wood Production

Forest structure was measured in selected FCE mangrove sites, including all Shark River sites and TS/Ph-8. Forest structure was not determined at TS/Ph-6 & 7 due to the stunted physiognomy (tree height ≤ 1.5 m) of the forest restricted dbh measurements. All trees with diameter at breast height (dbh) ≥ 2.5 cm were tagged and measured within each plot in all sites to determine species composition, basal area ($\text{m}^2 \text{ ha}^{-1}$), tree density (stems ha^{-1}), and tree height (m). All trees were initially measured in May 2001 and re-measured every year until May 2004. The spatial distribution and species composition of mangrove forests at the Shark River sites were also evaluated along transects using the point-center quarter method (PCQM; Cottam and Curtis 1956), with sampling points 10 m apart. As in the case of plot sampling, all trees with dbh ≥ 2.5 cm were tagged and measured along each transect in all sites to determine species composition, basal area, tree density, and tree height (m). All trees were initially measured in May 2002 and re-measured every year until May 2004. The height of all tagged trees within plots and along transects was recorded in 2002 using a laser rangefinder (Impulse 200 LR, Laser

Technology Inc., Tucson WY). Indices of structural development were calculated according to Holdridge et al. (1971) and Cintron and Schaeffer-Novelli (1984). The importance value (IV) for each species was calculated as the sum of relative density, relative dominance, and relative frequency divided by 3 (Cottam and Curtis 1956). The complexity index was calculated as basal area x tree density x canopy height x number of species x 10^{-5} (Holdridge et al. 1971). For this study, I only report on changes in forest structure between initial (2001 for plots and 2002 for transects) and final (2004 for both techniques) measurements for all selected sites due to the highest temporal variation in structural attributes was captured in this fashion, based on field observations.

Aboveground wood biomass was calculated for each individual tree tagged within plots and transects of selected sites using species-specific allometric equations published for the study area for the three major species (Smith and Whelan 2006). For *C. erectus*, there is no published allometric equation. Thus, I used the allometric equation for *L. racemosa* due to similarity in growth forms between these two species. For each individual tree, total biomass and leaf biomass were calculated using equations of Smith and Whelan. Wood biomass was estimated as the difference between total and leaf biomass for each individual tree. The annual net increase in wood biomass was calculated as the difference between the initial and final biomass within plots (2001 and 2004) and transects (2002 and 2004) of each individual tree. For the plot data, the sum of these differences was used to estimate wood biomass production for each site. For the transect data, the average of these biomass differences was then multiplied by the number of trees per hectare (tree density) to estimate wood biomass production. The corrections made above to calculate wood biomass from the allometric equations of Smith and Whelan (2006) were necessary since the total dry biomass equation of Smith and Whelan includes all aboveground

components (i.e., stem, branch, leaf, and prop roots in the case of *R. mangle*). Since I measured litterfall production directly as a component of NPP_A , using the total biomass equation would overestimate NPP_A for the selected sites. For TS/Ph-6 & 7, I used wood production values reported by Ewe et al. (2006) to estimate NPP_A in these two sites. I also used aboveground biomass estimates reported by Coronado-Molina et al. (2004) for these two sites. These estimates were calculated by applying allometric equations developed in that study for the Taylor River area.

Litterfall Production

Litter dynamics was monitored in selected mangrove sites, including all Shark River sites and TS/Ph-8 from January 2001 to December 2005. At TS/Ph-6 & 7, litterfall production was not estimated due to the stunted physiognomy (tree height ≤ 1.5 m) of the mangrove forest. Litterfall was collected in 0.25 m^2 wooden baskets supported approximately 1.5 m aboveground, and the bottom of each basket was constructed of fiberglass screening (1 mm mesh). In each mangrove site, ten litter baskets were randomly placed inside the two 20 by 20 m permanent plots (5 baskets per plot). Litterfall was collected at monthly basis from each site. Plant material within each basket was dried for 72 h at 60°C , sorted into leaves, fruits, flowers, stipules, and woody material, and weighed to within 0.1 g. Litterfall rates of each component were expressed in $\text{g m}^{-2} \text{d}^{-1}$. For TS/Ph-6 & 7, I used leaf fall rates reported by Ewe et al. (2006) to estimate NPP_A in these two sites. In this study, leaf turnover rates were used as a proxy to estimate leaf fall production.

Belowground Biomass and Production

A complete description of the methods and rates of root biomass and production in all six FCE mangrove sites is found in chapter two of this dissertation (Figs. 2.2 and 2.4). Total (to a

depth of 90 cm of mangrove soils) root biomass was used to calculate the root:shoot ratio for all six sites and total root production was used to estimate the contribution of NPP_B to NPP_T ($NPP_L + NPP_W + NPP_B$) of mangrove forests in this region. Total root production represents the sum of fine (< 2mm in diameter), small (2-5 mm), and coarse (5-20 mm) root size classes reported for this study. Root size classes >20 mm in diameter were not included in my study.

Statistical Analyses

All statistical analyses were performed using PROC MIXED (SAS Institute, Cary, NC, USA). Variation in basal area, tree density, and aboveground wood biomass and wood production was initially tested with a two-way ANOVA to determine differences between sampling techniques (plots vs. transects) and among sites (only Shark River sites). TS/Ph-8 was not included in this analysis since transects were not established in this site. I used repeated measures ANOVA to test for differences in basal area, tree density, and aboveground wood biomass among selected sites (Shark River sites and TS/Ph-8) and years, with year as the repeated measure. Wood production was tested for differences among selected sites with a one-way ANOVA. Seasonal and site (Shark River sites and TS/Ph-8) differences in total litterfall and each of its individual components (leaves, reproductive parts, twigs) were tested with a split-plot repeated measures analysis. The main plot tested the effect site and the subplot tested the season and year effects. Annual litterfall (2001-2004) was calculated for each sampling unit (basket), and a two-way ANOVA was used to test for differences among sites and years. Litterfall calculated for 2005 was not included in any of the statistical analysis due to the passage of Hurricane Wilma during October 2005. These rates were represented of a disturbance, and thus were atypical compared to previous years. Porewater variables were tested for differences among all six sites, seasons, and years using the same split-plot repeated measures ANOVA, with sites

considered as the main plot, and year and season as the subplot. Soil nutrients (total C, N, and P), organic matter content, and bulk density were tested independently for differences among all sites using a one-way ANOVA.

All effects were considered fixed for all analyses. Plots were nested within each site, considered random effects, and treated as experimental units. The ANOVA design was unbalanced for some of the variables analyzed due to differences in the total number of observations per plot in each site. The Kenward-Roger procedure was used to adjust the degrees of freedom of the F test statistics when the design was unbalanced or when an unequal variance model was significant (SAS Institute, Cary, NC, USA; Kenward and Roger 1997). Interaction effects were considered for all analyses. Pairwise comparisons were performed with Tukey's Honestly Significant Difference (HSD) test when significant differences ($p < 0.05$) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. The assumption of homocedasticity was tested using the "null model" likelihood ratio test of the residual errors with a chi square distribution. Wood production and soil N:P were log-transformed ($\ln(x + 1)$) prior to analysis to meet the ANOVA assumptions. Unless otherwise stated, data presented are means (± 1 SE – standard error) of untransformed data. Regression analyses were performed to test relationships between soil properties and forest structure, aboveground biomass, and NPP_A .

RESULTS

Hydroperiod

Hydroperiod showed contrasting spatial and seasonal trends between Shark River and Taylor River (Figs. 4.2 and 4.3). Water levels above the soil surface were higher during the wet season (June-November) compared to the dry season (December-May) at all sites, and decreased

with distance inland from the mouth of the Shark River estuary (Fig. 4.2). In TS/Ph-6 & 7, water levels were above soil surface for most of the year, indicating permanently flooded conditions, while in TS/Ph-8 water levels were above the soil surface during the wet season compared to the dry season (Fig. 4.2). Flooding duration averaged across five years (2001-2005) ranged from 3965 to 5592 h yr⁻¹ among the Shark River sites, and from 3541 to 8653 h yr⁻¹ in the Taylor River sites (Fig. 4.3a; Appendix B). At the Shark River sites, water levels flooded the soil surface 45-65% of each year, with flood duration decreasing in sites farther upstream of the estuary. TS/Ph-6 & 7 remained flooded almost 100% of each year, while TS/Ph-8 showed a similar annual flood duration (41%) compared to SRS-4 (Fig. 4.3a; Appendix B). Annual flood frequency ranged from 165 to 395 inundations per year indicating the tidal forcing effect along Shark River, compared to upstream sites (SRS-4 and SRS-5) of this estuary (Fig. 4.3b; Appendix B). In the Taylor River sites the tidal effect and thus number of annual inundations was negligible, although at TS/Ph-8 flood frequency was 48 inundations per year suggesting the microtidal (<0.2 m) influence of Florida Bay and the seasonality of cold fronts in this area (Fig. 4.3b; Appendix B).

Soil Properties

Soil total C, N, and P, C:N and N:P ratios, bulk density, and organic matter content did not differ significantly among sampling depths for each of the FCE mangrove sites. Thus, depth was removed from further statistical analyses and concentrations for these variables were expressed for the top 45 cm of mangrove soils. Bulk density ranged from $0.10 \pm 0.01 \text{ g cm}^{-3}$ (SRS-4) to $0.39 \pm 0.03 \text{ g cm}^{-3}$ (TS/Ph-6) across all sites, with significantly lower values at Shark River sites compared to Taylor River sites, except for TS/Ph-7 ($0.16 \pm 0.01 \text{ g cm}^{-3}$; Table 4.1). Organic matter content also varied significantly along Shark River and Taylor River estuaries,

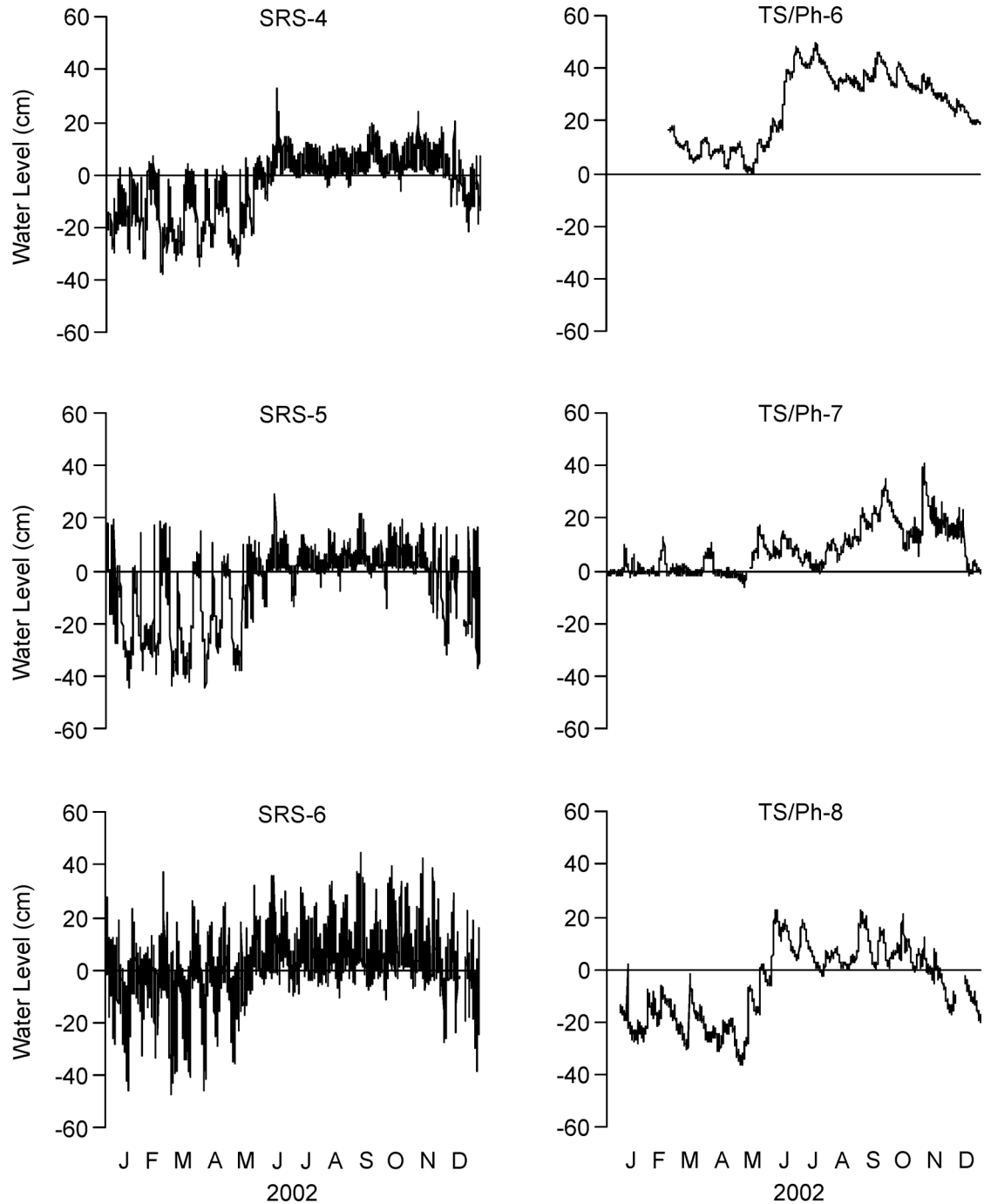


Fig. 4.2 Hydrographs in mangrove forests of the Florida Coastal Everglades during the dry and wet seasons of 2002. The zero mark is relative to the soil surface in each site. All water level data are not referenced to the North America Vertical Datum of 1988 (NAVD88).

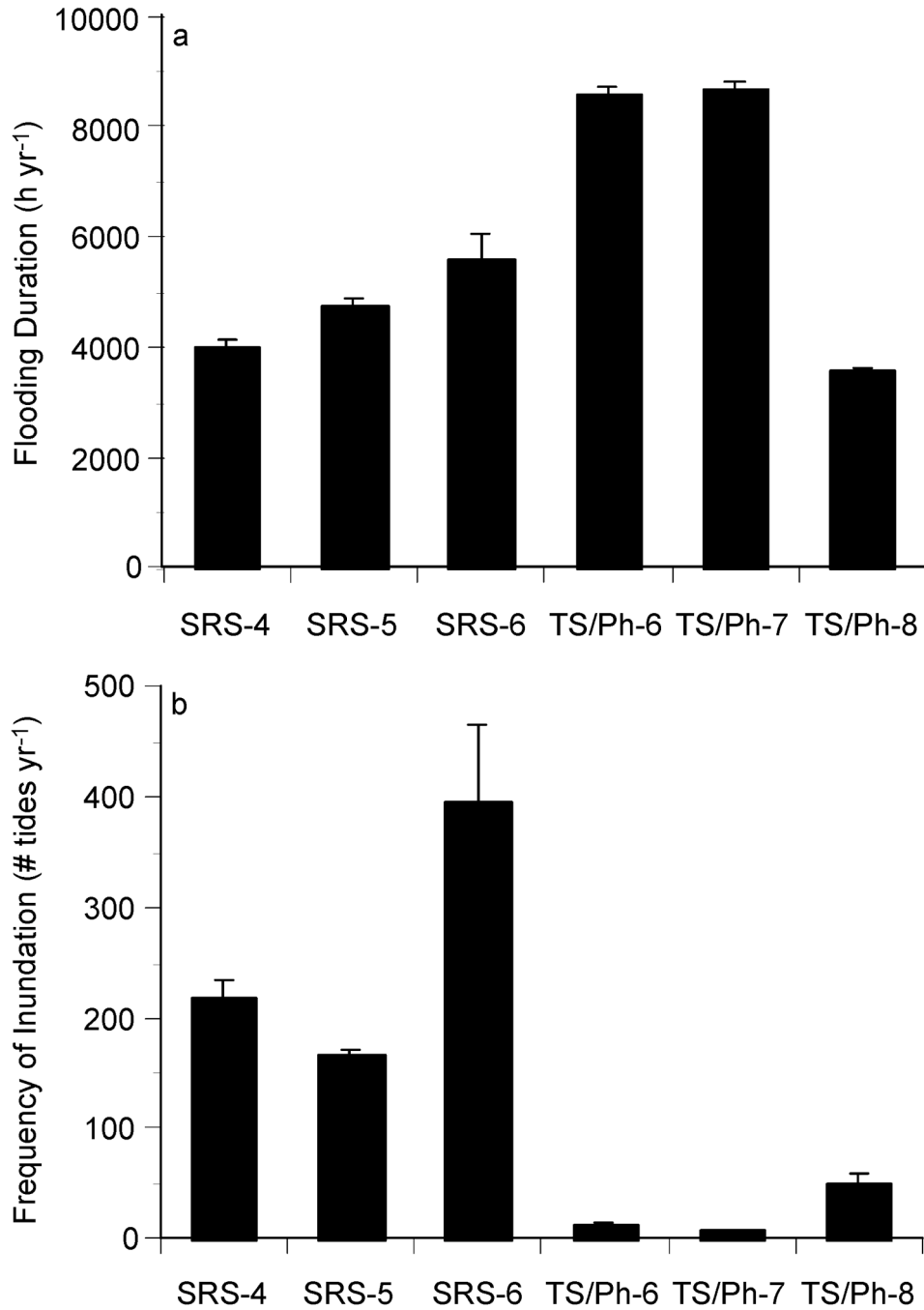


Figure 4.3 Flooding duration and frequency of inundation in mangrove forests of the Florida Coastal Everglades measured over the period 2001-2005.

with the highest content at SRS-5 ($119.3 \pm 2.7 \text{ mg cm}^{-3}$) and TS/Ph-7 ($114.5 \pm 5.4 \text{ mg cm}^{-3}$), respectively (Table 4.1). Overall, higher organic matter content was observed in the middle and downstream areas of each estuary relative to upstream (Table 4.1).

Soil total P concentrations indicated a fertility gradient along both Shark River and Taylor River estuaries, with a clear increase in soil total P from upstream to downstream along each estuary (Table 4.1). Soil total P density ranged from $0.05 \pm 0.004 \text{ mg cm}^{-3}$ (SRS-4) to $0.20 \pm 0.012 \text{ mg cm}^{-3}$ (SRS-6) along Shark River, and from $0.03 \pm 0.001 \text{ mg cm}^{-3}$ (TS/Ph-6) to $0.10 \pm 0.014 \text{ mg cm}^{-3}$ (TS/Ph-8) along Taylor River (Table 4.1). Soil total N density was not significantly different among sites, except for TS/Ph-6 ($1.7 \pm 0.1 \text{ mg cm}^{-3}$) that had the lowest nutrient density (Table 4.1). Overall, total N density ranged from 1.7 ± 0.1 to $2.5 \pm 0.3 \text{ mg cm}^{-3}$ across all sites (Table 4.1). Soil total C density did vary significantly along both Shark and Taylor River estuaries, with the highest nutrient density at SRS-5 ($52.9 \pm 1.6 \text{ mg cm}^{-3}$) and TS/Ph-6 ($60.7 \pm 2.9 \text{ mg cm}^{-3}$), respectively (Table 4.1). Overall, C density was lower in Shark River than at Taylor River, especially at SRS-4 and SRS-6 where C density was the lowest (Table 4.1). Soil atomic C:N ratios did not vary much across sites, except at TS/Ph-6 that had the highest value (44.6 ± 4.4 ; Table 4.1). In contrast to soil C:N, soil atomic N:P ratios showed a significant increase with distance inland from the mouth of each estuary (Table 4.1). Along Shark River, N:P ratios were 28 ± 1.8 at SRS-6, 46.2 ± 3.4 at SRS-5, and 105.3 ± 6.2 at SRS-6. Along Taylor River, N:P ratios were 66.1 ± 5.9 at TS/Ph-6, 101.9 ± 5.8 at TS/Ph-7, and 109.2 ± 5.9 at TS/Ph-8 (Table 4.1).

Porewater salinity decreased significantly with distance inland from the mouth of Shark River ranging from $27 \pm 2.6 \text{ g kg}^{-1}$ at SRS-6 to $4.6 \pm 1.1 \text{ g kg}^{-1}$ in SRS-4, while salinity along

Table 4.1 Statistical results of soil (top 45 cm) nutrients, C:N and N:P atomic ratios, bulk density and organic matter content measured in mangrove sites of the Florida Coastal Everglades. Means (\pm 1 SE) followed by different letters across each row are significantly different for each variable (Tukey HSD post hoc test, $p < 0.05$). Significant levels are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Variables	df ^a	F	p	Site					
				SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
Bulk density (g cm ⁻³)	5, 16.9	43.8	***	0.10 ^d (0.01)	0.17 ^c (0.01)	0.19 ^c (0.01)	0.39 ^a (0.03)	0.16 ^{cd} (0.01)	0.27 ^b (0.02)
Organic matter content (mg cm ⁻³)	5, 6.2	25.1	***	88.7 ^d (4.8)	119.3 ^a (2.7)	103.8 ^c (1.1)	54.3 ^e (4.4)	114.5 ^{ab} (5.4)	109.6 ^{bc} (3.2)
Total C (mg cm ⁻³)	5, 6.1	7.0	*	41.5 ^c (2.7)	52.9 ^{ab} (1.6)	40.6 ^c (0.9)	60.7 ^a (2.9)	50.0 ^{bc} (3.1)	51.6 ^{ab} (2.0)
Total N (mg cm ⁻³)	5, 17.1	5.1	**	2.3 ^{ab} (0.1)	2.4 ^a (0.1)	2.5 ^a (0.3)	1.7 ^b (0.1)	2.5 ^a (0.2)	2.4 ^a (0.1)
Total P (mg cm ⁻³)	5, 17.1	55.3	***	0.05 ^c (0.004)	0.12 ^b (0.006)	0.20 ^a (0.012)	0.03 ^c (0.001)	0.06 ^c (0.004)	0.10 ^b (0.014)
Atomic C:N	5, 17.1	19.3	***	21.3 ^b (1.2)	26.2 ^b (0.4)	19.1 ^b (2.1)	44.6 ^a (4.4)	23.4 ^b (0.6)	25.0 ^b (0.6)
Atomic N:P	5, 6.1	17.4	**	105.3 ^a (6.2)	46.2 ^b (3.4)	28.0 ^d (1.8)	109.2 ^a (5.9)	101.9 ^a (5.8)	66.1 ^b (5.9)

^a Degrees of freedom (df) of the denominator were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

Table 4.2 Statistical results of pore water variables measured in mangrove sites of the Florida Coastal Everglades. Mean (± 1 SE) followed by different letters across each row are significantly different within each effect (site, season, year; Tukey HSD post hoc test, $p < 0.05$). ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Variables	Site						Season		Year			
Salinity (g kg ⁻¹)	SRS-4 4.6 ^c (1.1)	SRS-5 20.8 ^b (3.1)	SRS-6 27.0 ^a (2.6)	TS/Ph-6 16.8 ^b (1.8)	TS/Ph-7 20.0 ^b (1.3)	TS/Ph-8 20.2 ^b (0.6)	Dry 20.9 ^a (1.8)	Wet 15.6 ^b (1.6)	2001 20.7 ^a (2.7)	2002 18.3 ^b (2.6)	2003 15.5 ^c (2.2)	2004 18.5 ^b (2.6)
Sulfide (mM)	0.05 ^c (0.02)	0.14 ^c (0.04)	0.01 ^c (0.01)	1.04 ^b (0.20)	0.86 ^b (0.12)	1.58 ^a (0.29)	0.50 ^b (0.12)	0.72 ^a (0.17)	0.59 ^a (0.27)	0.65 ^a (0.21)	0.66 ^a (0.20)	0.56 ^a (0.16)
DIN (μ M)	2.9 ^c (0.6)	4.1 ^c (0.8)	4.7 ^c (0.9)	21.8 ^a (6.2)	14.1 ^b (4.6)	8.8 ^b (4.0)	10.2 ^a (2.8)	8.9 ^a (2.0)	15.6 ^a (4.5)	6.7 ^b (1.6)	2.4 ^c (0.6)	13.0 ^a (4.1)
SRP (μ M)	0.7 ^b (0.3)	0.9 ^b (0.3)	1.4 ^a (0.4)	1.1 ^{ab} (0.3)	0.9 ^{ab} (0.2)	1.0 ^{ab} (0.3)	0.8 ^b (0.2)	1.2 ^a (0.1)	0.5 ^c (0.2)	0.8 ^b (0.2)	0.9 ^b (0.2)	1.8 ^a (0.3)
ANOVA source ^a :	Salinity		Sulfide		DIN		SRP					
Site	F _{5,6.1} = 95.4***		F _{5,6.6} = 46.2***		F _{5,47.1} = 17.2***		F _{5,6.4} = 4.0*					
Year	F _{3,289} = 62.2***		F _{3,293} = 0.8 ^{ns}		F _{3,292} = 28.2***		F _{3,291} = 61.4***					
Season	F _{1,290} = 361.8***		F _{1,295} = 17.1***		F _{1,293} = 1.6 ^{ns}		F _{1,293} = 27.0***					
Site*Year	F _{15,289} = 11.9***		F _{15,290} = 3.4***		F _{15,289} = 6.9***		F _{15,288} = 3.1***					
Site*Season	F _{5,289} = 97.9***		F _{5,292} = 7.7***		F _{5,291} = 2.9*		F _{5,290} = 16.0***					
Season*Year	F _{3,289} = 18.9***		F _{3,293} = 17.2***		F _{3,292} = 5.2**		F _{3,291} = 53.0***					
Site*Year*Season	F _{15,289} = 5.7***		F _{15,290} = 6.5***		F _{15,289} = 4.4***		F _{15,288} = 9.5***					

^a Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

Taylor River remained fairly constant at about 17-20 g kg⁻¹ (Table 4.2). Salinity was significantly higher during the dry season (20.9 g kg⁻¹) compared to the wet season (15.6 g kg⁻¹; Table 4.2). However, there was a significant site and season interaction, with higher salinity during the dry season compared to the wet season at all Shark River sites, while in the Taylor River sites salinity did not differ significantly between seasons (Table 4.2; Fig 4.4a). Salinity was higher during 2001 (20.7 ± 2.7) and lower during 2003 (15.5 ± 2.2 g kg⁻¹; Table 4.2). There was a significant interaction between year and season, with higher salinity during the dry season of all years compared to the wet season (Table 4.2).

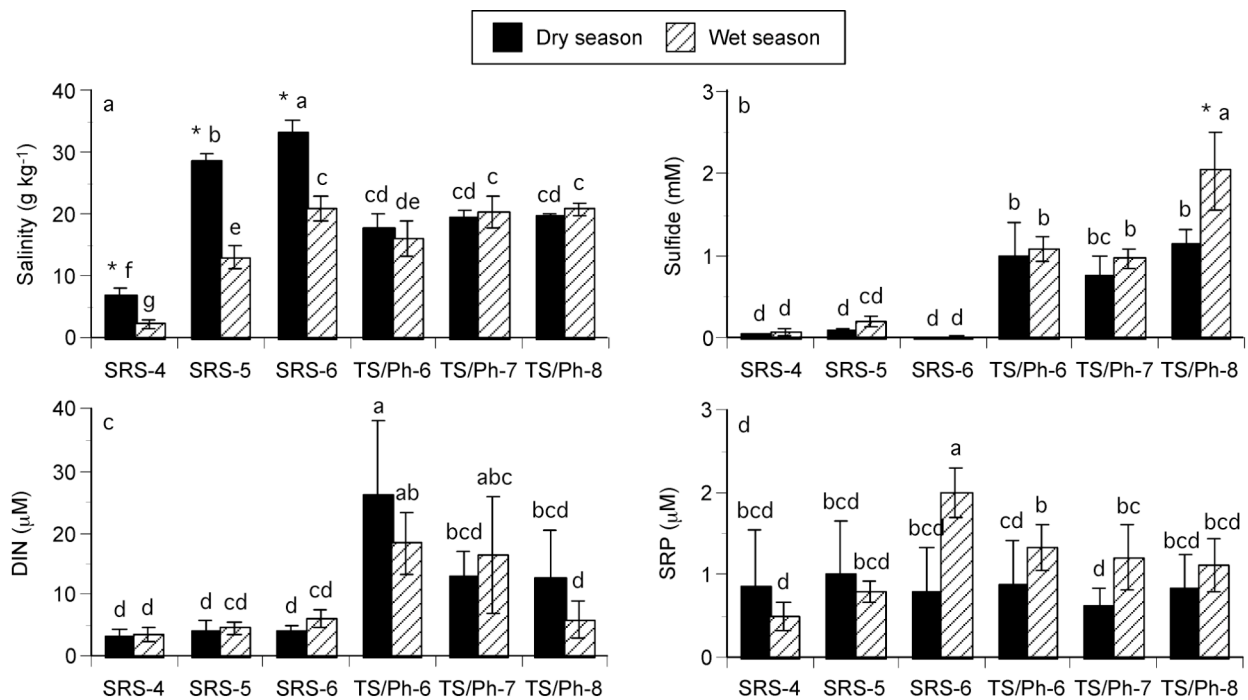


Fig. 4.4 Spatial and seasonal variation in soil properties including salinity (a), sulfide concentrations (b), dissolved inorganic nitrogen (DIN (c), and soluble reactive phosphorus (SRP (d) measured in mangrove sites of the Florida Coastal Everglades during the period 2001-2004. Asterisks indicate significant differences ($p < 0.05$) within each site. Means (± 1 SE) with different letters within each panel are significantly different ($p < 0.05$) across sites and seasons.

Sulfide concentrations were significantly higher at the Taylor River sites compared to all Shark River sites (Table 4.2). In Taylor River, TS/Ph-8 (1.58 ± 0.3 mM) had the highest sulfide concentrations and TS/Ph-7 (0.86 ± 0.1 mM) the lowest (Table 4.2). Along Shark River, sulfide concentrations were <0.14 mM (Table 4.2). Sulfide concentrations were higher during the wet season (0.72 ± 0.2 mM) compared to the dry season (0.50 ± 0.1 ; Table 4.2). However, there was a significant interaction between site and season, with no significant differences in sulfide concentrations between seasons for most of the sites, except for TS/Ph-8 (Table 4.2; Fig. 4.4b). Sulfide concentrations did not vary significantly from 2001 to 2004, and ranged from 0.56 ± 0.1 to 0.66 ± 0.2 (Table 4.2). Soil redox potential (Eh) did vary significantly among sites ($F_{5,68} = 4.2$, $p = 0.0023$) ranging from 42 ± 28 to 133.5 ± 13.8 mv across all six sites. Soil Eh also was significantly ($F_{2,68} = 37.2$, $p = 0.0023$) higher at 0 cm (125.3 ± 10 mv) and 10 cm (103.8 ± 12.7 mv) depths compared to 45 cm (-14.6 ± 16 mv). Overall, the Shark River sites (range: 73.2 ± 15.8 to 133.5 ± 13.8 mv) had higher soil Eh values compared to Taylor River sites (range: 42.0 ± 28.2 to 57.6 ± 28.3 mv). However, soil Eh values indicated slightly reducing conditions across all sites and depths. Soil Eh did not differ among seasons or years, and there were no significant interactions for site and season, site and depth, and season and depth ($p > 0.05$).

Porewater NO_2^- and NO_3^- concentrations were often <0.5 μM across all sites and seasons. Thus, values for NO_2^- , NO_3^- , and NH_4^+ were pooled together to determine dissolved inorganic nitrogen concentrations (DIN; Table 4.2; Fig. 4.4c). DIN concentrations were significantly higher at all the Taylor River sites compared to the Shark River sites, with the highest concentration at TS/Ph-6 (21.8 ± 6.2 μM) and the lowest at SRS-4 (2.9 ± 0.6 μM ; Table 4.2). Along Shark River, DIN concentrations did not vary significantly among sites and were <4.7 μM (Table 4.2). There was a significant interaction between site and season for DIN concentrations,

although no significant differences between seasons were observed for any of the sites (Table 4.2; Fig. 4.4c). Among years, DIN concentrations were higher during 2001 ($15.6 \pm 4.5 \mu\text{M}$) and 2004 ($13 \pm 4.1 \mu\text{M}$) compared to other years (Table 4.2).

Soluble reactive phosphorus (SRP) concentrations were significantly different among sites, especially along Shark River where concentrations increased from upstream to downstream the estuary (Table 4.2). Overall, SRP concentrations ranged from $0.7 \pm 0.3 \mu\text{M}$ (SRS-4) to $1.4 \pm 0.4 \mu\text{M}$ (SRS-6) along Shark River, and from $0.9 \pm 0.2 \mu\text{M}$ (TS/Ph-7) to $1.1 \pm 0.3 \mu\text{M}$ (TS/Ph-6) along Taylor River (Table 4.2). Overall, SRP concentrations were significantly higher during the wet season ($1.2 \pm 0.1 \mu\text{M}$) compared to the dry season ($0.8 \pm 0.2 \mu\text{M}$; Table 4.2). There was a significant interaction between site and season, with the highest SRP concentration at SRS-6 ($2.0 \pm 0.3 \mu\text{M}$) during the wet season (Table 4.2; Fig. 4.4d). SRP concentrations at SRS-4, SRS-5, and TS/Ph-8 were not significantly different between seasons (Fig. 4.4d). Across years, SRP concentrations ranged from 0.5 ± 0.2 to $1.8 \pm 0.3 \mu\text{M}$, with the highest concentration during 2004 (Table 4.2).

Forest Structure, Aboveground Biomass and Wood Production

Basal area, aboveground wood biomass and wood production did not differ significantly among plots and transects within a site for any of the Shark River sites (Table 4.3). Thus, data for plots and transects was pooled together within a site to run further analyses and to make comparisons for each of these variables across selected sites, except for tree density that varied significantly between plots and transects for most of selected sites (Table 4.3). Basal area differed significantly among selected sites and ranged from $1.2 \pm 0.3 \text{ m}^2 \text{ ha}^{-1}$ (TS/Ph-8) to $38.3 \pm 1.8 \text{ m}^2 \text{ ha}^{-1}$ (SRS-6; Tables 4.3 and 4.4). Along Shark River, basal area was significantly higher in SRS-6 compared to SRS-5 and SRS-4 that had basal areas at about $20 \text{ m}^2 \text{ ha}^{-1}$ (Table 4.4). *R.*

mangle, *L. racemosa* and *A. germinans* were found in SRS-5 and SRS-6, while the later species was not observed in the upstream part (SRS-4) of the estuary; *C. erectus* only occurred in this site (Table 4.4). *L. racemosa* ($18.0 \pm 3.5 \text{ m}^2 \text{ ha}^{-1}$) contributed more to total basal area in SRS-6, while *R. mangle* had the greatest basal area in SRS-4 ($12.4 \pm 1.3 \text{ m}^2 \text{ ha}^{-1}$) and SRS-5 ($20.5 \pm 1.8 \text{ m}^2 \text{ ha}^{-1}$; Table 4.4). In TS/Ph-8, *C. erectus* accounted for 92% of the total basal area (Table 4.4). There were neither significant differences in basal area among years nor a significant interaction between sites and years, indicating that the variation in basal area among sites is independent of time (Table 4.3).

Table 4.3 Statistical results of forest structural attributes, aboveground biomass and wood production in mangrove forests of the Florida Coastal Everglades. ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Source of variation	df ^a	F	p	Source of variation	df ^a	F	p
Basal area				Basal area			
Site	2, 3	14.5	*	Site	3, 4.5	40.1	***
Method	1, 15	1.5	ns	Year	1, 16.5	0.8	ns
Site*Method	2, 15	11.6	***	Site*Year	3, 16.5	0.1	ns
Tree density				Tree density			
Site	2, 3	70.8	**	Site	3, 4.9	55.1	***
Method	1, 15	233.8	***	Year	1, 17	0.2	ns
Site*Method	2, 15	113.1	***	Site*Year	3, 17	0.1	ns
Aboveground Biomass				Aboveground Biomass			
Site	2, 3	9.0	*	Site	3, 4.5	40.8	**
Method	1, 15	2.3	ns	Year	1, 16.5	0.9	ns
Site*Method	2, 15	11.5	***	Site*Year	3, 16.5	0.1	ns
Aboveground Wood Production				Aboveground Wood Production			
Site	2, 29	2.8	*	Site	3, 10	12.1	**
Method	1, 29	0.05	ns				
Site*Method	2, 29	0.3	ns				

^a Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

Table 4.4 Structural characteristics measured in plots and transects at mangrove sites in the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different for each variable (Tukey HSD post hoc test, $p < 0.05$).

Variable Species	Plots						Transects		
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8	SRS-4	SRS-5	SRS-6
Tree height (m)	6.0 (0.2)	8.3 (0.1)	13.0 (0.2)	—	—	3.2 (0.1)	-	-	-
Basal area (m ² ha ⁻¹)							-	-	-
<i>A. germinans</i>	-	1.2	11.4	—	—	-	-	-	-
<i>L. racemosa</i>	4.6	2.0	18.0	—	—	0.2	-	-	-
<i>R. mangle</i>	12.4	20.5	8.9	—	—	-	-	-	-
<i>C. erectus</i>	4.1	-	-	—	—	1.1	-	-	-
Total	21.1 ^b (1.3)	23.8 ^b (1.6)	38.3 ^a (1.8)	—	—	1.2 ^c (0.3)	-	-	-
Total tree density (trees ha ⁻¹) dbh ≥ 2.5 cm									
<i>A. germinans</i>	-	56	550	—	—	-	-	121	499
<i>L. racemosa</i>	1433	75	1075	—	—	150	465	151	562
<i>R. mangle</i>	5408	2644	1225	—	—	-	3310	2518	708
<i>C. erectus</i>	1000	-	-	—	—	900	337	-	-
Total	7842 ^a (208)	2775 ^{cd} (288)	2850 ^c (13)	—	—	1050 ^e (350)	4112 ^b (356)	2790 ^{cd} (520)	1770 ^d (29)
Importance value (IV)									
<i>A. germinans</i>	-	4	23	—	—	-	-	-	-
<i>L. racemosa</i>	22	4	43	—	—	35	-	-	-
<i>R. mangle</i>	61	92	34	—	—	-	-	-	-
<i>C. erectus</i>	17	-	-	—	—	65	-	-	-
Total	100	100	100	—	—	100	-	-	-
Complexity index (CI)	33.0	14.0	45.0	—	—	0.12	13.0	18.0	26.0

— Not determined

Tree density varied significantly between sampling methods (plots vs. transects) and selected sites, and there was a significant site and method interaction (Table 4.3). Tree density in SRS-4 and SRS-6 plots (7842 ± 208 and 2850 ± 13 trees ha⁻¹) was significantly higher compared to transect data (4112 ± 356 and 1770 ± 29 trees ha⁻¹, respectively; Table 4.4). TS/Ph-8 showed the lowest tree density compared to selected sites (Table 4.4). Tree density did not vary significantly among years and there was no significant interaction for site and year (Table 4.3). *R. mangle* occurred in all Shark River sites and represented 40% (SRS-6, transects) to 96% (SRS-5, plots) of total tree density across plots and transects at selected sites (Table 4.4). Along Shark River, the density of larger trees (dbh > 10 cm) decreased with distance inland from the mouth of the estuary for both plots and transects, and ranged from 550 trees ha⁻¹ (SRS-4) to 1388 trees ha⁻¹ (SRS-6) for plots, and from 809 trees ha⁻¹ (SRS-4) to 1123 trees ha⁻¹ (SRS-6) for transects (Fig. 4.5). However, total density of all trees with dbh > 2.5 cm was significantly higher in SRS-4 compared to SRS-5 and SRS-6 for both plots and transects (Table 4.4). The SRS-4 plots were characterized with a higher density of trees with dbh < 5 cm (4208 trees ha⁻¹) and dbh < 10 cm (3258 trees ha⁻¹) compared to SRS-4 transects and other selected sites (Fig. 4.5). In TS/Ph-8 plots, the density of smaller trees (dbh < 5 cm) accounted for 86% of the total density (1050 trees ha⁻¹; Fig 4.5; Table 4.4). Mean tree height decreased from 13 ± 0.2 m in SRS-6 to 6 ± 0.2 m in SRS-4 upstream the estuary. In TS/Ph-8, the average tree height was 3.2 ± 0.1 m (Table 4.4).

The relative importance value (IV) of *R. mangle* was higher in SRS-4 (61) and SRS-5 (92), while in SRS-6 *L. racemosa* (43) had the highest IV and *A. germinans* (23) the lowest. At TS/Ph-8, *C. erectus* was the dominant species (IV = 65) and co-existed with *L. racemosa* (Table 4.4). Along transects, the IV for all species had similar trends across all Shark River sites as the

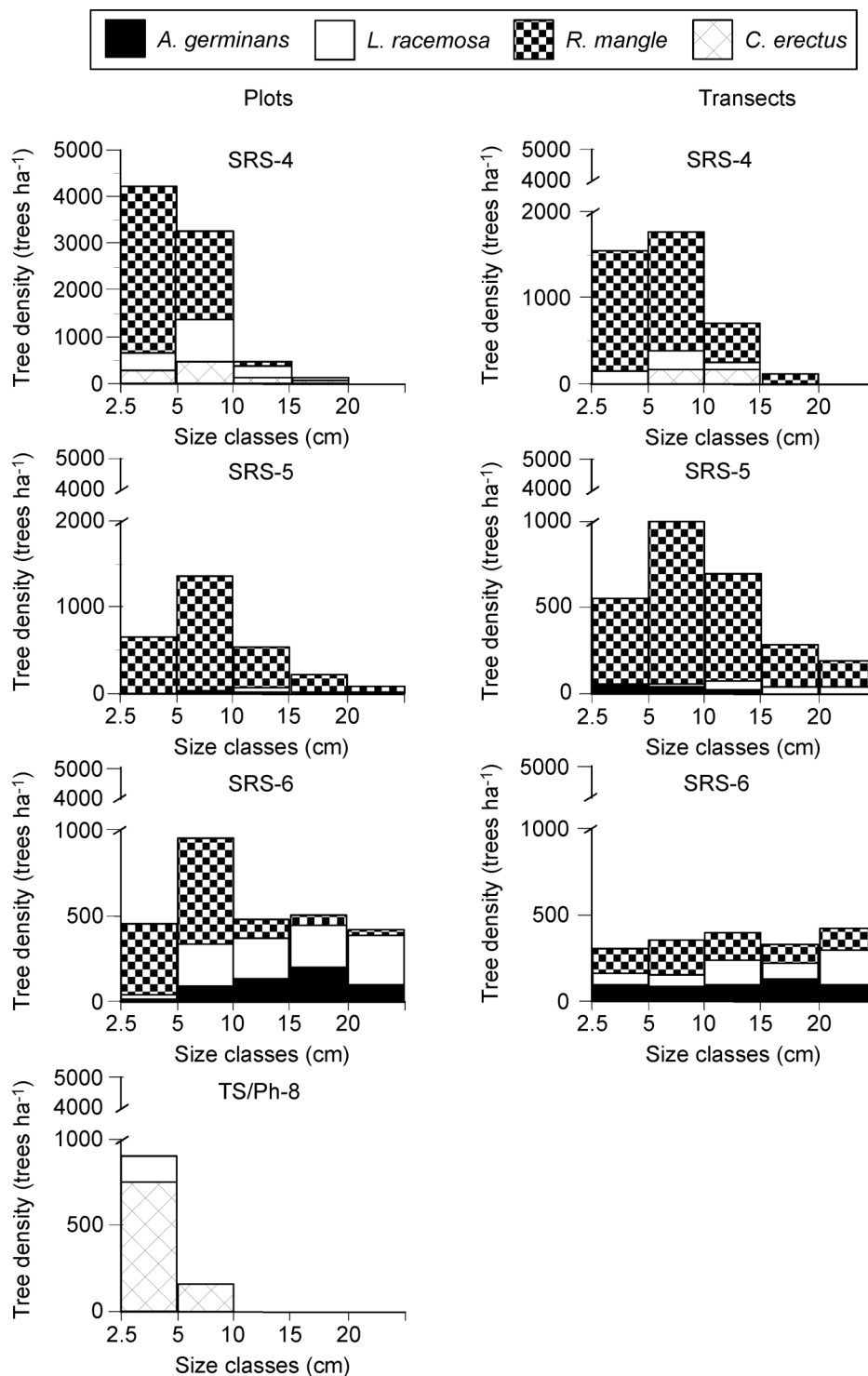


Fig. 4.5 Tree size class distribution of mangrove species along Shark River estuary and at TS/Ph-8 in Joe Bay measured in permanent vegetation plots and transects during the period 2001-2004.

plot data (data not shown). The complexity index (CI) of vegetation reflected the low structural development of TS/Ph-8 compared to Shark River sites. Along this estuary, SRS-6 had the highest complexity index (45 and 26) for plots and transects, respectively (Table 4.4). SRS-4 plots (CI = 33) had a higher complexity index compared to transects (CI = 13) due to the higher density of smaller trees within plots; SRS-5 had a similar complexity index for plots and transects (Table 4.4).

Mean aboveground wood biomass varied significantly among selected sites ranging from $447 \pm 46 \text{ g m}^{-2}$ (TS/Ph-8) to $15,207 \pm 609 \text{ g m}^{-2}$ (SRS-6; Fig. 4.6a). Along Shark River, wood biomass was significantly higher in SRS-6 compared to SRS-4 ($9772 \pm 702 \text{ g m}^{-2}$) and SRS-5 ($10,879 \pm 567 \text{ g m}^{-2}$; Fig. 4.6a). Wood biomass in TS/Ph-6 & 7 was 1250 g m^{-2} (after Coronado-Molina et al. 2004; Fig. 4.6a). *R. mangle* comprised 66.8 % (SRA-4), 87.1 % (SRS-5), 26% (SRS-6), and 100% (TS/Ph-6 & 7) of the total biomass at each site, while *L. racemosa* and *A. germinans* accounted for 43 and 31% of the total biomass at SRS-6, respectively. At TS/Ph-8, *C. erectus* comprised 90% of the total biomass (Fig. 4.6a).

Total (0-90 cm) belowground biomass varied significantly among all six sites ranging from $2404 \pm 329 \text{ g m}^{-2}$ to $4673 \pm 401 \text{ g m}^{-2}$ (Fig. 4.6a; see chapter 2 for a complete description of results). Estimates of total belowground biomass followed the trend TS/Ph-7 > SRS-5 > TS/Ph-8 > SRS-4 > SRS-6 > TS/Ph-6 (Fig. 4.6a). The biomass root:shoot ratio in the Shark River sites was lower compared to all Taylor sites. Root:shoot ratio ranged from 0.33 ± 0.04 to 0.17 ± 0.01 in the Shark River sites, and from 1.92 to 9.75 ± 1.0 in the Taylor River sites (Fig. 4.6b).

Average wood production for mangrove species ranged from 0.18 ± 0.13 to $3.28 \pm 0.48 \text{ kg tree}^{-1} \text{ yr}^{-1}$ across selected sites (Table 4.5). *L. racemosa* had the highest wood production in SRS-5 ($3.28 \pm 0.48 \text{ kg tree}^{-1} \text{ yr}^{-1}$) and SRS-6 ($2.85 \pm 0.45 \text{ kg tree}^{-1} \text{ yr}^{-1}$; Table 4.5). Average

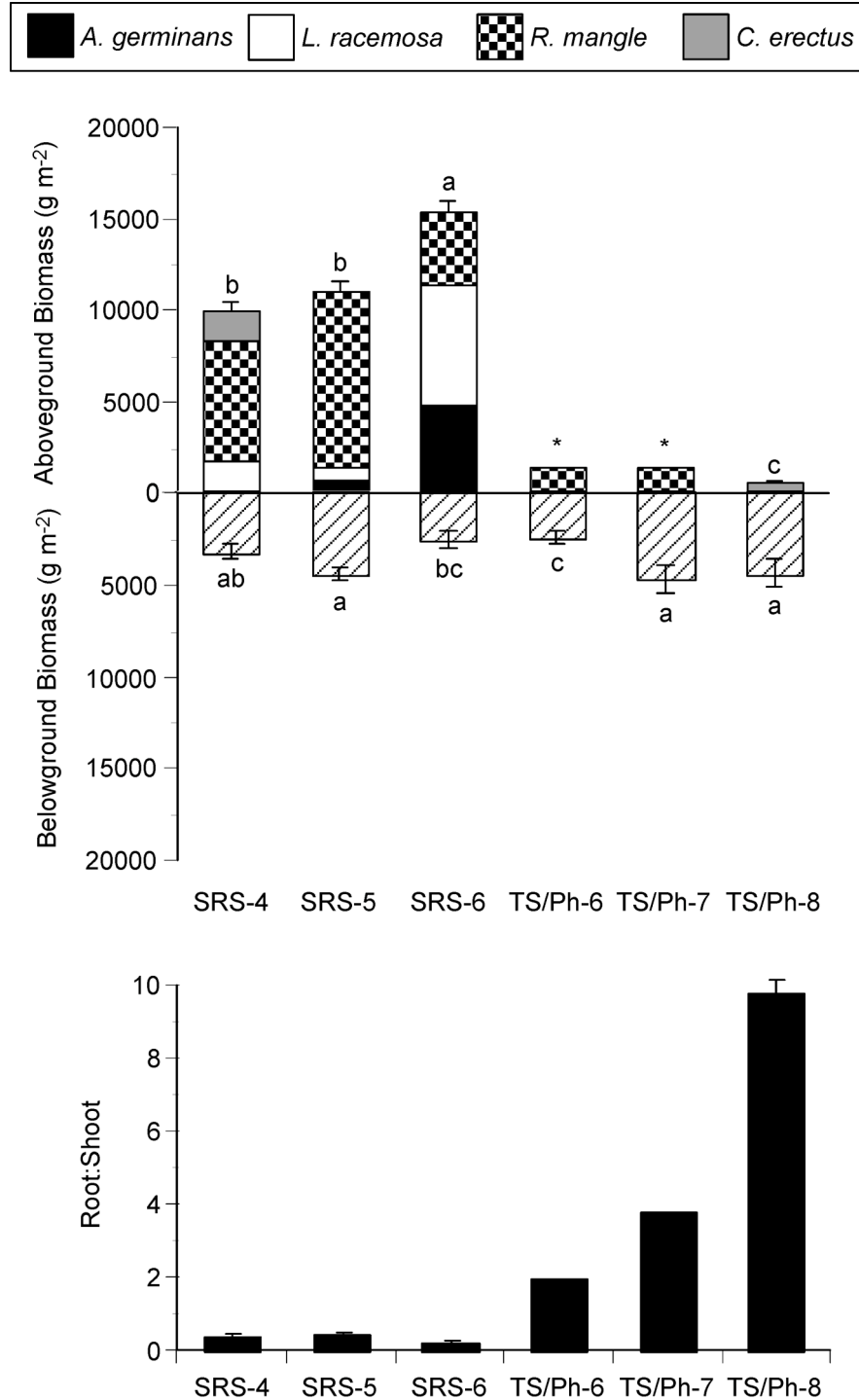


Fig. 4.6 Total aboveground wood biomass and belowground biomass (a) and root:shoot ratios (b) in mangrove forests of the Florida Coastal Everglades. Means (± 1 SE) with different letters are significantly different ($p < 0.05$) among sites for each component of biomass. Asterisks indicate data from Coronado-Molina et al. (2004), and were not included in the statistical analysis.

wood production for *A. germinans* and *R. mangle* were highest in SRS-6 (Table 4.5). Along Shark River, average total wood production decreased from $5.26 \pm 0.53 \text{ kg tree}^{-1} \text{ yr}^{-1}$ in SRS-6 to $2.11 \pm 0.1 \text{ kg tree}^{-1} \text{ yr}^{-1}$ in SRS-4 (Table 4.5). At TS/Ph-8, average total wood production was $0.54 \pm 0.05 \text{ kg tree}^{-1} \text{ yr}^{-1}$, and lower compared to Shark River sites (Table 4.5).

Table 4.5 Average wood production per tree and total annual basal area increment in mangrove forests of the Florida Coastal Everglades.

Variable Species	Sites					
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
Average wood production ($\text{kg tree}^{-1} \text{ yr}^{-1}$)						
<i>A. germinans</i>	-	0.18 (0.13)	1.03 (0.23)	—	—	-
<i>L. racemosa</i>	0.65 (0.15)	3.28 (0.48)	2.85 (0.45)	—	—	0.05 (0.05)
<i>R. mangle</i>	0.43 (0.03)	0.65 (0.20)	1.38 (0.32)	—	—	-
<i>C. erectus</i>	1.03 (0.23)	-	-	—	—	0.49 (0.01)
Total	2.11 (0.1)	4.11 (0.8)	5.26 (0.53)	—	—	0.54 (0.05)
Basal area increment ($\text{cm}^2 \text{ m}^{-2} \text{ yr}^{-1}$)						
<i>A. germinans</i>	-	0.01 (0.00)	0.12 (0.03)	—	—	-
<i>L. racemosa</i>	0.16 (0.09)	0.10 (0.06)	0.59 (0.07)	—	—	0.008 (0.00)
<i>R. mangle</i>	0.39 (0.08)	0.39 (0.14)	0.31 (0.03)	—	—	-
<i>C. erectus</i>	0.13 (0.03)	-	-	—	—	0.12 (0.07)
Total	0.68 (0.19)	0.50 (0.19)	1.02 (0.06)	—	—	0.12 (0.06)

— Not determined

The annual increments in total basal area also decreased from the mouth of Shark River estuary (SRS-6) to farther upstream (SRS-4), and ranged from $0.01 \pm 0.00 \text{ cm}^2 \text{ m}^{-2} \text{ yr}^{-1}$ (*A. germinans*) to $0.59 \pm 0.07 \text{ cm}^2 \text{ m}^{-2} \text{ yr}^{-1}$ (*L. racemosa*) across selected sites (Table 4.5). *R. mangle* contributed 57% (SRS-4) and 75% (SRS-5) of total growth increment in the upstream sites, while *L. racemosa* accounted for 58% of the total productivity in SRS-6 (Table 4.5). In TS/Ph-8, annual increment in total basal area was 8.5 times lower compared to that of SRS-6 (Table 4.5).

Total annual wood production varied significantly among selected sites, with the highest wood production in SRS-6 ($384.0 \pm 34.2 \text{ g m}^{-2} \text{ yr}^{-1}$) and the lowest in TS/Ph-8 ($47.6 \pm 23.5 \text{ g m}^{-2} \text{ yr}^{-1}$; Table 4.6), and showed the same spatial trend as the individual tree growth rates (Table 4.5). Along Shark River, annual wood production was higher in SRS-6 and lower at sites upstream the estuary (Table 4.6). *L. racemosa* (SRS-6) had the highest wood production across selected sites, while *R. mangle* dominated wood productivity in the upstream sites (SRS-4 and SRS-5; Table 4.6). In TS/Ph-6 & 7 annual wood production ranged from 64 to 75 $\text{g m}^{-2} \text{ yr}^{-1}$, respectively (after Ewe et al. 2006; Table 4.6).

Litterfall Production

There was a consistent seasonal pattern of total litterfall and each of its components (leaves, reproductive parts, and wood) across the 4-year period (2001-2004) of study (Fig. 4.7). Litterfall production for all components was significantly higher during the wet season (June-November) compared to the dry season (December-May), with higher rates for leaf fall ($2.18 \pm 0.14 \text{ g m}^{-2} \text{ d}^{-1}$) and lower rates for reproductive parts ($0.63 \pm 0.01 \text{ g m}^{-2} \text{ d}^{-1}$) and wood ($0.24 \pm 0.03 \text{ g m}^{-2} \text{ d}^{-1}$; Fig. 4.7; Table 4.7). Mean total litterfall ranged from 1.26 ± 0.1 to $3.04 \pm 0.2 \text{ g m}^{-2} \text{ d}^{-1}$ for the dry and wet seasons, respectively (Table 4.7). Mean rates of total litterfall ranged

Table 4.6 Aboveground NPP (NPP_A : $\text{g m}^{-2} \text{ yr}^{-1}$) of mangrove forests in the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different for each variable (Tukey HSD post hoc test, $p < 0.05$).

Variable	Sites					
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
Wood production (NPP_W)						
<i>A. germinans</i>		2.7 (1.4)	50.6 (12.2)	-	-	-
<i>L. racemosa</i>	53.5 (25.1)	36.3 (19.9)	210.4 (26.5)	-	-	3.2 (0.0)
<i>R. mangle</i>	179.6 (28.8)	167.2 (56.5)	123.0 (4.5)	64.0 *	75.0 *	
<i>C. erectus</i>	46.8 (10.2)	-	-	-	-	44.4 (25.1)
Total	279.9 ^{ab} (64.0)	206.0 ^{bc} (77.8)	384.0 ^a (34.2)	64.0 *	75.0 *	47.6 ^d (23.5)
Litterfall production (NPP_L)						
Leaves	534.6 (38.6)	581.2 (40.3)	741.4 (47.5)	258.0 *	303.0 *	230.7 (20.5)
Reproductive parts	196.4 (24.4)	123.7 (10.5)	184.9 (17.7)			45.2 (5.3)
Wood	79.6 (19.2)	62.4 (13.8)	87.7 (18.1)			9.3 (3.2)
Total	810.6 ^b (75.1)	767.3 ^b (53.0)	1014.1 ^a (74.0)	258.0 *	303.0 *	285.2 ^c (25.0)
$\text{NPP}_A = \text{NPP}_W + \text{NPP}_L$	1090.5	973.3	1398.1	322.0 *	378.0 *	332.8

* Data from Ewe et al. (2006); not included in any of the statistical analysis

Table 4.7 Statistical results for each component of daily ($\text{g m}^{-2} \text{d}^{-1}$) litterfall in mangrove sites of the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different within each effect (site, season, year; Tukey HSD post hoc test, $p < 0.05$). ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Variables	Site						Season		Year			
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8	Dry	Wet	2001	2002	2003	2004
Total	2.41 ^b (0.25)	2.27 ^b (0.29)	2.95 ^a (0.36)	—	—	0.98 ^c (0.09)	1.26 ^b (0.09)	3.04 ^a (0.21)	1.97 ^b (0.34)	1.97 ^b (0.31)	2.31 ^a (0.28)	2.36 ^a (0.36)
Leaves	1.59 ^b (0.15)	1.72 ^b (0.21)	2.15 ^a (0.25)	—	—	0.80 ^c (0.07)	0.95 ^b (0.06)	2.18 ^a (0.14)	1.45 ^{bc} (0.22)	1.44 ^c (0.21)	1.70 ^a (0.20)	1.67 ^{ab} (0.24)
Reproductive parts	0.59 ^a (0.07)	0.37 ^{ab} (0.06)	0.56 ^a (0.09)	—	—	0.14 ^b (0.02)	0.21 ^b (0.02)	0.63 ^a (0.06)	0.39 ^a (0.08)	0.40 ^a (0.08)	0.41 ^a (0.07)	0.46 ^a (0.09)
Wood	0.23 ^a (0.05)	0.18 ^{ab} (0.04)	0.24 ^a (0.04)	—	—	0.03 ^b (0.01)	0.10 ^b (0.02)	0.24 ^a (0.03)	0.12 ^{bc} (0.04)	0.13 ^c (0.04)	0.20 ^{ab} (0.04)	0.22 ^a (0.05)
ANOVA source ^a :	Total		Leaves		Reproductive parts		Wood					
Site	$F_{3,36} = 34.2^{***}$		$F_{3,36} = 26.4^{***}$		$F_{3,5.2} = 15.8^{**}$		$F_{3,4} = 14.0^*$					
Year	$F_{3,1801} = 9.9^{***}$		$F_{3,1801} = 7.1^{***}$		$F_{3,1503} = 1.8^{ns}$		$F_{3,1722} = 8.7^{***}$					
Season	$F_{1,1801} = 819.5^{***}$		$F_{1,1801} = 687.1^{***}$		$F_{1,1630} = 298.3^{***}$		$F_{1,1765} = 45.0^{***}$					
Site*Year	$F_{9,1801} = 1.9^{ns}$		$F_{9,1801} = 0.9^{ns}$		$F_{9,1546} = 2.9^*$		$F_{9,1736} = 2.8^{**}$					
Site*Season	$F_{3,1801} = 52.7^{***}$		$F_{3,1801} = 43.0^{***}$		$F_{3,1613} = 24.5^{***}$		$F_{3,1759} = 3.1^*$					
Season*Year	$F_{3,1801} = 3.8^{**}$		$F_{3,1801} = 1.4^{ns}$		$F_{3,1503} = 3.0^*$		$F_{3,1722} = 3.2^*$					
Site*Year*Season	$F_{9,1801} = 3.8^{***}$		$F_{9,1801} = 3.7^{***}$		$F_{9,1546} = 2.0^*$		$F_{9,1736} = 1.6^{ns}$					

^a Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

— Not measured in these sites

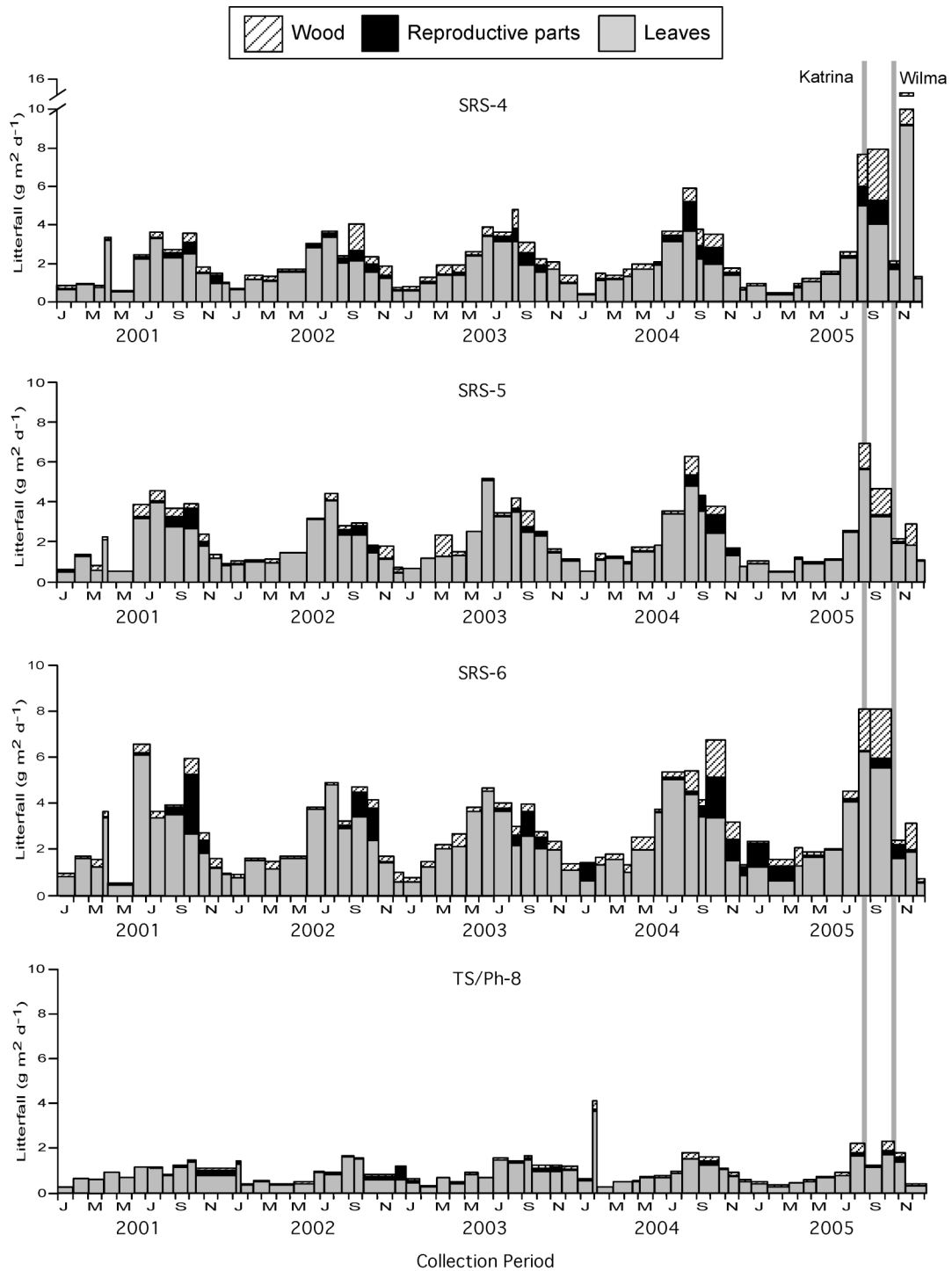


Fig. 4.7 Daily rates of litterfall components (leaves, reproductive parts, and wood) in mangrove forests along Shark River estuary and at TS/Ph-8 during the period 2001-2005. The width of the bars represents the time period over which collections were made. The vertical gray boxes represent the approximate time of hurricane events affecting the study area. Note the y-axis break in the top panel (SRS-4) of the figure relative to other panels.

from $0.98 \pm 0.1 \text{ g m}^{-2} \text{ d}^{-1}$ (TS/Ph-8) to $2.95 \pm 0.4 \text{ g m}^{-2} \text{ d}^{-1}$ (SRS-6) across selected sites, and followed the pattern $\text{SRS-6} > \text{SRS-4} = \text{SRS-5} > \text{TS/Ph-8}$ (Table 4.7). Leaf fall followed the same pattern as total litterfall; whereas rates for reproductive parts and wood were significantly higher in SRS-4 and SRS-6 and lower in TS/Ph-8 (Table 4.7).

There was a significant site and season interaction on total litterfall and each of its components (Table 4.7). Mean total litterfall was significantly higher during the wet season compared to the dry season for selected sites, with the highest rates at SRS-6 ($4.27 \pm 0.3 \text{ g m}^{-2} \text{ d}^{-1}$) and the lowest at TS/Ph-8 ($0.73 \pm 0.13 \text{ g m}^{-2} \text{ d}^{-1}$) during the dry season (Fig. 4.8a). Along Shark River, total rates were higher in SRS-6 and significantly lower in the upstream sites (SRS-4 and SRS-5; Fig. 4.8a). Leaf fall comprised most of the total litterfall in selected sites ranging from 66% (SRS-4) to 81% (TS/Ph-8). Wood fall accounted for 16% (SRS-5 and TS/Ph-8) to 24% (SRS-4) of the total litter production, while reproductive parts had the smallest contribution (<10%) among selected sites (Fig. 4.8b).

There were also significant differences among years for total, leaf, and wood, with higher rates during 2003 and 2004 compared to 2001 and 2002 (Table 4.7). Mean daily rates of total litterfall ranged from 1.97 ± 0.31 to $2.36 \pm 0.36 \text{ g m}^{-2} \text{ d}^{-1}$ across all years, with an overall increase in rates from 2001 to 2004 (Table 4.7). There was a significant season and year interaction for total, reproductive parts and wood (Table 4.7). Overall, litterfall was higher during the wet season for all years compared to the dry season. There was no significant interaction between sites and years for total litter and leaf fall production (Table 4.7).

Annual litterfall ranged from $285 \pm 25 \text{ g m}^{-2} \text{ yr}^{-1}$ (TS/Ph-8) to $1014.1 \pm 74 \text{ g m}^{-2} \text{ yr}^{-1}$ (SRS-6) across selected sites, and followed the pattern $\text{SRS-6} > \text{SRS-4} = \text{SRS-5} > \text{TS/Ph-8}$ (Table 4.8). Along Shark River, annual total litterfall was approximately 1.3 times lower in

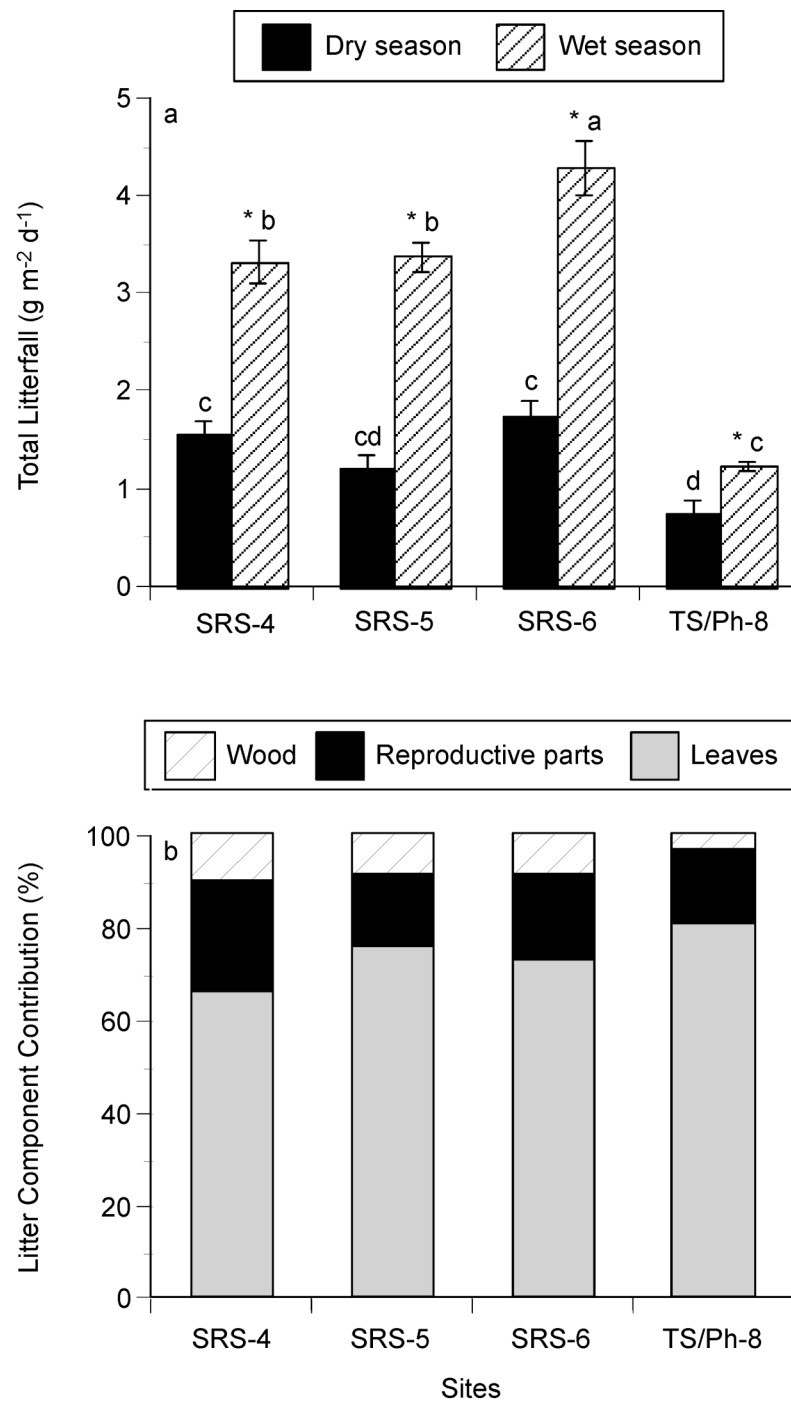


Fig. 4.8 Seasonal variation in daily total litterfall production (a) and litter component contribution (b) in mangrove forests along Shark River estuary and at TS/Ph-8 averaged over the period 2001-2004. Asterisks indicate significant differences ($p < 0.05$) within each site. Means (± 1 SE) with different letters are significantly different ($p < 0.05$) across sites and seasons.

the upstream sites (SRS-4 and SRS-5) compared to SRS-6 (Table 4.8). Annual leaf fall followed the same trend as total litterfall ranging from 230.7 ± 21 to 741.4 ± 48 g m⁻² yr⁻¹ among selected sites (Table 4.8). Across all years, total litterfall was significantly higher in 2004 compared to 2001 and 2002, with rates ranging from 505 ± 87 to 840.1 g m⁻² yr⁻¹ (Table 4.8). Annual rates for leaf fall and reproductive parts were significantly higher during 2002-2004 compared to 2001. Rates for wood fall showed a similar trend to that of annual total litterfall (Table 4.8). There was not a significant site and year interaction for all litterfall components, except for wood (Table 4.8). During 2005, total litterfall had a significant increase in selected sites when compared to previous years due to the passage of Hurricane Wilma across FCE during October 2005. Total litterfall was 1628 ± 58 g m⁻² yr⁻¹ for SRS-4, 859 ± 6 g m⁻² yr⁻¹ for SRS-5, 1339 ± 83 g m⁻² yr⁻¹ for SRS-6, and 325 ± 10 g m⁻² yr⁻¹ for TS/Ph-8. These litterfall rates were 1.1-1.3 times higher in SRS-5, SRS-6, and TS/Ph-8 and double the rates in SRS-4 relative to average annual rates in each site prior to the storm. The daily total litterfall in SRS-4 was 15.4 g m⁻² d⁻¹ during November 2005 after the passage of Hurricane Wilma (Fig. 4.7).

Total Annual Net Primary Productivity (NPP_T)

Annual NPP_A (NPP_L + NPP_W) ranged from 322 g m⁻² yr⁻¹ (TS/Ph-6) to 1398 g m⁻² yr⁻¹ (SRS-6) across all six sites, with higher NPP_A rates in the Shark River sites compared to the Taylor River sites (Table 4.6). Average NPP_A was 3.4 times greater in the Shark River sites (1154 ± 127 g m⁻² yr⁻¹) compared to the Taylor River sites (344 ± 17 g m⁻² yr⁻¹). The NPP_L had the highest contribution to NPP_A accounting for 75 and 85% of the total NPP_A in Shark River and Taylor River, respectively (Table 4.6).

Estimates of NPP_B (0-90 cm) did not differ significantly among all six sites, and ranged from 407 ± 23 g m⁻² yr⁻¹ (TS/Ph-7) to 643 ± 93 g m⁻² yr⁻¹ (SRS-5; Fig. 4.9a; see chapter 2

Table 4.8 Statistical results for each component of annual ($\text{g m}^{-2} \text{ yr}^{-1}$) litterfall in mangrove sites of the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different within each effect (site, season, year; Tukey HSD post hoc test, $p < 0.05$). ANOVA source with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant.

Variables	Site						Year			
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8	2001	2002	2003	2004
Total	810.6 ^b (75.1)	767.3 ^b (53.0)	1014.1 ^a (74.0)	—	—	285.2 ^c (25.0)	504.8 ^c (86.8)	728.1 ^b (102.8)	804.2 ^{ab} (104.9)	840.1 ^a (128.9)
Leaves	534.6 ^b (38.6)	581.2 ^b (40.3)	741.4 ^a (47.5)	—	—	230.7 ^c (20.5)	370.2 ^b (57.1)	535.9 ^a (74.7)	594.2 ^a (72.3)	587.6 ^a (81.0)
Reproductive parts	196.4 ^a (24.4)	123.7 ^{ab} (10.5)	184.9 ^a (17.7)	—	—	45.2 ^b (5.3)	98.0 ^b (19.9)	144.1 ^a (23.0)	139.9 ^a (26.6)	168.1 ^a (33.2)
Wood	79.6 ^a (19.2)	62.4 ^a (13.8)	87.7 ^a (18.1)	—	—	9.3 ^b (3.2)	36.5 ^c (12.7)	48.2 ^b (14.6)	70.0 ^{ab} (20.2)	84.4 ^a (21.3)
ANOVA source ^a :	Total		Leaves		Reproductive parts		Wood			
Site	$F_{3, 3.9} = 61.7^{***}$		$F_{3, 165} = 63.6^{***}$		$F_{3, 4.0} = 19.7^{**}$		$F_{3, 4} = 35.5^*$			
Year	$F_{3, 162} = 23.3^{***}$		$F_{3, 165} = 20.9^{***}$		$F_{3, 162} = 10.8^{***}$		$F_{3, 162} = 14.9^{***}$			
Site*Year	$F_{9, 162} = 1.5^{\text{ns}}$		$F_{9, 165} = 0.7^{\text{ns}}$		$F_{9, 162} = 2.5^*$		$F_{9, 162} = 1.6^{\text{ns}}$			

^a Degrees of freedom (df) of the denominator for each effect were adjusted with the Kenward-Roger method when required, SAS Proc Mixed

— Not measured in these sites

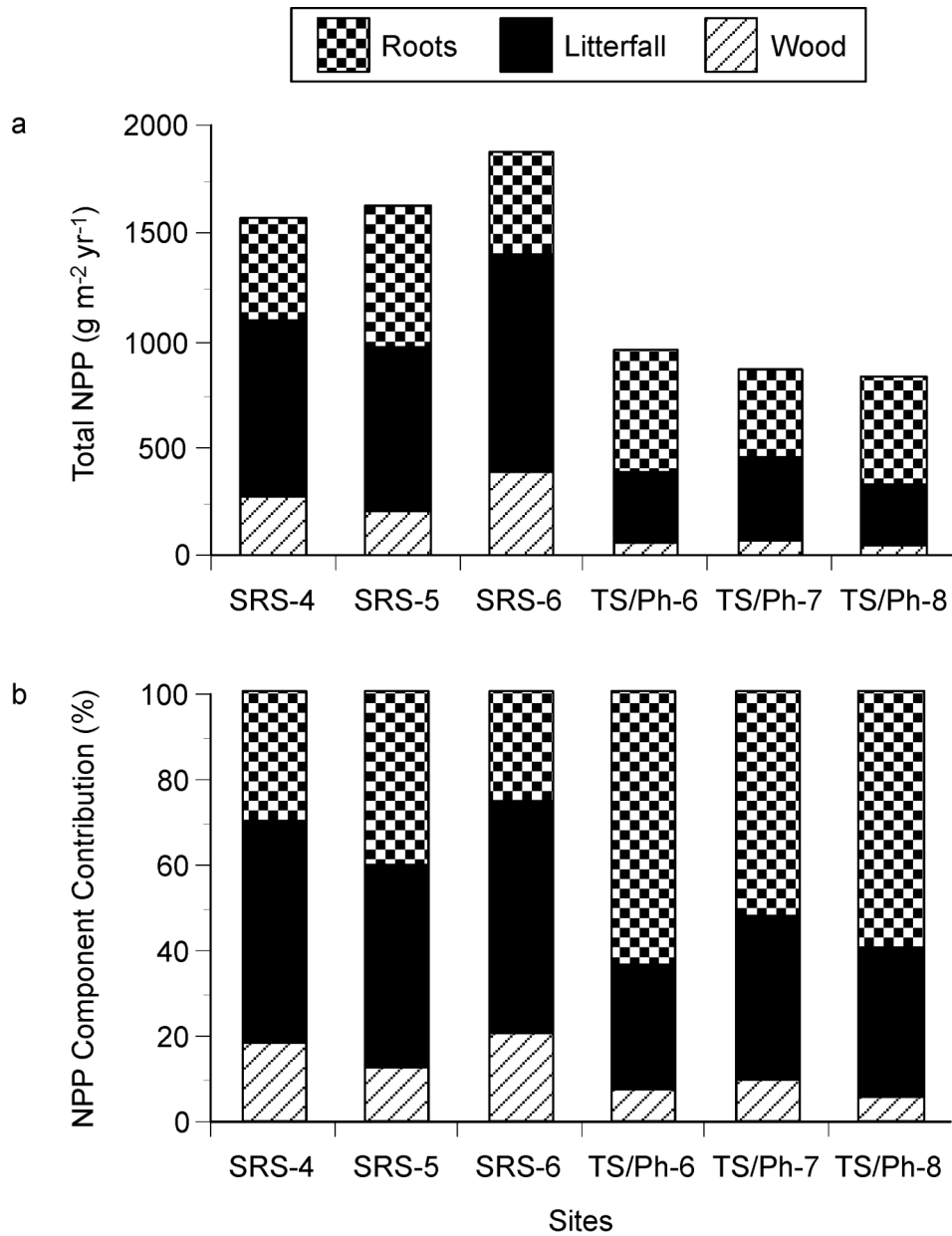


Fig. 4.9 Total net primary productivity (NPP_T) including root, litterfall, and wood production (a) and NPP_T component contribution (b) in mangrove forests of the Florida Coastal Everglades during the period 2001-2004.

for a complete description of results). NPP_T ($NPP_A + NPP_B$) ranged from $785 \text{ g m}^{-2} \text{ yr}^{-1}$ (TS/Ph-7) to $1867 \text{ g m}^{-2} \text{ yr}^{-1}$ (SRS-6) across all six sites, with higher NPP_T rates in all Shark River sites compared to Taylor River sites (Fig. 4.9a). Average NPP_T was twice in Shark River ($1680 \pm 95 \text{ g}$

$\text{m}^{-2} \text{yr}^{-1}$) compared to Taylor River ($829 \pm 29 \text{ g m}^{-2} \text{yr}^{-1}$). On average, NPP_L accounted for 51% (Shark River) and 34% (Taylor River) of the NPP_T , while NPP_W only contributed 17% (Shark River) and 8% (Taylor River) to NPP_T (Fig 4.9b). NPP_B had a significant contribution to NPP_T ranging from 32% in the Shark River sites to 58% in the Taylor River sites (Fig. 4.9b). The contribution of fine roots ($<2 \text{ mm}$ diameter) to NPP_T was 50% of the total NPP_B estimated for both Shark River and Taylor River estuaries.

DISCUSSION

This study investigated spatial and temporal landscape patterns of community structure, biomass and NPP of mangrove forests along two FCE estuaries, Shark River and Taylor River. I tested the hypothesis that the allocation of biomass and NPP between above- and belowground is regulated by the interplay of resources, regulators and hydroperiod gradients across the coastal landscape. I also evaluated whether pulsing disturbances such as hurricanes are significant to soil nutrient inventories and vertical accretion of mangrove forests in FCE. The passage of Hurricane Wilma across FCE during October 2005 allowed me to test if there are gradients in storm-related sediment and nutrient inputs to the mangroves of FCE, and how these pulses of sediment deposition maintain landscape patterns of soil fertility and vertical accretion. While these results are specific to the conditions of Hurricane Wilma, they support the hypothesis that the redistribution of nutrients during hurricanes influences long-term mangrove forest dynamics in this oligotrophic P-limited carbonate-based setting. Results from this study demonstrate that the degree of interaction among factors such as soil P fertility, sulfide concentrations, and hydroperiod control mangrove vegetation patterns, which result in distinct riverine and scrub mangrove ecotypes at the same latitudinal gradient across the coastal landscape (Twilley and Rivera-Monroy 2005; Ewe et al. 2006; Mancera-Pineda et al. 2009). In fact, regression analyses

confirm that the cumulative effect of these three environmental gradients (i.e., soil P fertility, hydroperiod, and sulfide concentrations) explains between 40-85% of the total variability in forest structure and productivity across my mangrove sites (Table 4.9; Koch 1997; Koch and Snedaker 1997; Chen and Twilley 1999b; Krauss et al. 2006).

Table 4.9 Summary of linear regression analyses between forest structure and productivity and soil properties and hydroperiod. N = 12 (N = 8 for basal area).

Dependent variable Independent variable	df	F	p	Parameter Estimates	r ² model
Basal area					
Soil total P	1, 6	3.6	0.0105	151.4	0.38
Frequency of inundation	1, 6	43.2	0.0006	0.1	0.88
Sulfide	1, 6	18.2	0.0053	-17.4	0.75
Aboveground biomass					
Soil total P	1, 10	9.5	0.0115	71468.1	0.49
Frequency of inundation	1, 10	82.8	0.0001	0.9	39.4
Sulfide	1, 10	38.4	0.0001	-8513.3	0.79
Wood production					
Soil total P	1, 10	7.1	0.0236	1524.1	0.42
Frequency of inundation	1, 10	55.7	0.0001	0.887	0.85
Sulfide	1, 10	24.2	0.0006	-185.8	0.71
Litterfall production					
Soil total P	1, 10	6.7	0.0275	3519.7	0.40
Frequency of inundation	1, 10	53.4	0.0001	2.1	0.84
Sulfide	1, 10	29.7	0.0003	-450.3	0.75
Root:Shoot					
Sulfide	1, 10	27.2	0.0004	5.4	0.73

Salinity has usually been considered an important factor in regulating community structure, productivity, and zonation of mangroves species, particularly in drier environmental settings, with higher salinities restricting growth and forest development (Lugo and Snedaker 1974; Pool

et al. 1977; Cintron et al. 1978; Castañeda-Moya et al. 2006). Yet, variations in salinity ($<30 \text{ g kg}^{-1}$; Table 4.2) across my mangrove sites were below the critical value (65 g kg^{-1}) that influences mangrove forest structure and mortality (Cintorn et al. 1978), and thus could not explain the variability in forest structure and productivity between Shark River and Taylor River.

Mangrove forests along both estuaries are characterized by a distinct gradient in P fertility and corresponding shift in N:P ratios with distance inland from the mouth of each estuary (Table 4.1; Chen and Twilley 1999a, b; Chambers and Pederson 2006; Mancera Pineda et al. 2009). Riverine mangroves along Shark River are influenced by a significant tidal regime with higher duration, frequency, and magnitude of inundation in the more fertile site (SRS-6) downstream compared to P-limited sites (SRS-4 & 5) upstream in the estuary (Figs. 4.2, 4.3; Chen and Twilley 1999b; Krauss et al. 2006). Along Taylor River, P-limited scrub forests have no tidal influence and remain flooded almost 100% of the year, particularly at TS/Ph-6 & 7 (Figs. 4.2, 4.3). These two sites are isolated from the direct influence of Florida Bay by a geologic berm (Davis et al. 2004), in contrast to TS/Ph-8 (i.e., in Joe Bay) that is hydrologically connected to Florida Bay (Castañeda-Moya et al. 2010). Hydroperiod in TS/Ph-8 is more variable than other areas of Taylor River due the microtidal influence of the Bay and the seasonal effect of cold fronts, although significantly lower compared to Shark River sites. These contrasting conditions in hydroperiod between Shark River and Taylor River determine the degree of regulator gradients such as salinity and sulfide concentrations across the coastal landscape. The Shark River estuary has a salinity gradient that increases from 5 g kg^{-1} in SRS-4 to 27 g kg^{-1} in SRS-6; whereas in Taylor River salinity remains constant throughout the year at about $\sim 20 \text{ g kg}^{-1}$ along the estuary (Table 4.2). In addition, sulfide concentrations are

significantly higher in all Taylor River sites compared to the Shark River sites, reflecting the lack of a tidal signature and water turnover in Taylor River (Table 4.2; Mancera Pineda et al. 2009).

Mangroves along Shark River also exhibit higher community structure compared those in Taylor River, with average basal areas 23 times greater in Shark River compared to TS/Ph-8 (Table 4.4). Along Shark River, forest structure follows the soil P fertility gradient, with basal areas twice higher in the more fertile site of SRS-6 relative to the P-limited sites upstream in the estuary (Table 4.4; Chen and Twilley 1999b). The total density of trees shows the opposite trend, with higher tree density in SRS-4 relative to SRS-6 (Table 4.4; Fig. 4.5). There is also a shift in species dominance along the estuary, with *R. mangle* dominating sites upstream and *L. racemosa* dominating the forest downstream (SRS-6; Fig. 4.5). This, coupled with the higher growth rate of this species in SRS-6 (Table 4.5) suggest that P availability is a controlling factor on forest structure and productivity across FCE mangroves, as has been demonstrated in previous studies in the neotropics (McKee 1995; Chen and Twilley 1998; 1999b). The inverse relationship between tree density and tree diameter as well as the observed shift in species dominance along the estuary reflects the lower forest structure of mangrove sites upstream relative to mangroves adjacent to the mouth of the estuary (SRS-6; Chen and Twilley 1999b).

Patterns in aboveground wood biomass also follow the soil P fertility gradient along the estuary, with wood biomass estimates 1.5 times greater in SRS-6 compared to SRS4 & 5 (Chen and Twilley 1999b), and on average 12 times greater in riverine mangroves along Shark River compared to scrub forests in Taylor River. These observations are consistent with other mangrove studies in the neotropics, indicating differences in aboveground biomass allocation among mangrove ecotypes (Appendix C). Biomass allocation patterns between above- and belowground are also distinct between these estuaries, with root:shoot ratios 17 times higher in

Taylor River relative to Shark River (Fig. 4.6). This indicates that scrub forests in Taylor River allocate a large proportion of their biomass belowground relative to aboveground in response to P limitation and flooded hydroperiods (Koch 1997; Koch and Snedaker 1997; Ewe et al. 2006). In fact, root:shoot ratios increased with increasing sulfide concentrations across my mangrove sites ($r^2 = 0.73$, $p < 0.001$; Table 4.9), suggesting that the flooded hydroperiods observed in the Taylor River sites causes the build up of sulfide in the soil relative to Shark River sites, where sulfide concentrations were nearly below detection limits (<0.03 mM; Table 4.2; Mancera Pineda et al. 2009). These results are in accordance with resource limitation and biomass allocation theories for terrestrial forests (Gleeson and Tilman 1992; Chapin et al. 1987), and demonstrate that mangroves allocate a large proportion of their total biomass to belowground in response to nutrient limitation and soil stress conditions (Saenger 1982; Lugo 1990; Komiyama et al. 2000; Sherman et al. 2003; Krauss et al. 2006; Lopez-Hoffman et al. 2007).

Root dynamics also respond to P availability and hydroperiod gradients across FCE. The significant increase in fine root biomass allocation with increasing P limitation and decreasing frequency of inundation reflects an adaptation of mangroves to facilitate nutrient acquisition, but also minimize stress from high sulfide concentrations in flooded soils (Krauss et al. 2006; Lovelock 2008). In contrast to fine root biomass, fine root production shows a different pattern. Shark River has higher fine root production compared to Taylor River suggesting that the extreme P-limited conditions coupled to the lack of a tidal inundation and flooded hydroperiods in Taylor River reduces root production and turnover (McKee et al. 2007). In fact, fine root turnover significantly decreased with increasing soil N:P ratios across FCE mangroves, indicating a strong coupling between P availability and carbon allocation to fine root production. In conclusion, mangroves in Taylor River tend to produce roots with greater longevity and low

morphological plasticity as a mechanism of nutrient conservation in nutrient-poor environments, while mangroves at the more fertile region of Shark River should produce short-lived roots with rapid potential rates of nutrient uptake and rapid growth rates (Eissenstat and Yanai 1997).

Patterns in NPP_A also correspond to soil P fertility and hydroperiod gradients, with average NPP_A 3.4 times greater in Shark River compared to Taylor River, and similar to values reported for other mangrove forests in the neotropics (Appendix C; Ewe et al. 2006). The NPP_L has the highest contribution to NPP_A accounting for 75 and 85% of the total NPP_A in Shark River and Taylor River, respectively. In addition, the allocation of production between above- and belowground was also distinct between estuaries. Average NPP_T is twice higher in Shark River compared to Taylor River. NPP_L accounts for 51% (Shark River) and 34% (Taylor River) of the NPP_T , while NPP_W only contributes 17% (Shark River) and 8% (Taylor River). The contribution of NPP_B to NPP_T is significant accounting for 32% (Shark River) and 58% (Taylor River). The contribution of fine roots to NPP_T is 50% of the total root production estimated for both Shark River and Taylor River estuaries. These findings are consistent with global estimates of NPP_T for mangrove forests suggesting the significant contribution of NPP_B (38%) to the overall production, while the contribution of NPP_L and NPP_W is about 31% (Bouillon et al. 2008).

These results support the hypothesis that scrub mangrove forests along Taylor River allocate more belowground biomass (i.e., high root:shoot ratios) and production relative to aboveground compartments (litter and wood) in response to P limitation and high soil stress conditions, at expenses of aboveground growth and development (Lovelock 2008). These tradeoffs suggest a strong link between biomass and NPP allocation patterns and the morphological and physiological plasticity of mangrove species in response to environmental

gradients across the FCE landscape, in order to maximize efficiency of resource use and conserve the most limiting nutrient (Chapin et al. 1987).

Hurricane disturbances are a major feature of south Florida (Smith et al. 1994, 2009; Zhang et al. 2008). These pulsing events not only play an important role in inducing changes to vegetation but also by distributing sediment and nutrients at fine spatial and temporal scales that can influence mangrove regeneration and vegetation patterns (Smith et al. 1994; Lugo 2000, 2008; Castañeda-Moya et al. 2010). Hurricane Wilma had significant effects on hydrology, sediment deposition, and nutrient biogeochemistry of mangroves across the coastal landscape. Allochthonous mineral inputs from Wilma were localized within 10 km inland from the Gulf of Mexico, with maximal deposition in areas close to the mouth of Shark River (SRS-6) and no deposition in upstream areas of this estuary (SRS-4; Castañeda-Moya et al. 2010). Storm-derived sediments were not observed in mangroves areas of TS/Ph-6 & 7 as a result of the Buttonwood Ridge, where most of the sediments were deposited (Castañeda-Moya et al. 2010). There was also a strong gradient in P deposition from west (Broad Creek and SRS-6) to east (TS/Ph-8) across FCE indicating an enrichment of total P in the bulk sediments deposited by the storm (Castañeda-Moya et al. 2010). This gradient in P deposition from shore to inland areas of Shark River, and from west to east across FCE is coincidental with observed pulses in P fertility associated with hurricanes, and subsequent patterns in forest structure and productivity across the Florida Everglades (Chen and Twilley 1999a, b; Ewe et al. 2006; Simard et al. 2006). In addition, the lower P loading in mangrove areas to the east of Taylor River (i.e., TS/Ph-8) is coincidental with the observed P limitation condition in this region (Koch 1997; Ewe et al. 2006; Mancera Pineda et al. 2009).

These allochthonous mineral inputs from Hurricane Wilma are an important contribution to soil P fertility of mangroves forests in near-shore mangroves in western Everglades (Chen and Twilley 1999a, b; Twilley and Rivera-Monroy 2009; Castañeda-Moya et al. 2010). Mangroves areas that do not receive this pulse of P including upstream areas of western FCE, inland areas of Taylor River, and those further east of Florida Bay have lower accumulation of total P in soils (Castañeda-Moya et al. 2010). These gradients in storm surge and nutrient deposition establish the oligotrophic condition of this ecosystem, and evidently influence the observed patterns of mangrove vegetation across the coastal landscape. In addition to the significant input of P to the nutrient inventory of mangrove soils across FCE, Hurricane Wilma significantly contributed to the long-term vertical accretion and stability of mangrove soils. Vertical accretion resulting from hurricane deposition – in a single pulsing event – was one order of magnitude greater than the annual vertical accretion rate averaged over the past 50 years (Castañeda-Moya et al. 2010).

My study provides evidence that landscape patterns of mangrove forests in the FCE represent the degree of interaction of three environmental gradients, resources, regulators, and hydroperiod that define a constraint envelope for determining the community structure and productivity of mangrove wetlands. Hurricanes disturbances, as pulsing events also play a major role in the nutrient biogeochemistry and soil vertical accretion of mangroves at different spatial and temporal scales. Therefore, the juxtaposition of these conditions determines the differential above- and belowground allocation patterns of biomass and NPP of mangroves across the coastal landscape. In addition, the feedback of mangroves to theses pulses of P fertility and mineral sediments during hurricanes may be an adaptation of mangroves in the Caribbean region to self-adjust to current changes in sea level.

SUMMARY

Allocation patterns of biomass and NPP of mangroves between above- and belowground responded to the degree of interaction among factors such as P availability, sulfide, and hydroperiod, resulting in distinct riverine and scrub mangrove ecotypes at the same latitudinal gradient across the FCE landscape. There was a strong gradient in soil P density and corresponding shift in N:P ratios along both estuaries, with P limitation increasing with distance inland from the mouth of the estuary. Riverine mangroves along Shark River have a significant tidal regime, with higher flood duration, frequency, and magnitude in the more fertile site of SRS-6 compared to sites (SRS4 & 5) upstream the estuary. In contrast, P-limited scrub forests in Taylor River are not influenced by tides and have flooded hydroperiods, particularly at TS/Ph-6 & 7. This distinct hydroperiod between Shark River and Taylor River determines gradients in regulators such as sulfide concentrations, with higher concentrations in the Taylor River sites compared to Shark River sites, where concentrations are significantly lower.

The Shark River sites exhibited higher forest structure compared to TS/Ph-8. Along Shark River there was a distinct gradient in forest structure, with basal area, density of larger (dbh > 10 cm) trees, aboveground wood biomass and wood production, and tree height decreasing with distance inland from the mouth of the estuary. In contrast, total density of trees was greater in SRS-4 relative to SRS-5 and SRS-6. There was also a shift in the community composition of mangrove species along the estuary, with the dominance of *R. mangle* in sites upstream the estuary and *L. racemosa* in SRS-6. In TS/Ph-8, the forest was comprised mostly of smaller (dbh < 2.5 cm) trees of *C. erectus* with significantly lower basal areas compared to Shark River sites, reflecting the lower forest structure. The average biomass root:shoot ratio was 17

times higher in Taylor River relative to Shark River, indicating that scrub mangroves allocate a larger proportion of their total biomass to belowground.

Average NPP_A was 3.4 times greater in the Shark River sites ($1154 \pm 127 \text{ g m}^{-2} \text{ yr}^{-1}$) compared to the Taylor River sites ($344 \pm 17 \text{ g m}^{-2} \text{ yr}^{-1}$). Litterfall production had the highest contribution to NPP_A accounting for 75 and 85% of the total NPP_A in Shark River and Taylor River, respectively. Average NPP_T was twice in Shark River ($1680 \pm 95 \text{ g m}^{-2} \text{ yr}^{-1}$) compared to Taylor River ($829 \pm 29 \text{ g m}^{-2} \text{ yr}^{-1}$). Litterfall production accounted for 51% (Shark River) and 34% (Taylor River) of the NPP_T , while wood production only contributed 17% (Shark River) and 8% (Taylor River). Total root production made a significant contribution to NPP_T accounting for 32% (Shark River) and 58% (Taylor River). The contribution of fine roots (<2 mm diameter) to NPP_T was 50% of the total root production estimated for both Shark River and Taylor River estuaries. The higher contribution of root production to NPP_T in the Taylor River sites is associated to an adaptation of allocating more belowground biomass (i.e., high root:shoot ratios) and production relative to aboveground compartments in response to P limitation and high sulfide concentrations in these scrub forests.

Regression analyses support these findings since the cumulative effect of soil P fertility, hydroperiod, and sulfide concentrations explained between 40-85% of the total variability in forest structure and productivity across FCE mangroves. On the contrary, salinity ($<30 \text{ g kg}^{-1}$) variation across my sites was below the critical value (65 g kg^{-1}) that influences mangrove forest structure and mortality, and thus it could not be considered a controlling factor for forest structure and productivity between Shark River and Taylor River.

This information on how mangrove biomass and NPP are distinctly allocated between above- and belowground in response to environmental gradients across the FCE will be used to

develop carbon budgets (storage, production and allocation) before and after major disturbances (i.e., hurricanes) and to improve our understanding of carbon dynamics in neotropical mangrove forests.

REFERENCES

- Alongi, D.M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science* 76: 1-13.
- Arreola-Lizarraga, J.A., F. Flores-Verdugo, and A. Ortega-Rubio. 2004. Structure and litterfall of an arid mangrove stand on the Gulf of California, Mexico. *Aquatic Botany* 79: 137-143.
- Aspila, K.I., H. Agemian, and S.Y. Chau. 1976. A semi-automated method for the determination of inorganic, organic and total phosphate in sediments. *Analyst* 101: 187-197.
- Boto, K.G., and J.T. Wellington. 1984. Soil characteristics and nutrients status in a northern Australian Mangrove Forest. *Estuaries* 7: 61-69.
- Bouillon, S., A.V. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N.C. Duke, E. Kristensen, S.Y. Lee, C. Marchand, J.J. Middleburg, V. Rivera-Monroy, T.J.I. Smith, and R.R. Twilley. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles* 22: GB2013, doi:2010.1029/2007GB003052.
- Cahoon, D.R., P. Hensel, J. Rybczyk, K.L. McKee, E. Proffitt, and B.C. Perez. 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology* 91: 1093-1105.
- Cardona-Olarte, P., R.R. Twilley, K.W. Krauss, and V.H. Rivera-Monroy. 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. *Hydrobiologia* 569: 325-341.
- Castañeda-Moya, E., V.H. Rivera-Monroy, and R.R. Twilley. 2006. Mangrove zonation in the dry life zone of the Gulf of Fonseca, Honduras. *Estuaries and Coasts* 29: 751-764.
- Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, K. Zhang, S.E. Davis, III., and M. Ross. 2010. Sediment and nutrient deposition associated with Hurricane Wilma in mangroves of the Florida Coastal Everglades. *Estuaries and Coasts* 33: 45-58.
- Chambers, R.M., and K.A. Pederson. 2006. Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands. *Hydrobiologia* 569: 63-70.
- Chapin, F.S.I., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* 37: 49-57.

- Chen, R., and R.R. Twilley. 1998. A gap dynamic model of mangrove forest development along gradients of salinity and nutrient resources. *Journal of Ecology* 86: 37-51.
- Chen, R., and R.R. Twilley. 1999a. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44: 93-118.
- Chen, R., and R.R. Twilley. 1999b. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22: 955-970.
- Childers, D.L. 2006. A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia* 569: 531-544.
- Childers, D.L., J.N. Boyer, S.E. Davis, C.J. Madden, and D.T. Rudnick. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades. *Limnology and Oceanography* 51: 602-616.
- Chmura, G.L., S.C. Anisfeld, D.R. Cahoon, and J.C. Lynch. 2003. Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles* 17: 1111, doi:1110.1029/2002GB001917.
- Cintron, G., A.E. Lugo, D. Douglas, J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10: 110-121.
- Clark, D.A., S. Brown, D.W. Kicklighter, J.Q. Chambers, J.R. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: Concepts and field methods. *Ecological Applications* 11: 356-370.
- Clough, B.F. 1992. Primary productivity and growth of mangrove forests. In *Tropical Mangrove Ecosystems*, eds. A. I. Robertson and D. M. Alongi, 225-249. Washington, DC.: American Geophysical Union.
- Coronado-Molina, C., J.W.J. Day, E. Reyes, and B.C. Perez. 2004. Standing crop and aboveground biomass partitioning of a dwarf mangrove forests in Taylor River Slough, Florida. *Wetlands Ecology and Management* 12: 157-164.
- Cottam, G., and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- Davies, B.E. 1974. Loss-on-ignition as an estimate of soil organic matter. *Soil Science Society of American Proceedings* 38: 150-151.
- Davis, S.E.I., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W.J. Day, C.D. Huttel, C.J. Madden, E. Reyes, D. Rudnick, and F. Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida Gulf coast estuary. *Journal of Coastal Research* 20: 1198-1208.

- Davis, S.M. 1994. Phosphorus inputs and vegetation sensitivity in the Everglades. In *Everglades. The ecosystem and its restoration* eds. S. M. Davis and J. C. Ogden, 357-378. Delray Beach, Florida: St. Lucie Press.
- Day, J.W., W.H. Conner, F. Ley-Lou, R.H. Day, and A.M. Navarro. 1987. The productivity and composition of mangrove forests, Laguna de Terminos, Mexico. *Aquatic Botany* 27: 267-284.
- Day, J.W., C. Coronado-Molina, F.R. Vera-Herrera, R.R. Twilley, V.H. Rivera-Monroy, H. Alvarez-Guillen, R. Day, and W. Conner. 1996. A 7-year record of above-ground net primary production in a southeastern Mexican mangrove forest. *Aquatic Botany* 55: 39-60.
- Duarte, C.M., and J. Cebrian. 1996. The fate of marine autotrophic production. *Limnology and Oceanography* 41: 1758-1766.
- Duarte, C.M., J.J. Middleburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2: 1-8.
- Eissenstat, D.M., and R.D. Yanai. 1997. The ecology of root lifespan. *Advances in Ecological Research* 27: 1-60.
- Ewe, S.M.L., E.E. Gaiser, D.L. Childers, D. Iwaniec, V. Rivera-Monroy, and R.R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along tow freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* 569: 459-474.
- Ewel, K., R.R. Twilley, and J.E. Ong. 1998. Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* 7: 83-94.
- FAO. 2003. Status and trends in mangrove area extent worldwide. *Forest Resources Assessment Working Paper No. 63* Forest Resources Division, FAO, Rome.
- Feller, I.C., K.L. McKee, D.F. Whigham, and J.P. O'Neill. 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145-175.
- Feller, I.C., D.F. Whigham, K.L. McKee, and C.E. Lovelock. 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia* 134: 405-414.
- Fiala, K., and L. Hernandez. 1993. Root biomass of a mangrove forest in southwestern Cuba (Majana). *Ekologia (Bratislava)* 12: 15-30.
- Field, C.D. 1995. Impact of expected climate change on mangroves. *Hydrobiologia* 295: 75-81.

- Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37: 162-171.
- Giraldo, B. 2005. Belowground productivity of mangrove forests in southwest Florida. Ph.D. Dissertation. Louisiana State University, Baton Rouge.
- Gleeson, S.K., and D. Tilman. 1992. Plant allocation and the multiple limitation hypothesis. *The American Naturalist* 139: 1322-1343.
- Golley, F., H.T. Odum, and R.F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9-19.
- Golley, F.B., J.T. McGinnis, R.G. Clements, G.I. Child, and M.J. Duever. 1975. Mineral cycling in a tropical moist forest ecosystem, Athens, GA.: University of Georgia Press.
- Hargis, T.G., and R.R. Twilley. 1994. Multi-depth probes for measuring Oxidation-Reduction (Redox) Potential in wetland soils. *Journal of Sedimentary Research* A64: 684-685.
- Heald, E.J. 1969. The production of organic detritus in a south Florida estuary. Ph.D. Dissertation. University of Miami, Coral Gables, Florida.
- Holdridge, L.R., W.C. Grenke, W.H. Hatheway, T. Liang, and J.A. Tosi, Jr. 1971. Forest environments in tropical life zones: A pilot study, New York: Pergamon Press Inc.
- Imbert, D., A. Rousteau, and P. Scherrer. 2000. Ecology of mangrove growth and recovery in the Lesser Antilles. *Restoration Ecology* 8: 230-236.
- Jennerjahn, T.C., and V. Ittekkot. 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften* 89: 23-30.
- Kenward, M., and J. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983-997.
- Koch, M.S. 1997. *Rhizophora mangle* L. seedling development into the sapling stage across resource and stress gradients in subtropical Florida. *Biotropica* 29: 427-439.
- Koch, M.S., and J.G. Snedaker. 1997. Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. *Aquatic Botany* 59: 87-98.
- Komiyama, A., S. Havanond, W. Srisawatt, Y. Mochida, K. Fujimoto, T. Ohnishi, S. Ishihara, and T. Miyagi. 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) forest. *Forest Ecology and Management* 139: 127-134.

- Krauss, K.W., T.W. Doyle, R.R. Twilley, V. Rivera-Monroy, and J.K. Sullivan. 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia* 569: 311-324.
- Kristensen, E., S. Bouillon, T. Dittmar, and C. Marchand. 2008. Organic carbon dynamics in mangrove ecosystems: A review. *Aquatic Botany* 89: 201-219.
- Lodge, T.E. 2005. *The Everglades Handbook: Understanding the Ecosystem*, 2nd edition. Boca Raton, Florida: CRC Press.
- Lopez-Hoffman, L., N.P.R. Anten, M. Martinez-Ramos, and D.D. Ackerly. 2007. Salinity and light interactively affect neotropical mangrove seedlings at the leaf and whole plant levels. *Oecologia* 150: 545-556.
- Lovelock, C.E. 2008. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 11: 342-354.
- Lovelock, C.E., M.C. Ball, B. Choat, B.M.J. Engelbrecht, N.M. Holbrook, and I.C. Feller. 2006. Linking physiological processes with mangrove forest structure: Phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant, Cell and Environment* 29: 793-802.
- Lovelock, C.E., I.C. Feller, K.L. McKee, B.M. Engelbrecht, and M.C. Ball. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology* 18: 25-33.
- Lugo, A.E. 1990. Fringe wetlands. In *Ecosystems of the World 15, Forested Wetlands*, eds. A. E. Lugo, M. Brinson, and S. Brown, 143-169. Amsterdam: Elsevier.
- Lugo, A.E. 2000. Effects and outcomes of Caribbean hurricanes in a climatic change scenario. *The Science of the Total Environment* 262: 243-251.
- Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology* 33: 368-398.
- Lugo, A.E., and S.C. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5: 39-64.
- Mancera Pineda, J.E., R.R. Twilley, and V.H. Rivera-Monroy. 2009. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic discrimination in mangroves in Florida Coastal Everglades as a function of environmental stress. *Contributions in Marine Science* 38: 109-129.
- McKee, K.L. 1993. Soil physicochemical patterns and mangrove species distribution - reciprocal effects? *Journal of Ecology* 81: 477-487.

- McKee, K.L. 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. *Oecologia* 101: 448-460.
- McKee, K.L., D.R. Cahoon, and I.C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545-556.
- McKee, K.L., and P. Faulkner. 2000. Restoration of biogeochemical function in mangrove forests. *Restoration Ecology* 8: 247-259.
- McNaughton, S.J., M. Oesterheld, D.A. Frank, and K.J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341: 142-144.
- Meriwether, J.R., W.-J. Sheu, C. Hardaway, and J.N. Beck. 1996. Coring sampler for chemical analyses of soft sediments. *Microchemical Journal* 53: 201-206.
- Nagelkerken, I., S.J.M. Blaber, S. Bouillon, P. Green, M. Haywood, L.G. Kirton, J.O. Meynecke, J. Pawlik, H.M. Penrose, A. Sasekumar, and P.J. Somerfield. 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany* 89: 155-185.
- Naidoo, G. 2006. Factors contributing to dwarfing in the mangrove *Avicennia marina*. *Annals of Botany* 97: 1095-1101.
- Noe, G.B., D.L. Childers, and R.D. Jones. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: why is the Everglades so unique? *Ecosystems* 4: 603-624.
- Pool, D.J., A.E. Lugo, and S.C. Snedaker. 1975. Litter production in mangrove forests of southern Florida and Puerto Rico. Pages 213-237 in G. E. Walsh, S. C. Snedaker, and H. J. Teas, editors. *Proceedings of the International Symposium on Biology and Management of Mangroves*, East-West Center, Honolulu, Hawaii.
- Pool, D.J., S.C. Snedaker, and A.E. Lugo. 1977. Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. *Biotropica* 9: 195-212.
- Saenger, P. 1982. Morphological, anatomical and reproductive adaptations of Australian mangroves. In *Mangrove ecosystems in Australia: Structure, function and management*, eds. B. F. Clough, Canberra, Australia: Australian National University Press.
- Saenger, P., and S.C. Snedaker. 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* 96: 293-299.
- Sala, O.E., and A.T. Austin. 2000. Methods of estimating aboveground net primary productivity. In *Methods in Ecosystem Science*, eds. O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, 31-43. New York, NY.: Springer-Verlag.

- Sherman, R.E., T.J. Fahey, and P. Martinez. 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems* 6: 384-398.
- Simard, M., K. Zhang, V. Rivera-Monroy, M.S. Ross, P.L. Ruiz, E. Castaneda-Moya, R.R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. *Photogrammetric Engineering and Remote Sensing* 72: 299-311.
- Smith, T.J.I., G.H. Anderson, K. Balentine, G. Tiling, and G.A. Ward. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: Sediment deposition, storm surge and vegetation. *Wetlands* 29: 24-34.
- Smith, T.J.I., M.B. Robblee, H.R. Wanless, and T.W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44: 256-262.
- Smith, T.J.I., and K.R.T. Whelan. 2006. Development of allometric relations for three mangrove species in south Florida for use in the Greater Everglades Ecosystem restoration. *Wetlands Ecology and Management* 14: 409-419.
- Sobrado, M.A., and M.C. Ball. 1999. Light use in relation to carbon gain in the mangrove, *Avicennia marina*, under hypersaline conditions. *Australian Journal of Plant Physiology* 26: 245-251.
- Thom, B.G. 1982. Mangrove ecology - a geomorphological perspective. In *Mangrove Ecosystems in Australia*, eds. B. F. Clough, 3-17. Canberra: Australian National University Press.
- Twilley, R.R. 1995. Properties of mangrove ecosystems related to the energy signature of coastal environments. In *Maximum power: the ideas and applications of H. T. Odum*, eds. C. A. S. Hall, 43-62. Niwot, Colorado: University Press of Colorado.
- Twilley, R.R., R.H. Chen, and T. Hargis. 1992. Carbon sinks in mangroves and theirs implications to carbon budget of tropical coastal ecosystems. *Water, Air, and Soil Pollution* 64: 265-288.
- Twilley, R.R., A.E. Lugo, and C. Patterson-Zucca. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology* 67: 670-683.
- Twilley, R.R., M. Pozo, V.H. Garcia, V.H. Rivera-Monroy, R. Zambrano, and A. Boderó. 1997. Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia* 111: 109-122.
- Twilley, R.R., and V. Rivera-Monroy. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research* 40: 79-93.

- Twilley, R.R., and V. Rivera-Monroy. 2009. Ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. In *Coastal Wetlands: An integrated ecosystem approach*, eds. G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and M. M. Brinson, 641-683. Elsevier B.V.
- Walters, B.B., P. Ronnback, J.M. Kovacs, B. Crona, S.A. Hussain, R. Badola, J.H. Primavera, E. Barbier, and F. Dahdouh-Guebas. 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. *Aquatic Botany* 89: 220-236.
- Wanless, H.R., R.W. Parkinson, and L.P. Tedesco. 1994. Sea level control on stability of Everglades wetlands. In *Everglades. The ecosystem and its restoration* eds. S. M. Davis and J. C. Ogden, 199-223. Delray Beach, Florida: St. Lucie Press.
- Zhang, K., M. Simard, M.S. Ross, V. Rivera-Monroy, P. Houle, P.L. Ruiz, R.R. Twilley, and K.R.T. Whelan. 2008. Airborne laser scanning quantification of disturbances from hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA. *Sensors* 8: 2262-2292.

CHAPTER 5 SUMMARY

This study investigated landscape patterns of community structure, biomass and NPP of mangrove forests along two FCE estuaries, Shark River and Taylor River. I tested the hypothesis that the allocation of biomass and NPP between above- and belowground is regulated by the interplay of resources, regulators and hydroperiod gradients across the coastal landscape. I also quantified sediment and nutrient deposition associated with the passage of Hurricane Wilma across FCE in October 2005, and evaluated whether these pulsing disturbances are significant to soil nutrient inventories and vertical accretion of mangrove forests in FCE. Results from this study demonstrated that the landscape vegetation patterns of mangroves in FCE represent the outcome of three environmental gradients including soil P fertility, sulfide concentrations, and hydroperiod that define a constraint envelope for determining the structure and productivity of mangrove wetlands. On the contrary, variations in salinity ($<30 \text{ g kg}^{-1}$) across my mangrove sites were below the critical value (65 g kg^{-1}) that influences mangrove forest structure and mortality, and thus could not explain the variability in forest structure and productivity between Shark River and Taylor River.

Mangrove forests along both estuaries showed a distinct gradient in P availability and corresponding shifts in N:P ratios with distance inland from the mouth of each estuary. Riverine mangroves along Shark River have a distinct tidal regime, with higher flooding, frequency, and depth of inundation in the most fertile site of SRS-6 compared to P-limited sites (SRS-4 & 5) upstream in the estuary. In contrast, P-limited scrub forests along Taylor River are not influenced by tides and remained flooded almost 100% during the year, particularly at TS/Ph-6 & 7. At TS/Ph-8, the hydroperiod is more variable due to the influence of Florida Bay and the seasonal effect of cold fronts. The relative lack of a strong tidal signature and permanent flooding

conditions in Taylor River are associated with the higher concentrations of sulfide and more anaerobic conditions in the soil compared to Shark River, where concentrations were negligible.

Mangrove forests along Shark River also showed higher forest structure compared to Taylor River. Basal area and tree height were significantly higher in Shark River relative to Taylor River. Along Shark River, basal area was 1.7 times greater in SRS-6 relative to sites (SRS-4 & 5) upstream in the estuary, and followed the observed soil fertility gradient. In contrast, total density of trees was higher in SRS-4 relative to SRS-6. There was also a shift in species dominance along the estuary, with *R. mangle* dominating sites upstream and *L. racemosa* dominating the forest downstream. These observations reflect the decrease in forest structure with distance inland from the mouth of Shark River estuary.

Changes in aboveground wood biomass also followed the observed P fertility gradient along Shark River estuary, with wood biomass estimates 1.5 times greater in SRS-6 compared to sites upstream the estuary (SRS-4 and SRS-5). And on average wood biomass was 12 times greater in the Shark River sites compared to scrub forests in Taylor River. There was a distinct trend in biomass allocation between above- and belowground components across FCE mangroves, with root:shoot ratios 17 times higher in the Taylor River sites compared to Shark River sites. Riverine mangroves along Shark River allocated 3.5 times more biomass aboveground compared to roots, resulting in lower root:shoot ratios; whereas in the scrub forests of Taylor River root biomass allocation was 3.8 times greater relative to aboveground allocation. These results suggest an adaptation of these scrub forests to P limitation and flooded hydroperiods in this region of FCE.

Patterns of root dynamics responded to P availability and hydroperiod gradients across FCE. The significant increase in fine root biomass allocation with increasing P limitation and

decreasing frequency of inundation reflects an adaptation of mangroves to facilitate nutrient acquisition, but also minimize stress from high sulfide concentrations in flooded soils. In contrast to fine root biomass, fine root production showed a different pattern. Shark River had higher fine root production compared to Taylor River suggesting that the extreme P-limited conditions coupled to the lack of a tidal inundation and flooded hydroperiods in Taylor River reduces root production and turnover. In fact, fine root turnover significantly decreased with increasing soil N:P ratios across FCE mangroves, indicating a strong coupling between P availability and carbon allocation to fine root production. Therefore, mangroves in Taylor River tend to produce roots with greater longevity and low morphological plasticity as a mechanism of nutrient conservation in nutrient-poor environments, while mangroves at the more fertile region of Shark River should produce short-lived roots with rapid potential rates of nutrient uptake and rapid growth rates.

Aboveground NPP (NPP_A) was consistently higher in the riverine mangroves of Shark River sites compared to scrub forests along Taylor River. Litterfall production had the highest contribution to NPP_A accounting for 75 and 85% of the total NPP_A in Shark River and Taylor River, respectively. Average NPP_T was twice in Shark River ($1680 \pm 95 \text{ g m}^{-2} \text{ yr}^{-1}$) compared to Taylor River ($829 \pm 29 \text{ g m}^{-2} \text{ yr}^{-1}$). Average NPP_A accounted for 68% (Shark River) and 42% (Taylor River) of the NPP_T . Total root production had an opposite trend, with higher contribution in Taylor River (58%) relative to Shark River (32%). The higher contribution of root production to NPP_T in Taylor River is associated to an adaptation of allocating more belowground biomass (i.e., high root:shoot ratios) and production relative to aboveground compartments in response to P limitation and high sulfide concentrations in these scrub forests.

The passage of Hurricane Wilma through FCE had significant effects on local hydrology, sediment deposition, and nutrient biogeochemistry of mangrove soils. The storm surge within

mangroves was ~3 m at the mouth of Shark River estuary and decreased to 0.50 m at the upper mangrove sites about 18 km from the mouth of the estuary. Large amounts of sediment from the coastal shelf were redistributed and deposited across mangrove forests of FCE, with maximal deposition in mangrove areas adjacent to the mouth of Shark River and no storm deposits in upstream areas (SRS-4) of this estuary. In addition, storm deposits were not observable in mangrove areas of TS/Ph-6 & 7 as a result of the Buttonwood Ridge, where most of the sediments were deposited. There was a gradient in total P input across mangrove zones located near shore from west (Broad Creek and SRS-6) to east (TS/Ph-8) across FCE, indicating an enrichment of total P in the bulk sediments deposited by the storm. This P gradient from west to east may also result in a gradient of P input associated with sediment deposition during storm events in this region, contributing to gradients in mangrove productivity. In addition, sediment deposition estimated in SRS-6 and TS/Ph-8 plots resulting from this storm event was 8 and 17 times greater than the annual vertical accretion rate (0.30 ± 0.03 and 0.27 ± 0.03 cm yr⁻¹, respectively) based on ¹³⁷Cs data.

This research contributes to a better understanding of how the allocation of biomass and NPP in mangrove forests between above- and belowground is regulated by the interplay of resources, regulators, and hydroperiod gradients across the FCE landscape. Hurricane disturbances not only play a major role in inducing changes to vegetation, but also by distributing sediments and nutrients at fine spatial and temporal scales that can influence mangrove forest regeneration. Therefore, the interaction of these environmental gradients and hurricane disturbances that operate at different spatial and temporal scales determine the contrasting vegetation patterns across FCE. In addition, the feedback of hurricane disturbance on sediment deposition, accretion and nutrient deposition in this P-limited carbonate ecosystem may

have important implications as to how soil formation and accretion serve as adaptations of mangroves to future impacts of sea-level rise.

APPENDIX A
LETTER OF PERMISSION

SPRINGER LICENSE TERMS AND CONDITIONS

May 12, 2010

This is a License Agreement between **Edward Castaneda** ("You") and **Springer** ("Springer") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by Springer, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	2426550760241
License date	May 12, 2010
Licensed content publisher	Springer
Licensed content publication	Estuaries and Coasts
Licensed content title	Sediment and Nutrient Deposition Associated with Hurricane Wilma in Mangroves of the Florida Coastal Everglades
Licensed content author	Edward Castañeda-Moya
Licensed content date	Jan 1, 2009
Volume number	33
Issue number	1
Type of Use	Thesis/Dissertation
Portion	Full text
Number of copies	1
Author of this Springer article	Yes and you are the sole author of the new work
Order reference number	

Title of your thesis / dissertation	Landscape patterns of community structure, biomass and net primary productivity of mangrove forests in the Florida Coastal Everglades as a function of resources, regulators, hydroperiod, and hurricane disturbance
Expected completion date	May 2010
Estimated size(pages)	200
Total	0.00 USD

Terms and Conditions

Introduction

The publisher for this copyrighted material is Springer Science + Business Media. By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the Billing and Payment terms and conditions established by Copyright Clearance Center, Inc. ("CCC"), at the time that you opened your Rightslink account and that are available at any time at <http://myaccount.copyright.com>).

Limited License

With reference to your request to reprint in your thesis material on which Springer Science and Business Media control the copyright, permission is granted, free of charge, for the use indicated in your enquiry. Licenses are for one-time use only with a maximum distribution equal to the number that you identified in the licensing process.

This License includes use in an electronic form, provided it is password protected or on the university's intranet, destined to microfilming by UMI and University repository. For any other electronic use, please contact Springer at (permissions.dordrecht@springer.com or permissions.heidelberg@springer.com)

The material can only be used for the purpose of defending your thesis, and with a maximum of 100 extra copies in paper.

Although Springer holds copyright to the material and is entitled to negotiate on rights, this license is only valid, provided permission is also obtained from the (co) author (address is given with the article/chapter) and provided it concerns original material which does not carry references to other sources (if material in question appears with credit to another source, authorization from that source is required as well). Permission free of charge on this occasion does not prejudice any rights we might have to charge for reproduction of our copyrighted material in the future.

Altering/Modifying Material: Not Permitted

However figures and illustrations may be altered minimally to serve your work. Any other abbreviations, additions, deletions and/or any other alterations shall be made only with prior

written authorization of the author(s) and/or Springer Science + Business Media. (Please contact Springer at permissions.dordrecht@springer.com or permissions.heidelberg@springer.com)

Reservation of Rights

Springer Science + Business Media reserves all rights not specifically granted in the combination of (i) the license details provided by you and accepted in the course of this licensing transaction, (ii) these terms and conditions and (iii) CCC's Billing and Payment terms and conditions.

Copyright Notice:

Please include the following copyright citation referencing the publication in which the material was originally published. Where wording is within brackets, please include verbatim.

"With kind permission from Springer Science+Business Media: <book/journal title, chapter/article title, volume, year of publication, page, name(s) of author(s), figure number(s), and any original (first) copyright notice displayed with material>."

Warranties: Springer Science + Business Media makes no representations or warranties with respect to the licensed material.

Indemnity

You hereby indemnify and agree to hold harmless Springer Science + Business Media and CCC, and their respective officers, directors, employees and agents, from and against any and all claims arising out of your use of the licensed material other than as specifically authorized pursuant to this license.

No Transfer of License

This license is personal to you and may not be sublicensed, assigned, or transferred by you to any other person without Springer Science + Business Media's written permission.

No Amendment Except in Writing

This license may not be amended except in a writing signed by both parties (or, in the case of Springer Science + Business Media, by CCC on Springer Science + Business Media's behalf).

Objection to Contrary Terms

Springer Science + Business Media hereby objects to any terms contained in any purchase order, acknowledgment, check endorsement or other writing prepared by you, which terms are inconsistent with these terms and conditions or CCC's Billing and Payment terms and conditions. These terms and conditions, together with CCC's Billing and Payment terms and conditions (which are incorporated herein), comprise the entire agreement between you and Springer Science + Business Media (and CCC) concerning this licensing transaction. In the event of any conflict between your obligations established by these terms and conditions and those established by CCC's Billing and Payment terms and conditions, these terms and conditions shall control.

Jurisdiction

All disputes that may arise in connection with this present License, or the breach thereof, shall be settled exclusively by the country's law in which the work was originally published.

Other terms and conditions:

v1.2

Gratis licenses (referencing \$0 in the Total field) are free. Please retain this printable license for your reference. No payment is required.

If you would like to pay for this license now, please remit this license along with your payment made payable to "COPYRIGHT CLEARANCE CENTER" otherwise you will be invoiced within 48 hours of the license date. Payment should be in the form of a check or money order referencing your account number and this invoice number RLNK10783115.

Once you receive your invoice for this order, you may pay your invoice by credit card. Please follow instructions provided at that time.

Make Payment To:
Copyright Clearance Center
Dept 001
P.O. Box 843006
Boston, MA 02284-3006

If you find copyrighted material related to this license will not be used and wish to cancel, please contact us referencing this license number 2426550760241 and noting the reason for cancellation.

Questions? customercare@copyright.com or +1-877-622-5543 (toll free in the US) or +1-978-646-2777.

APPENDIX B
HYDROPERIOD IN MANGROVE FORESTS OF THE FLORIDA COASTAL
EVERGLADES

Appendix B. Comparison of hydroperiod in mangrove forests of the Florida Coastal Everglades during the period 2001-2006. Values are the mean (\pm 1 SE).

Sites	Hydroperiod	
	Flooding duration (h yr ⁻¹)	Frequency of inundation (# tides yr ⁻¹)
SRS-4	3965 (163)	217 (16)
SRS-5	4716 (168)	165 (7)
SRS-6	5592 (433)	395 (70)
TS/Ph-6	8566 (144)	12 (1)
TS/Ph-7	8653 (150)	6 (2)
TS/Ph-8	3541 (50)	48 (10)

APPENDIX C
SUMMARY OF ABOVEGROUND BIOMASS, LITTERFALL, AND WOOD PRODUCTION OF NEOTROPICAL MANGROVE FORESTS

Site	Mangrove type	Aboveground biomass (g m ⁻²)	Litterfall Production (g m ⁻² yr ⁻¹)	Wood Production (g m ⁻² yr ⁻¹)	Reference
Shark River (TS/Ph-6), Florida (USA)	Scrub	1250 ^a	258 ^b	64 ^b	This study
Shark River (TS/Ph-7), Florida (USA)	Scrub	1250 ^a	303 ^b	75 ^b	This study
Shark River (TS/Ph-8), Florida (USA)	Scrub	447	285	48	This study
Turkey Point, Florida (USA)	Scrub	790	85		Pool et al. 1975
					Lugo and Snedaker 1974
Biscayne Bay, Florida (USA)	Scrub	2230	590	220	Ross et al. 2001
Gulf of California (Mexico)	Scrub		175		Arreola-Lizarraga et al. 2004
Rookery Bay, Florida (USA)	Scrub		101		Giraldo 2005
Bocas del Toro (Panama)	Scrub		34		Guzman et al. 2005
Twin Cays (Belize)	Scrub		280		McKee et al. 2007
Shark River (SRS-4), Florida (USA)	Riverine	9770	811	280	This study
Shark River (SRS-5), Florida (USA)	Riverine	10,880	767	206	This study
Shark River (SRS-6), Florida (USA)	Riverine	15,210	1014	384	This study
Panama	Riverine	28,000	710		Golley et al. 1975
Vacia Talega (Puerto Rico)	Riverine		1445		Pool et al. 1975
Chokoloskee Bay, Florida (USA)	Riverine		1175	731	Sell 1977
Chokoloskee Bay, Florida (USA)	Riverine		1183	986	Sell 1977
Gordon River, SW Florida (USA)	Riverine		909	1333	Sell 1977
Gordon River, SW Florida (USA)	Riverine		1443	1679	Sell 1977
Ten Thousand Is., Florida (USA)	Riverine	13,550	1066		Snedaker and Brown 1981
					Lugo and Snedaker 1974
Ten Thousand Is., Florida (USA)	Riverine		1173		Snedaker and Brown 1981
Boca Chica, Terminos Lagoon (Mexico)	Riverine	13,500	1252	1206	Day et al. 1987
Agua Brava, Nayarit (Mexico)	Riverine		1015		Ramirez 1987

Appendix C cont.

Site	Mangrove type	Aboveground biomass (g m ⁻²)	Litterfall Production (g m ⁻² yr ⁻¹)	Wood Production (g m ⁻² yr ⁻¹)	Reference
La Mancha Lagoon, Veracruz (Mexico)	Riverine		1263		Flores-Verdugo et al. 1992
Guayas River (Ecuador)	Riverine		647		Twilley et al. 1997
Guayas River (Ecuador)	Riverine		787		Twilley et al. 1997
Guayas River (Ecuador)	Riverine	30,000	1064		Twilley et al. 1997
French Guiana	Riverine	15,540			Fromard et al. 1998
Shark River (SRS-4), Florida (USA)	Riverine			420	Chen and Twilley 1999b
Shark River (SRS-5), Florida (USA)	Riverine			320	Chen and Twilley 1999b
Shark River (SRS-6), Florida (USA)	Riverine			1200	Chen and Twilley 1999b
Potengi estuary (northern Brazil)	Riverine		1230		Silva et al. 2007
La Parguera (Puerto Rico)	Fringe		475	307	Golley et al. 1962
North River, Florida (USA)	Fringe		876		Heald 1969
La Ceiba (Puerto Rico)	Fringe		664		Pool et al. 1975
Ten Thousand Is., Florida (USA)	Fringe		771		Pool et al. 1975
Ten Thousand Is., Florida (USA)	Fringe	11,890	1002		Snedaker and Brown 1981
					Lugo and Snedaker 1974
Turkey Point, Florida (USA)	Fringe		1082		Snedaker and Brown 1981
Estero Pargo, Terminos Lagoon (Mexico)	Fringe	12,000	834	772	Day et al. 1987
El Verde Lagoon, Sinaloa (Mexico)	Fringe		1100		Flores-Verdugo et al. 1987
Agua Brava, Nayarit (Mexico)	Fringe		1417		Ramirez 1987
Rookery Bay, Florida (USA)	Fringe		929		Steyer 1988
Terminos Lagoon (Mexico)	Fringe	16,400	793		Day et al. 1996
French Guiana	Fringe	4610			Fromard et al. 1998
Biscayne Bay, Florida (USA)	Fringe	5600	1220	1390	Ross et al. 2001
Quintana Roo (Mexico)	Fringe		261		Navarrete and Oliva 2002
Samana Bay (Dominican Republic)	Fringe	19,540	1020	660	Sherman et al. 2003
Samana Bay (Dominican Republic)	Fringe	26,940		1180	Sherman et al. 2003
Rookery Bay, Florida (USA)	Fringe		213		Giraldo 2005
Twin Cays (Belize)	Fringe		700		McKee et al. 2007

Appendix C cont.

Site	Mangrove type	Aboveground biomass (g m ⁻²)	Litterfall Production (g m ⁻² yr ⁻¹)	Wood Production (g m ⁻² yr ⁻¹)	Reference
Twin Cays (Belize)	Fringe		450		McKee et al. 2007
Piñones (Puerto Rico)	Basin		970		Pool et al. 1975
Clam Bay, SW Florida (USA)	Basin		579		Heald et al. 1979
Tabasco (Mexico)	Basin		614		Lopez-Portillo and Ezcurra 1985
Rookery Bay, Florida (USA)	Basin		751		Twilley et al. 1986
Rookery Bay, Florida (USA)	Basin		538		Twilley et al. 1986
Rookery Bay, Florida (USA)	Basin		469		Twilley et al. 1986
Fort Myers, Florida (USA)	Basin		868		Twilley et al. 1986
Fort Myers, Florida (USA)	Basin		351		Twilley et al. 1986
Agua Brava, Nayarit (Mexico)	Basin		1263		Ramirez 1987
Agua Brava, Nayarit (Mexico)	Basin		521		Ramirez 1987
Rookery Bay, Florida (USA)	Basin		917	69	Steyer 1988
Rookery Bay, Florida (USA)	Basin		565		Steyer 1988
Rookery Bay, Florida (USA)	Basin	8000	740		Twilley 1995
					Lugo and Snedaker 1975
Terminos Lagoon (Mexico)	Basin	4940	496	167	Day et al. 1996
French Guiana	Basin	24,750			Fromard et al. 1998
Barra de Tecoaapa, Guerrero (Mexico)	Basin		949		Hernandez and Espino 1999
Naples Bay, Florida (USA)	Basin		652		McKee and Faulkner 2000
Naples Bay, Florida (USA)	Basin		543		McKee and Faulkner 2000
Rookery Bay, Florida (USA)	Basin		739		McKee and Faulkner 2000
Rookery Bay, Florida (USA)	Basin		804		McKee and Faulkner 2000
Samana Bay (Dominican Republic)	Basin	18,190	1280		Sherman et al. 2003
Samana Bay (Dominican Republic)	Basin	16,750		1630	Sherman et al. 2003
Rookery Bay, Florida (USA)	Basin		219		Giraldo 2005
Rookery Bay, Florida (USA)	Basin		177		Giraldo 2005

^a Data from Coronado-Molina et al. (2004)

^b Data from Ewe et al. (2006)

VITA

Edward Castaneda was born in Bogotá, Colombia, South America in 1973. After high school graduation, he enrolled in the army in 1989. He received a Bachelor of Science in Marine Biology in May 1998 from Universidad Jorge Tadeo Lozano, Colombia. After graduation he accepted a full-time position as a research associate at the Institute for Coastal and Marine Research INVEMAR in Santa Marta, Colombia. He worked for two years in a mangrove rehabilitation project in the Ciénaga Grande de Santa Marta, Colombia, under supervision of Dr. Victor H. Rivera-Monroy and Dr. Robert R. Twilley. In August 2000, he enrolled in the University of Louisiana at Lafayette, Louisiana, and earned a Master of Science in biology in December 2003 under guidance of Dr. Robert Twilley. In August 2004, Edward began his doctoral program at Louisiana State University in Baton Rouge, Louisiana, and concluded his doctorate in oceanography and coastal sciences with an official minor in applied statistics in August 2010 under supervision of Dr. Robert Twilley. He has dedicated his entire undergraduate and graduate research to studying the ecology of mangroves in different regions in the neotropics.