



Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA



Edward Castañeda-Moya*, Robert R. Twilley, Victor H. Rivera-Monroy

Department of Oceanography and Coastal Sciences, School of the Coast and Environment, Louisiana State University, Baton Rouge, LA 70803, USA

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ABSTRACT

Vegetation patterns of mangroves in the Florida Coastal Everglades (FCE) result from the interaction of environmental gradients and natural disturbances (i.e., hurricanes), creating an array of distinct riverine and scrub mangroves across the landscape. We investigated how landscape patterns of biomass and total net primary productivity (NPP_T), including allocation in above- and below-ground mangrove components, vary inter-annually (2001–2004) across gradients in soil properties and hydroperiod in two distinct FCE basins: Shark River Estuary and Taylor River Slough. We propose that the allocation of belowground biomass and productivity (NPP_B) relative to aboveground allocation is greater in regions with P limitation and permanent flooding. Porewater sulfide was significantly higher in Taylor River (1.2 ± 0.3 mM) compared to Shark River (0.1 ± 0.03 mM) indicating the lack of a tidal signature and more permanent flooding in this basin. There was a decrease in soil P density and corresponding increase in soil N:P from the mouth (28) to upstream locations (46–105) in Shark River that was consistent with previous results in this region. Taylor River sites showed the highest P limitation (soil N:P > 60). Average NPP_T was double in higher P environments (17.0 ± 1.1 Mg ha⁻¹ yr⁻¹) compared to lower P regions (8.3 ± 0.3 Mg ha⁻¹ yr⁻¹). Root biomass to aboveground wood biomass (BGB:AWB) ratio was 17 times higher in P-limited environments demonstrating the allocation strategies of mangroves under resource limitation. Riverine mangroves allocated most of the NPP_T to aboveground (69%) while scrub mangroves showed the highest allocation to belowground (58%). The total production to biomass (P:B) ratios were lower in Shark River sites (0.11 yr⁻¹); whereas in Taylor River sites P:B ratios were higher and more variable (0.13 – 0.24 yr⁻¹). Our results suggest that the interaction of lower P availability in Taylor River relative to Shark River basin, along with higher sulfide and permanent flooding account for higher allocation of belowground biomass and production, at expenses of aboveground growth and wood biomass. These distinct patterns of carbon partitioning between riverine and scrub mangroves in response to environmental stress support our hypothesis that belowground allocation is a significant contribution to soil carbon storage in forested wetlands across FCE, particularly in P-limited scrub mangroves. Elucidating these biomass strategies will improve analysis of carbon budgets (storage and production) in neotropical mangroves and understanding what conditions lead to net carbon sinks in the tropical coastal zone.

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1. Introduction

Primary productivity represents the major input of carbon and biological energy into world's ecosystems and can be considered as an integrative measure of ecosystem functioning (McNaughton et al., 1989; Sala and Austin, 2000). Mangrove forests dominate tropical and subtropical coastlines and are among the most productive marine ecosystems in the world, ranking second in terms of net primary productivity (NPP) only to coral reefs (Duarte and Cebrian, 1996). Mangrove forests produce organic carbon well in excess of ecosystem respiration and are considered important sites

for carbon burial (~10%) and carbon export (~40%) to adjacent coastal waters, indicating 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 137,760 km², which represents 0.7% of total tropical forests of the world (Giri et al., 2011); yet these forested wetlands are a significant site of carbon sequestration within the coastal zone (Twilley et al., 1992; Bouillon et al., 2008; Breithaupt et al., 2012).

The productivity of mangroves represents the outcome and interactions of several factors that operate at distinct global, regional, and local scales (Twilley, 1995). Climate and the relative role of regional geophysical processes (river input, tides, and waves)

* Corresponding author. Tel.: +1 225 578 6422; fax: +1 225 578 6423.
E-mail address: ecastal1@tigers.lsu.edu (E. Castañeda-Moya).

within a coastal landform are the dominant forcing functions that control the basic patterns of mangrove forest structure and function (Thom, 1982; Twilley, 1995). At the local scale, variation in topography and hydrology within a coastal landform influence the distribution of soil resources and abiotic regulators, and along with hydroperiod, produce gradients resulting in the development of distinct ecological types of mangroves such as riverine, fringe, basin, scrub, and overwash forests (Lugo and Snedaker, 1974; Twilley and Rivera-Monroy, 2009). The magnitude and interaction of these environmental gradients including regulators (i.e., soil salinity, sulfide), resources (e.g., light, nutrients), and hydroperiod (e.g., frequency, duration, and depth of flooding) define a constraint envelope that determines mangrove productivity within a coastal setting (Twilley and Rivera-Monroy, 2005).

Mangrove species adjust morphological and physiological traits in response to availability of nutrient resources, concentration of regulators, and hydroperiod conditions along these environmental gradients in the intertidal zone (Twilley and Rivera-Monroy, 2009; Krauss et al., 2008). For example, long-term fertilization studies of *Rhizophora mangle* found in scrub stands in different neotropical regions suggest that these forests respond positively to P additions increasing aboveground net primary productivity (NPP_A) and shifting resource allocation from roots to shoots (Koch and Snedaker, 1997; Feller et al., 2003a,b; Lovelock et al., 2004, 2006). Salinity has also been recognized to control the spatial distribution and productivity of mangrove species, particularly in drier coastal settings (Lugo and Snedaker, 1974; Pool et al., 1977; Cintron et al., 1978; Castañeda-Moya et al., 2006). Moreover, changes in above- and belowground biomass and productivity in mangroves also respond to changes in hydroperiod (Krauss et al., 2008). Higher frequency of inundation can maximize growth and aboveground productivity (Twilley et al., 1986; Krauss et al., 2006), while permanent flooding can stimulate fine root biomass allocation due to more soil reducing conditions and sulfide accumulation (Castañeda-Moya et al., 2011).

Understanding the allocation of carbon to above- and belowground biomass and productivity along these environmental gradients is significant to estimating global carbon budgets of mangrove ecosystems (Bouillon et al., 2008). Current estimates indicate that litterfall (NPP_L), along with wood (NPP_W) and root production (NPP_B), account for ~31%, 31%, and 38%, respectively, of the total net productivity (NPP_T) on a global basis (Bouillon et al., 2008). These estimates underscore the significant contribution of NPP_W and NPP_B to NPP_T of mangrove forests worldwide. Recent summaries indicate few examples of simultaneous measurements of both the aboveground components of NPP (NPP_A = NPP_L + NPP_W) and belowground components (NPP_B) to accurately estimate NPP_T of neotropical mangroves along natural environmental gradients. There are few long-term studies that test the temporal and spatial variation in carbon allocation to above- and belowground production (NPP_B:NPP_A ratio) of mangrove forests, and/or the production:biomass ratio of these coastal wetland forests. Studies of belowground components are particularly lacking in the neotropics (see Castañeda-Moya et al., 2011; Donato et al., 2011; Rivera-Monroy et al., 2013). Our study will contribute to a better understanding of the landscape patterns of NPP_T and carbon allocation of neotropical mangrove forests responding to distinct gradients in environmental settings.

We 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 two distinct basins of the Florida Coastal Everglades (FCE) landscape. We focused on Shark River Estuary and Taylor River Slough to test the generality that allocation patterns of biomass and NPP of mangroves respond to the interaction of environmental gradients resulting in distinct productivity trends across the

southern Everglades (Ewe et al., 2006; Rivera-Monroy et al., 2011). We hypothesized that the allocation of belowground biomass and NPP_B relative to aboveground allocations is greater in the Taylor River sites compared to the Shark River sites, reflecting mangrove vegetation strategies associated with P limitation and permanent flooding conditions. We addressed the following questions: (1) What is the long-term inter-annual variation in community structure and NPP of mangrove forests across a P-limited landscape as modified by different conditions of hydroperiod? (2) What is the production to biomass (P:B) ratio across mangrove sites in response to different nutrient and hydroperiod gradients? (3) What is the NPP_T in mangrove sites across nutrient and hydroperiod gradients, and what is the relative contribution of NPP_B to NPP_T across these gradients? Estimates of both belowground biomass and productivity for our six mangrove sites were not determined during this study, but were obtained from the literature (Castañeda-Moya et al., 2011). This information is used in the context of this study to estimate the total (above- and belowground) biomass and productivity of mangroves in the FCE.

2. Materials and methods

2.1. Study site

This study was conducted in mangrove forests of Everglades National Park (ENP), south Florida (Fig. 1) as part of the Florida Coastal Everglades Long Term Ecological Research (FCE-LTER) program (Childers, 2006; <http://fcelter.fiu.edu/>). Mangrove forests of ENP are distributed along the coastal margin and occupy 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). A full site description can be found in Chen and Twilley (1999b) and Castañeda-Moya et al. (2010). Briefly, 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) basins. Riverine mangroves along Shark River (southwestern ENP) contain mixed-species of *R. 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 upstream, respectively (Fig. 1). Mangrove tree height decreases with distance inland from the mouth of the estuary, and ranged between 5 and 13 m on average. All three sites have a distinct tidal hydroperiod, although SRS-4 is also influenced by runoff and groundwater particularly during the wet season (Chen and Twilley, 1999b; Castañeda-Moya, 2010; Saha et al., 2012). Mangrove sites along Taylor River (southeastern ENP: TS/Ph-7 & TS/Ph-6) are located approximately 1.5 and 4 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. The site TS/Ph-8 is located in Joe Bay, east of the Taylor River mouth (Fig. 1), with mangrove canopies averaging 3–4 m in height. *R. mangle* is the dominant species in the fringe areas and tidal creeks, while *C. erectus* is found in the interior parts; mangrove species also coexist with clusters of *C. jamaicense* (Ewe et al., 2006). Tides in 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 (Provost, 1973; Wanless et al., 1994). Mangrove waterways along Taylor River (e.g., TS/Ph-6 & 7) are non-tidal systems with flooded conditions (Castañeda-Moya, 2010) compared to Shark River, and water flow is determined by the interactions of seasonal precipitation, upland runoff, and wind (Sutula et al., 2001; Michot et al., 2011).

The south Florida's climate is subtropical savanna with a typical dry season from December through May, and a wet season from

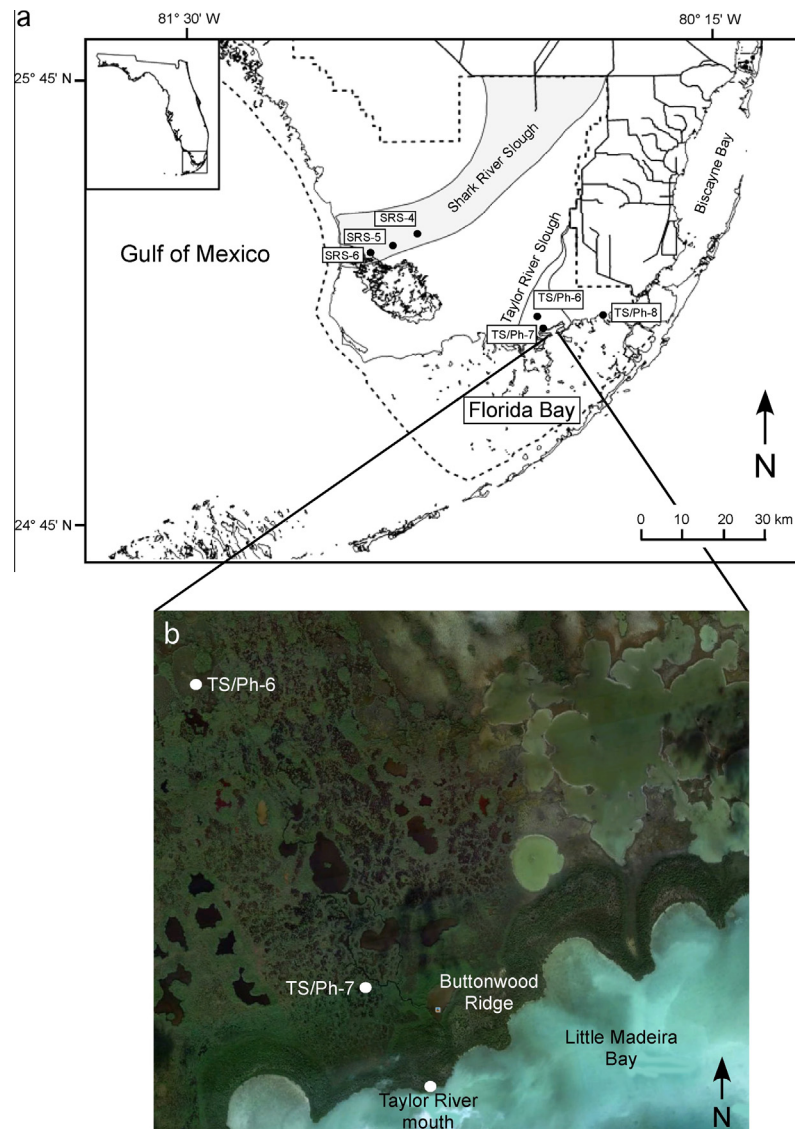


Fig. 1. Location of the study sites in the Florida Coastal Everglades (FCE), Everglades National Park (ENP) in south Florida, USA (a) and enlargement of the Taylor River basin indicating the location of the Buttonwood Ridge (b). Sites along Shark River Estuary include SRS-4, SRS-5, and SRS-6; sites along Taylor River Slough include TS/Ph-6 and TS/Ph-7, and TS/Ph-8 in Joe Bay. All sites are part of the FCE Long-Term Ecological Research (FCE-LTER) program.

June to November. Within these two seasons, the region experiences a transition period called the winter frontal season (during early dry season) and the hurricane season (during the wet season; Duever et al., 1994). Mean annual precipitation in the Everglades ranges from 120 to 160 cm, with 60% of the precipitation occurring during the wet season and only 25% during the dry season (Duever et al., 1994). Mean annual air temperature is 24 °C, with a seasonal range from 15 °C (winter) to 28 °C (summer; Thomas, 1974).

2.2. Experimental design

In all six FCE mangrove sites, two 20 × 20 m permanent vegetation plots (20-m apart) were established between 30 and 50 m from the shoreline to monitor forest structural attributes and soil biogeochemical properties. In addition, at the Shark River sites two transects (~20–40 m apart) 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 and composition of mangrove species.

2.3. Hydroperiod

Continuous water level recorders allowed us to measure frequency, duration, and depth of flooding in all six FCE-LTER mangrove sites from 2001 to 2005. Ultrasonic water level recorders (model 220, Infinites 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 for 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.

2.4. Soil properties

Porewater parameters were monitored in all six FCE mangrove sites. Within each site, four repeated sampling stations were ran-

domly established in each plot to measure porewater salinity, temperature (°C), porewater nutrient and sulfide concentrations, and soil redox potential (Eh). Porewater samples were collected at 30 cm depth using a rigid plastic probe (3/16" OD) attached to a suction device as described in McKee et al. (1988). Sampling was conducted 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 sulfide anti-oxidant buffer (SAOB, pH above 12; Thermo Orion operating instructions for model 9616BN silver/sulfide electrode) 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^-), and 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 carbon, nitrogen, and phosphorus), bulk density and organic matter 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 \times 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; in SRS-6, only three cores were processed and analyzed to determine soil properties. Soil samples were oven-dried at 60 °C to a constant weight and weighed to estimate soil bulk density (g dry mass per cm^3 of wet soil). Subsamples of soil cores were ground with a Wiley Mill to pass through a 250- μm mesh screen. Total organic matter (%DW) was determined by loss-on-ignition at 550 °C for 2 h (Davies, 1974). 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). Nutrient data were expressed on a volume basis using bulk density values.

2.5. 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 \leq 1.5 m) of the forest restricted standard (at 1.3 m above soil surface) tree diameter measurements. All trees with diameter at breast height (dbh, 1.3 m) \geq 2.5 cm were tagged and measured within each plot in all sampled 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 in all sites, except at TS/Ph-8 where trees were re-measured once during May 2003. 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. At TS/Ph-8, transects were not established due to the too narrow (<50 m) fringe mangrove zone. As in the case of plot sampling, all trees with

dbh \geq 2.5 cm were tagged and measured along both transects in all Shark River 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 \times tree density \times canopy height \times number of species $\times 10^{-5}$ (Holdridge et al., 1971).

Aboveground wood biomass (AWB) was calculated for each individual tree tagged within plots of selected sites using species-specific allometric equations published for the three dominant species in the study area (Smith and Whelan, 2006). There is no published allometric equation for *C. erectus*. Thus, we used the allometric equation for *L. racemosa* due to similarity in growth forms between these two species. For each individual tree, total 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 years of each individual tree. The sum of these differences was used to estimate wood production for each site. The corrections made above to calculate wood biomass from the allometric equations were necessary since the total dry biomass equation of Smith and Whelan includes all aboveground components (i.e., stem, branch, leaf, and prop root in the case of *R. mangle*). At TS/Ph-6 & 7, estimates of AWB and production were not determined during this study. We used published estimates of AWB (Coronado-Molina et al., 2004) and wood production (Ewe et al., 2006) for these two sites. The AWB estimates were calculated by applying allometric equations developed in that study for the Taylor River area.

2.6. Litterfall production

Litter dynamics were monitored in selected mangrove sites, including all Shark River sites and TS/Ph-8 from January 2001 to December 2005. 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 site, ten litter baskets were randomly placed inside the two 20 by 20 m permanent plots (5 baskets per plot). Litterfall was collected monthly 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 $\text{g m}^{-2} \text{d}^{-1}$. The low stature (tree height \leq 1.5 m) of the forest at TS/Ph-6 & 7 sites precluded the use of standard litter baskets to collect litterfall. Thus, we used published leaf fall rates reported by Ewe et al. (2006); in this study, leaf turnover rates were used as a proxy to estimate leaf fall production during 2001–2004.

2.7. Belowground biomass and production

Estimates of belowground biomass and productivity for all six FCE mangrove sites were not determined during this study but were obtained from the literature (Castañeda-Moya et al., 2011). A detailed description of the methods used to estimate belowground root biomass (BGB) and production can be found in Castañeda-Moya et al. (2011). We used total (to a depth of 90 cm of mangrove soils) root biomass to calculate the BGB:AWB ratio for all sites and total root production (NPP_B) to estimate its

contribution to NPP_T ($NPP_L + NPP_W + NPP_B$) for each mangrove site. Total root production represented the sum of fine (<2 mm in diameter), small (2–5 mm), and coarse (5–20 mm) root size classes.

2.8. Statistical analyses

All statistical analyses were performed using PROC MIXED (SAS Institute, Cary, NC, USA). We used repeated measures ANOVA (using plot data) to test for differences in basal area, tree density, aboveground wood biomass, and wood production among sites (Shark River) and years (2001–2004), with year as the repeated measure. TS/Ph-8 (2001 and 2003 data) was not included in any of these analyses due to unbalanced design compared to Shark River sites. Basal area and tree density were tested independently to determine differences between sampling techniques (plots vs. transects) and among sites (Shark River) using a two-way ANOVA. Seasonal, annual, and site (Shark River sites and TS/Ph-8) differences in total litterfall and each of its individual components (leaves, reproductive parts, woody material) 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 (Castañeda-Moya et al., 2010). These rates were representative of disturbance impacts, 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. Variation in soil nutrients (total C, N, and P), organic matter (%), and bulk density in the top 45 cm of mangrove soils was tested independently with a one-way ANOVA to determine differences among all sites. All main effects were considered fixed and interaction effects were included for all the analyses. Pairwise comparisons were described with a Tukey's Honestly Significant Difference (HSD) test. Regressions analyses were performed using step-wise and *r*-square methods to assess the effect of soil properties and hydroperiod on forest structure and productivity data. Multicollinearity was detected using the variance-inflation factor (VIF) and condition indices (CI). Regression models with low VIF's (<10) and CI's (<30), and the lowest Mallows' *C*(*p*) statistic were selected as the best fitted models (Freund and Wilson, 2003). Non-metric multi-dimensional scaling (nMDS) was also applied to the data to assess differences among sites following methods of Clarke and Warwick (2001), and using the Primer package (Clarke and Gorley, 2001). Data were standardized and similarity matrices were calculated using the Bray-Curtis similarity index (structure and productivity data) and Euclidean distance (environmental factors). The statistical significance of differences among sites was assessed using analysis of similarities (ANOSIM). A goodness-of-fit measure "Stress value" was used to evaluate how close the MDS ordination represented the distance or similarity data (Clarke and Warwick, 2001). The BIO-ENV procedure was used to explain how the variation in environmental factors accounts for the observed patterns in community structure and productivity across our sites (Clarke and Warwick, 2001).

3. Results

3.1. Hydroperiod

Hydroperiod showed contrasting spatial and seasonal trends between Shark River and Taylor River (Table 1 and Fig. 2). Water

levels above the soil surface were higher during the wet season (June–November) compared to the dry season (December–May) at all sites. In Shark River sites, water levels decreased with distance inland from the mouth of the estuary (Fig. 2). In Taylor River sites, water levels in TS/Ph-6 & 7 were above soil surface for most of the year, indicating permanently flooded conditions. In contrast, water levels in TS/Ph-8 were above the soil surface only during the wet season (Fig. 2). Annual flooding duration averaged across 5 years (2001–2005) ranged from 165 days (3965 h yr^{-1} , SRS-4) to 361 days (8653 h yr^{-1} , TS/Ph-7) across all sites (Table 1). At the Shark River sites, water levels flooded the soil surface 45–65% of each year. At TS/Ph-6 & 7, surface soils remained flooded almost 100% of each year, while TS/Ph-8 exhibited a similar annual flood duration (41%) compared to SRS-4 (Table 1). Annual flood frequency ranged from 165 to 395 inundations per year indicating the tidal forcing effect along Shark River (Table 1). 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 (Table 1).

3.2. Soil properties

Average 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 compared to Taylor River, except for TS/Ph-7 (Table 1). Organic matter had an opposite trend compared to that of bulk density, with the highest percentage at SRS-4 ($87.8 \pm 1.0\%$) and the lowest at TS/Ph-6 ($20.7 \pm 2.9\%$) across sites (Table 1). Soil (top 45 cm) total P concentrations indicated a fertility gradient along both Shark River and Taylor River sites, with an increase in soil total P from upstream to downstream along each estuary (Table 1). Overall, soil total P density ranged from $0.03 \pm 0.001 \text{ mg cm}^{-3}$ (TS/Ph-6) to $0.20 \pm 0.012 \text{ mg cm}^{-3}$ (SRS-6) across all sites (Table 1). Soil total N density was not significantly different among sites, except for TS/Ph-6 that had the lowest nutrient density (Table 1). Soil total C density did vary significantly along both Shark and Taylor River basins, with the highest C 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 1). Soil atomic C:N ratios did not vary across sites, except at TS/Ph-6 that had the highest value (Table 1); whereas soil N:P ratios showed a significant increase with distance inland from the mouth of each estuary (Table 1).

There was a significant ($p < 0.001$) site, season, and year interaction for all porewater variables. Salinity was higher during the dry season compared to the wet season across all sites and years, except in Taylor River where salinity did not differ between seasons and among sites and years. Along Shark River, salinity decreased with distance inland from the mouth the estuary ranging from 27 ± 2.6 at SRS-6 to 4.6 ± 1.1 in SRS-4; whereas along Taylor River salinity remained fairly constant at about 17–20 (Fig. 3a).

Sulfide concentrations were significantly higher at the Taylor River sites compared to all Shark River sites, and ranged from <0.02 mM (SRS-6) to $3.3 \pm 0.5 \text{ mM}$ (TS/Ph-8) across all years and seasons. There was an interaction between site and season, with no significant differences in sulfide concentrations between seasons for most of the sites, except for TS/Ph-8 (Fig. 3b). Sulfide concentrations along Shark River were <0.14 mM during the study period (Fig. 3b). Mean soil redox potential (Eh) did vary significantly ($p < 0.001$) among sites and depths ranging from $-88 \pm 30 \text{ mv}$ (TS/Ph-8, 45 cm) to $165 \pm 11 \text{ mv}$ (SRS-4, 10 cm; data not shown). Soil Eh was significantly ($F_{2, 68} = 41.1$, $p < 0.001$) higher at 0 cm ($125 \pm 10 \text{ mv}$) and 10 cm ($103 \pm 13 \text{ mv}$) depths compared to 45 cm ($-14 \pm 16 \text{ mv}$). Overall, soil Eh values indicated slightly reducing conditions across all sites and depths.

Table 1

Variation (plot data) in soil nutrients, C:N and N:P ratios, bulk density, organic matter content, and hydroperiod in mangrove sites of the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different (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	F	p	Site					
				SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
Frequency of inundation (# tides yr ⁻¹)				217 (16)	165 (7)	395 (70)	12 (1)	6 (2)	48 (10)
Flooding duration (h yr ⁻¹)				3965 (163)	4716 (168)	5592 (433)	8566 (144)	8653 (150)	3541 (50)
Bulk density (g cm ⁻³)	5, 16.9	43.8	***	0.10 ^{ad} (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 (%)	5, 6.1	83.3	***	87.8 ^a (1.0)	68.9 ^b (2.7)	55.2 ^c (1.8)	20.7 ^e (2.9)	71.2 ^b (1.4)	44.1 ^d (2.5)
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)
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 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)
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, 17.1	51.9	***	105.3 ^a (6.2)	46.2 ^b (3.4)	28.0 ^c (1.8)	109.0 ^a (5.6)	101.9 ^a (5.8)	66.1 ^b (5.9)

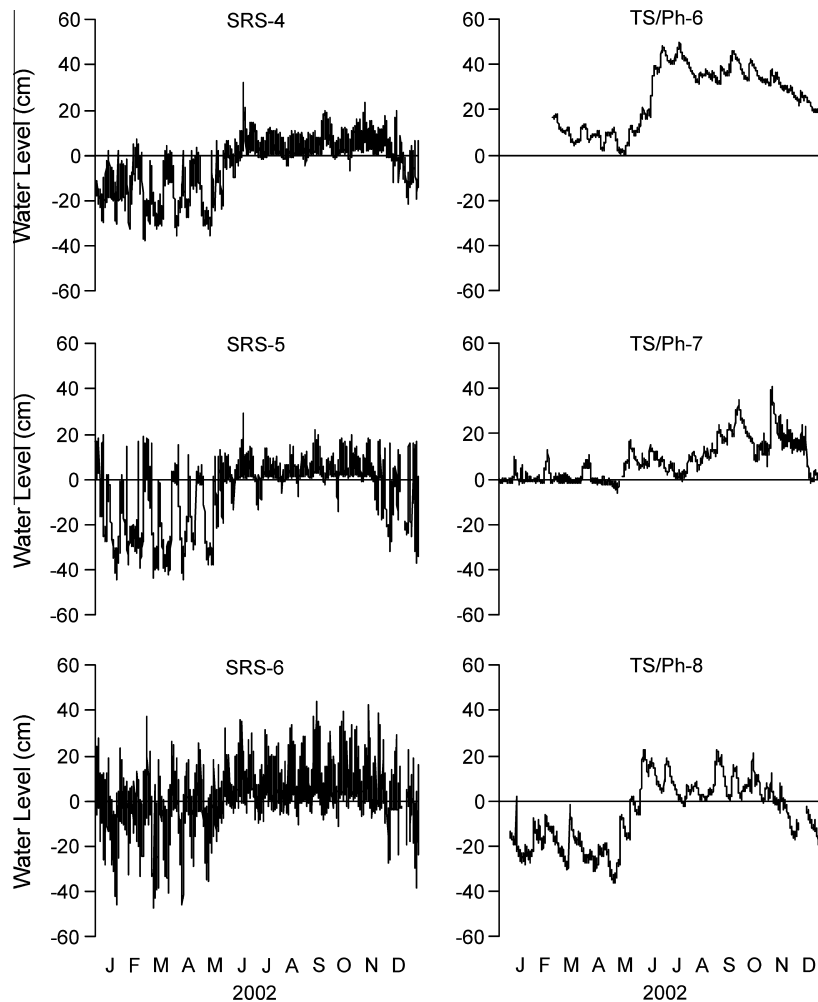


Fig. 2. Hydrographs in mangrove forests of the Florida Coastal Everglades during the dry and wet seasons of 2002. The zero mark is relative to the soil surface in each site. All water level data are not referenced to the North America Vertical Datum of 1988 (NAVD88).

Porewater NO_2^- and NO_3^- concentrations were often $< 0.5 \mu\text{M}$ across all sites, seasons, and years. Thus, values for NO_2^- , NO_3^- , and NH_4^+ were pooled to determine dissolved inorganic nitrogen concentrations (DIN; Fig. 3c). TS/Ph-6 & 7 had the highest DIN concentrations during all seasons and years compared to other sites, except during 2002 and 2003 where concentrations were lower and similar to Shark River sites. There were no significant differences in DIN concentrations between seasons for any of the sites, except at TS/Ph-8 (Fig. 3c).

Soluble reactive phosphorus (SRP) concentrations were significantly different among sites, especially along Shark River where concentrations increased from upstream to downstream during all seasons and years, except during 2001 (dry season) when SRP concentrations at SRS-6 were lower relative to upstream sites. SRP concentrations were higher during the wet season ($1.2 \pm 0.1 \mu\text{M}$) compared to the dry season ($0.8 \pm 0.2 \mu\text{M}$). 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 (Fig. 3d).

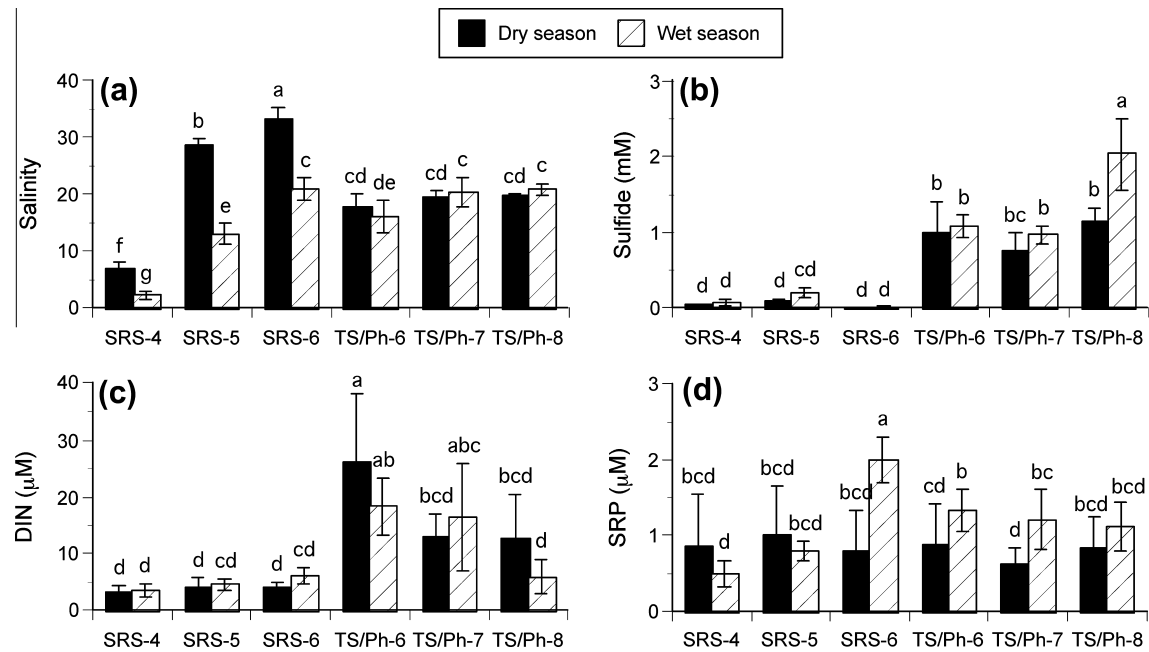


Fig. 3. Spatial and seasonal variation in soil properties including salinity (a), sulfide concentrations (b), dissolved inorganic nitrogen (DIN) (c), and soluble reactive phosphorus (SRP) (d) measured in mangrove sites of the Florida Coastal Everglades during the period 2001–2004. Means (± 1 SE) with different letters within each panel are significantly different ($p < 0.05$) across sites and seasons.

Table 2
Structural characteristics measured in plots at mangrove sites in the Florida Coastal Everglades during the period 2001–2004. Means (± 1 SE) followed by different letters across each row are significantly different (Tukey HSD post hoc test, $p < 0.05$).

Variable	Site			
	SRS-4	SRS-5	SRS-6	TS/Ph-8
Tree height (m)	6.0 (0.2)	8.3 (0.1)	13.0 (0.2)	3.2 (0.1)
Basal area ($\text{m}^2 \text{ha}^{-1}$)				
<i>A. germinans</i>	–	3.3	11.7	–
<i>L. racemosa</i>	6.9	1.6	22.5	0.2
<i>R. mangle</i>	10.9	17.4	6.7	–
<i>C. erectus</i>	5.7	–	–	1.1
Total	23.5 ^b (0.8)	22.3 ^b (0.1)	40.9 ^a (0.6)	1.3 ^a (0.1)
Total density (trees ha^{-1})				
<i>A. germinans</i>	–	100	528	–
<i>L. racemosa</i>	1438	100	1094	150
<i>R. mangle</i>	5333	2644	1216	–
<i>C. erectus</i>	975	–	–	900
Total	7746 ^a (83)	2844 ^b (15)	2838 ^b (31)	1050 ^a (350)
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)	32.8	15.8	45.3	0.13

^a Not included in any of the statistical analysis.

3.3. Forest structure, above- and belowground biomass, and wood production

Basal area varied significantly ($F_{2,3} = 11.5$, $p < 0.05$) among Shark River sites, with the highest values in SRS-6 ($40.9 \pm 0.6 \text{ m}^2 \text{ha}^{-1}$) compared to SRS-4 & 5 ($\sim 23 \text{ m}^2 \text{ha}^{-1}$; Table 2). Mean basal area in TS/Ph-8 was $1.3 \pm 0.1 \text{ m}^2 \text{ha}^{-1}$ (Table 2). *R. mangle*, *L. racemosa*, and *A. germinans* were found in SRS-5 & 6. Due to low pore-water salinity values at SRS-4, *A. germinans* was absent, while *C.*

erectus was only present in this site (Table 2). *L. racemosa* contributed more to total basal area in SRS-6, while *R. mangle* had the greatest basal area in SRS-4 & 5 (Table 2). In TS/Ph-8, *C. erectus* accounted for 81% of the total basal area (Table 2). Among years, basal area increased significantly ($F_{3,9} = 5.1$, $p < 0.05$) from 2001 ($27.3 \pm 1.9 \text{ m}^2 \text{ha}^{-1}$) to 2004 ($29.5 \pm 1.9 \text{ m}^2 \text{ha}^{-1}$). There was no significant ($F_{6,9} = 1.0$, $p = 0.5$) interaction between sites and years, indicating that the variation in basal area among sites is independent of time. When comparing plot vs. transect data, basal area did

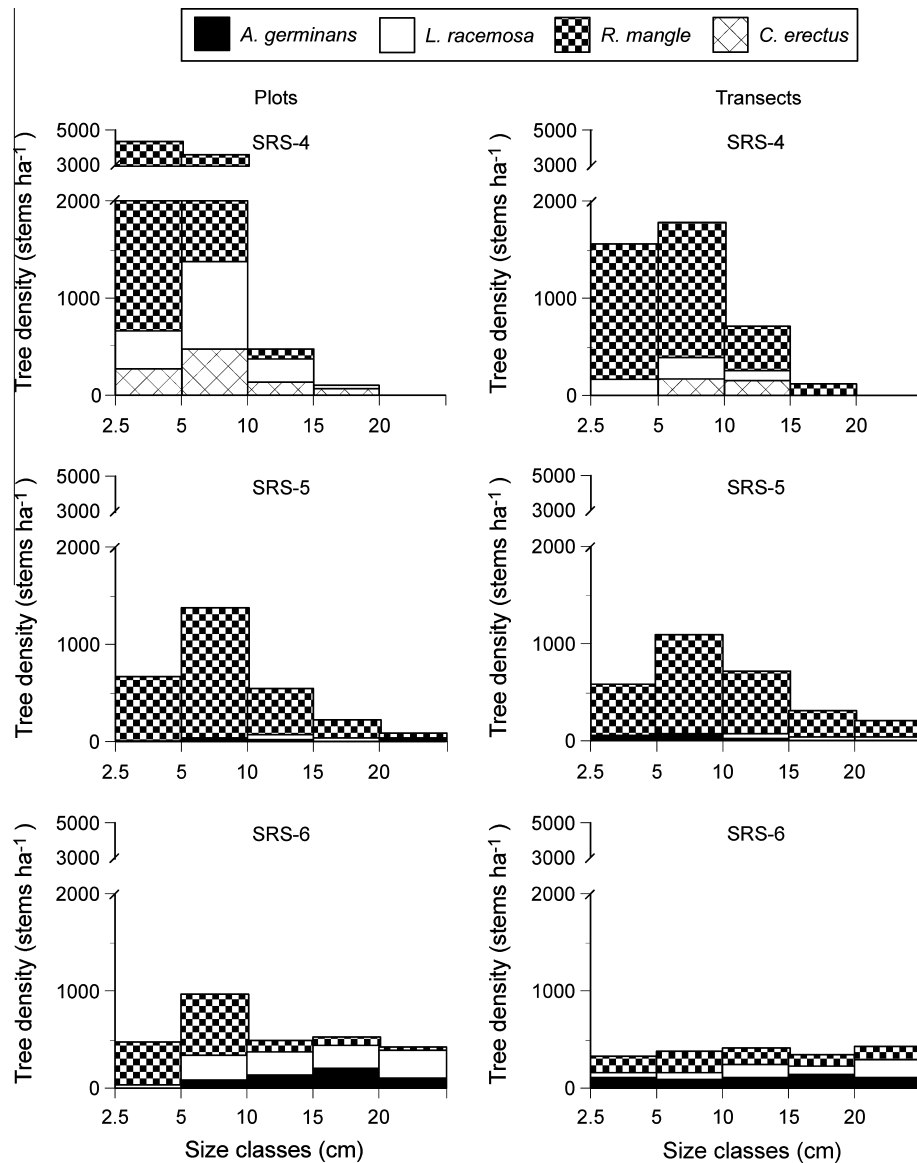


Fig. 4. Tree size class distribution of mangrove species along Shark River estuary measured in permanent plots and transects during the period 2001–2004.

not differ significantly ($F_{1, 15} = 1.5$, $p = 0.2$) within a site for any of the Shark River sites, and showed the same pattern along the estuary for both sampling methods (data not shown).

Total (all trees with dbh > 2.5 cm) tree density was significantly ($F_{2, 3} = 171.3$, $p < 0.001$) higher at SRS-4 (7746 ± 83 trees ha^{-1}) compared to SRS-5 & 6 (~ 2841 trees ha^{-1} ; Table 2). Tree density did not vary significantly ($F_{3, 9} = 0.9$, $p = 0.4$) among years and there was no significant ($F_{6, 9} = 2.0$, $p = 0.2$) interaction for site and year. When comparing total tree density between sampling methods (plots vs. transects), SRS-4 and SRS-6 plots (see above) had significantly ($F_{1, 15} = 233.8$, $p < 0.001$) higher densities compared to transect data (4112 ± 356 and 1770 ± 29 trees ha^{-1} , respectively); there was no significant difference in total tree density between SRS-5 plots (2844 ± 15 trees ha^{-1}) and transects (2790 ± 520 trees ha^{-1}). The distribution of trees by size classes also varied among sites (Fig. 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 670 trees ha^{-1} (SRS-4) to 1256 trees ha^{-1} (SRS-6; Fig. 4). In TS/Ph-8 plots, the density of smaller trees accounted for 86% of the total density (1050 trees ha^{-1}). Mean tree height decreased from 13 ± 0.2 m in

SRS-6 to 6 ± 0.2 m in SRS-4. In TS/Ph-8, the average tree height was 3.2 ± 0.1 m (Table 2) and all trees in TS/Ph-6 & 7 were <1.5 m.

The relative importance value (IV) of *R. mangle* was higher in upstream locations of Shark River, while in SRS-6 *L. racemosa* had the highest value. At TS/Ph-8, *C. erectus* was the dominant species and co-existed with *L. racemosa* (Table 2). The complexity index (CI) of vegetation reflected the low structural development of TS/Ph-8 compared to Shark River sites (Table 2).

Mean aboveground wood biomass (AWB) varied significantly ($F_{2, 3} = 8.8$, $p < 0.05$) among Shark River sites, with higher biomass in SRS-6 (162.2 ± 2.1 Mg ha^{-1}) compared to SRS-4 & 5 (~ 100 Mg ha^{-1} ; Fig. 5a). Wood biomass in TS/Ph-6 & 7 was 12.5 Mg ha^{-1} (after Coronado-Molina et al., 2004; Fig. 5a). *R. mangle* comprised 56% (SRS-4), 81% (SRS-5), 20% (SRS-6), and 100% (TS/Ph-6 & 7) of the total AWB at each site, while *L. racemosa* and *A. germinans* accounted for 51% and 30% of the total biomass at SRS-6, respectively. At TS/Ph-8, *C. erectus* comprised 83% of the AWB (Fig. 5a). Among years, wood biomass increased significantly ($F_{3, 9} = 5.1$, $p < 0.05$) from 2001 (117.6 ± 7.1 Mg ha^{-1}) to 2004 (126.4 ± 7.1 Mg ha^{-1}). There was no significant ($F_{6, 9} = 1.1$, $p = 0.4$) interaction between sites and years.

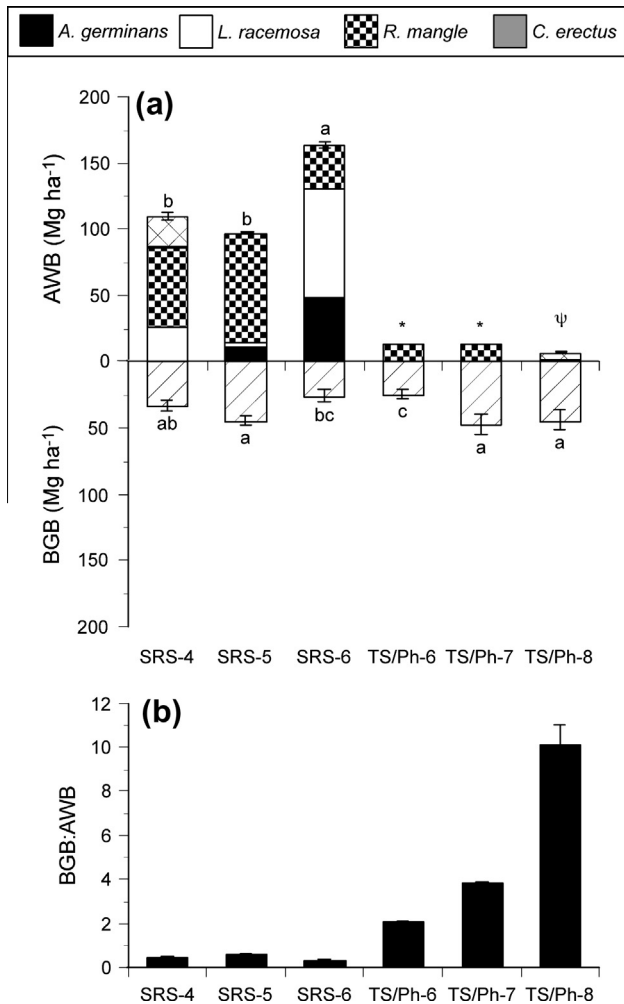


Fig. 5. Variation (plot data) in aboveground wood biomass (AWB) and belowground biomass (BGB) (a) and BGB:AWB ratios (b) in mangrove forests of the Florida Coastal Everglades. Means (± 1 SE) with different letters are significantly different ($p < 0.05$) among sites for each component of biomass. Asterisks indicate data from Coronado-Molina et al. (2004). Symbols ψ and * indicate data were not included in the statistical analysis.

Total (0–90 cm) belowground biomass (BGB) varied significantly among all six sites ranging from 24.0 ± 3.3 to 46.7 ± 7.5 Mg ha⁻¹ (Fig. 5a). Estimates of total BGB followed the trend TS/Ph-7 > SRS-5 > TS/Ph-8 > SRS-4 > SRS-6 > TS/Ph-6 (Fig. 5a; after Castañeda-Moya et al., 2011). The BGB:AWB ratio in the Shark River sites was lower compared to all Taylor River

Table 4

Average (plot data: 2001–2004) annual 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-8
<i>Average wood production (kg tree⁻¹ yr⁻¹)</i>				
<i>A. germinans</i>	–	0.14 (0.13)	1.24 (0.11)	–
<i>L. racemosa</i>	0.76 (0.22)	3.02 (0.38)	2.35 (0.17)	0.11 (0.05)
<i>R. mangle</i>	0.41 (0.06)	0.43 (0.03)	1.04 (0.15)	–
<i>C. erectus</i>	0.81 (0.16)	–	–	0.49 (0.01)
Total	1.98 (0.26)	3.59 (1.27)	4.63 (0.15)	0.60 (0.05)
<i>Basal area increment (m² ha⁻¹ yr⁻¹)</i>				
<i>A. germinans</i>	–	0.01 (0.001)	0.16 (0.02)	–
<i>L. racemosa</i>	0.23 (0.03)	0.10 (0.02)	0.70 (0.02)	0.008 (0.00)
<i>R. mangle</i>	0.42 (0.06)	0.25 (0.02)	0.29 (0.04)	–
<i>C. erectus</i>	0.16 (0.03)	–	–	0.12 (0.07)
Total	0.81 (0.10)	0.36 (0.01)	1.15 (0.07)	0.12 (0.06)

sites, and ranged from 0.17 to 0.33 in Shark River, and from 1.92 to 9.75 in Taylor River (Fig. 5b).

Total annual wood production differed significantly ($F_{2,9} = 7.3$, $p < 0.05$) among Shark River sites, with the highest wood production in SRS-6 (4.37 ± 0.29 Mg ha⁻¹ yr⁻¹) and the lowest in SRS-5 (1.45 ± 0.1 Mg ha⁻¹ yr⁻¹; Table 3). *L. racemosa* (SRS-6) had the highest wood production across all sites, while *R. mangle* dominated wood productivity in the upstream sites (SRS-4 & 5; Table 3). In contrast, there were no significant ($F_{2,9} = 0.1$, $p = 0.9$) differences in annual wood production among years and no significant ($F_{4,9} = 0.3$, $p = 0.8$) interaction between sites (i.e., Shark River) and years. At TS/Ph-6 & 7, annual wood production ranged from 0.64 to 0.75 Mg ha⁻¹ yr⁻¹, respectively (Table 3; after Ewe et al., 2006). Average wood production per tree ranged from 0.14 to 3.02 kg tree⁻¹ yr⁻¹ across all species and sites (Table 4). *L. racemosa* had the highest wood production in SRS-5 (3.02 kg tree⁻¹ yr⁻¹) and SRS-6 (2.35 kg tree⁻¹ yr⁻¹; Table 4). The annual increment in basal area ranged from 0.01 m² ha⁻¹ yr⁻¹ (*A. germinans*, SRS-5) to 0.70 m² ha⁻¹ yr⁻¹ (*L. racemosa*, SRS-6) among species at all sites (Table 4). *R. mangle* contributed 52% (SRS-4) and 69% (SRS-5) of total growth increment in the upstream sites, while *L. racemosa* accounted for 61% of the total productivity in SRS-6 (Table 4).

3.4. 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 (2001–2004) study period (Fig. 6). Daily rates of litterfall components were significantly ($p < 0.001$) higher during the wet season (June–November) compared to the dry season (December–May), with the highest rates observed for leaf fall (2.18 ± 0.14 g m⁻² d⁻¹) and the lowest for wood (0.24 ± 0.03 g m⁻² d⁻¹) in the wet season (Fig. 6). There was a

Table 3

Variation (plot data: 2001–2004) in wood production, total litterfall, and NPP_A in mangrove forests of 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	Site					
	SRS-4	SRS-5	SRS-6	TS/Ph-6	TS/Ph-7	TS/Ph-8
<i>Wood production (NPP_W) (Mg ha⁻¹ yr⁻¹)</i>						
<i>A. germinans</i>	–	0.01 (0.01)	0.63 (0.08)	–	–	–
<i>L. racemosa</i>	0.86 (0.11)	0.32 (0.07)	2.5 (0.09)	–	–	0.03 ^b (0.005)
<i>R. mangle</i>	2.11 (0.30)	1.12 (0.10)	1.24 (0.17)	0.64 ^a	0.75 ^a	–
<i>C. erectus</i>	0.60 (0.1)	–	–	–	–	0.44 ^b (0.20)
Total	3.57 ^{ab} (0.41)	1.45 ^b (0.05)	4.37 ^a (0.29)	0.64 ^{a,b}	0.75 ^{a,b}	0.47 ^b (0.23)
<i>Litterfall production (NPP_L) (Mg ha⁻¹ yr⁻¹)</i>						
	8.11 ^b (0.75)	7.67 ^b (0.53)	10.14 ^a (0.74)	2.58 ^{a,b}	3.03 ^{a,b}	2.85 ^c (0.25)
<i>NPP_A = NPP_W + NPP_L (Mg ha⁻¹ yr⁻¹)</i>						
	11.68 (1.38)	9.12 (0.73)	14.51 (1.07)	3.22 ^a	3.78 ^a	3.32 (0.52)

^a Data from Ewe et al. (2006).

^b Not included in any of the statistical analysis.

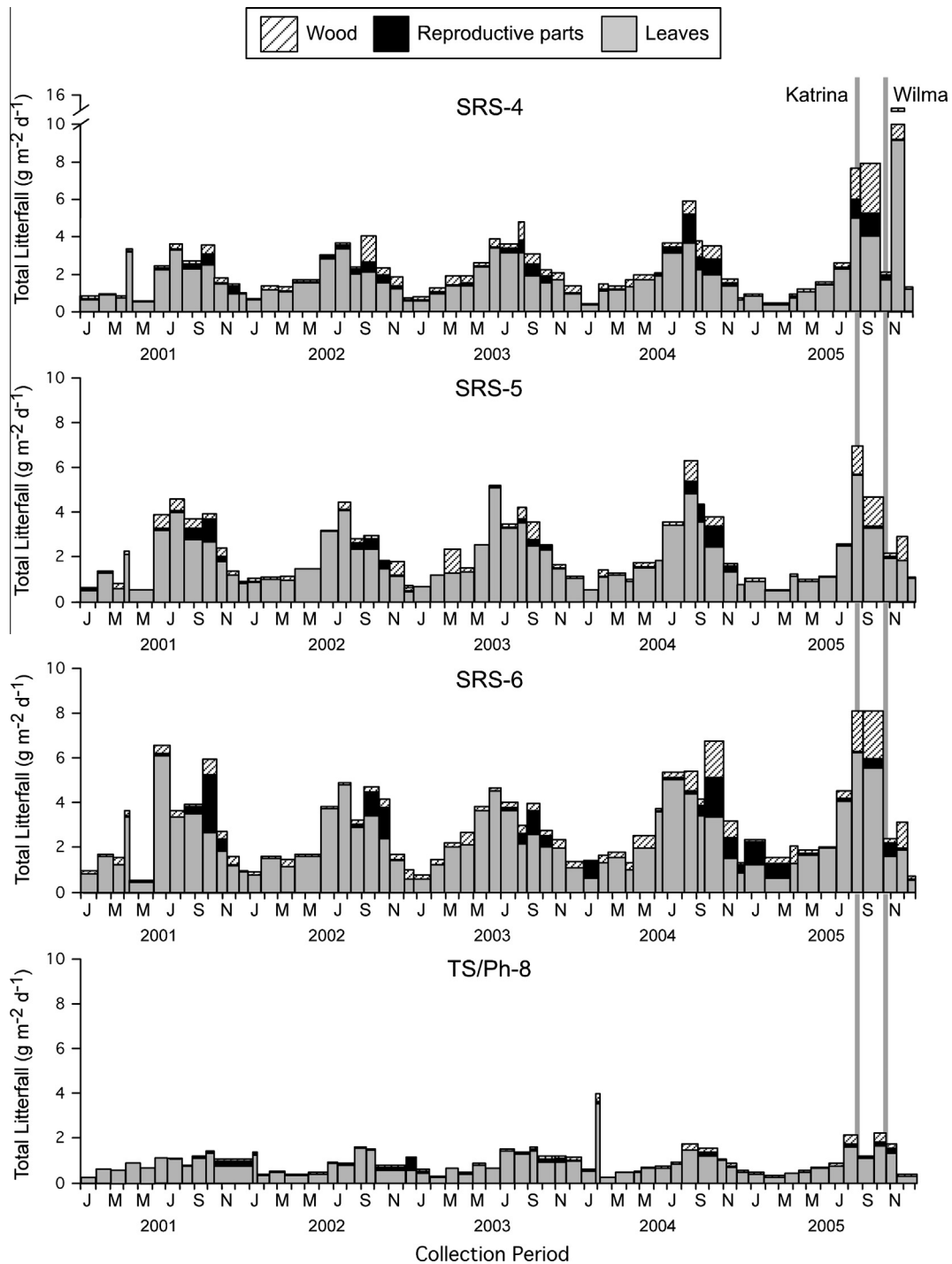


Fig. 6. Daily rates of litterfall components (leaves, reproductive parts, and twigs) in mangrove forests along Shark River estuary and at TS/Ph-8 during the period 2001–2005. The width of the bars represents the time period over which collections were made. The vertical gray boxes represent the approximate 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.

significant ($F_{3, 1801} = 52.7$, $p < 0.001$) site and season interaction on total daily litterfall. Mean daily rates ranged from $1.26 \pm 0.1 \text{ g m}^{-2} \text{ d}^{-1}$ (dry season) to $3.04 \pm 0.2 \text{ g m}^{-2} \text{ d}^{-1}$ (wet season), with the highest rates at SRS-6 ($4.27 \pm 0.3 \text{ g m}^{-2} \text{ d}^{-1}$) during the wet season and the lowest at TS/Ph-8 ($0.73 \pm 0.13 \text{ g m}^{-2} \text{ d}^{-1}$) during the dry season (Fig. 7). 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.

Annual litterfall ranged from $2.85 \pm 0.25 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (TS/Ph-8) to $10.14 \pm 0.74 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (SRS-6) across sites, and followed the pattern $\text{SRS-6} > \text{SRS-4} = \text{SRS-5} > \text{TS/Ph-8}$ (Table 5).

Annual total litterfall was approximately 1.3 times lower in Shark River upstream sites (SRS-4 and SRS-5) compared to SRS-6 (Table 5). Across all years, total litterfall was significantly higher in 2004 compared to 2001 and 2002. There was no significant interaction between site and year for all litterfall components, except for wood (Table 5). During 2005, total litterfall had a significant increase in all sites when compared to previous years due to

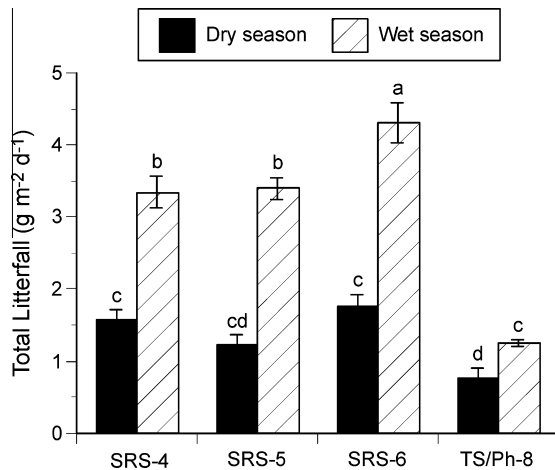


Fig. 7. Seasonal variation in daily rates of total litterfall production in mangrove forests along Shark River estuary and at TS/Ph-8 averaged over the period 2001–2004. Means (± 1 SE) with different letters are significantly different ($p < 0.05$) across sites and seasons.

the passage of Hurricane Wilma across FCE in October 2005. Total litterfall was $16.28 \pm 0.58 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for SRS-4, $8.59 \pm 0.10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for SRS-5, $13.39 \pm 0.83 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for SRS-6, and $3.25 \pm 0.10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ 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 ($15.4 \text{ g m}^{-2} \text{ d}^{-1}$) during November 2005 was 6.4 times higher than the average (2001–2004) rate prior to the storm (Fig. 6). In TS/Ph-6 & 7, annual litterfall was 2.58 and $3.03 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively (Table 3; after Ewe et al., 2006).

3.5. Total annual net primary productivity (NPP_T)

Annual NPP_A ($\text{NPP}_L + \text{NPP}_W$) ranged from $3.22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (TS/Ph-6) to $14.51 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (SRS-6) across all six sites (Table 3). Average NPP_A was 3.4 times higher in the Shark River sites ($11.77 \pm 1.56 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) compared to the Taylor River sites ($3.44 \pm 0.17 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Overall, NPP_L had the highest contribution to NPP_A accounting for 69–86% of the total NPP_A in both basins (Table 3). Estimates of NPP_B (0–90 cm) did not differ significantly among all six sites, and ranged from $4.07 \pm 0.23 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (TS/Ph-7) to $6.43 \pm 0.93 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (SRS-5; Fig. 8; after Castañeda-Moya et al., 2011). NPP_T ($\text{NPP}_A + \text{NPP}_B$) ranged from $7.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (TS/Ph-7) to $19.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (SRS-6) across all sites, with average NPP_T twice as high in Shark River ($17.0 \pm 1.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) compared to Taylor River ($8.3 \pm 0.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Fig. 8).

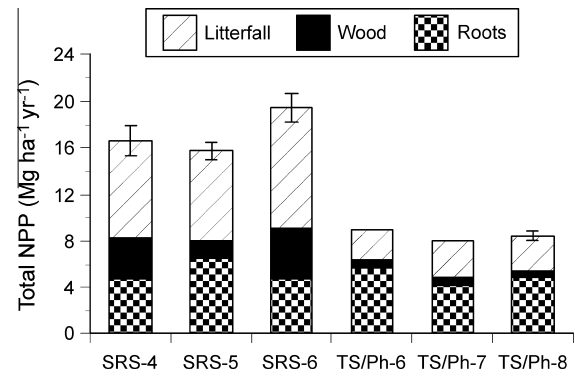


Fig. 8. Total annual net primary productivity (NPP_T) including litterfall, wood, and root production in mangrove forests of the Florida Coastal Everglades during the period 2001–2004 (plot data).

Overall, NPP_L accounted for 51% (Shark River) and 34% (Taylor River) of the NPP_T , while NPP_W only contributed 18% (Shark River) and 8% (Taylor River) to NPP_T (Fig. 8). NPP_B had a significant contribution to NPP_T ranging from 31% in the Shark River sites to 58% in the Taylor River sites (Fig. 8). The contribution of fine roots ($< 2 \text{ mm}$ diameter) was 50% of the total NPP_B estimated for all sites. The ratios of NPP_T to biomass (P:B) were consistently lower in all Shark River sites ranging from 0.10 to 0.12 yr^{-1} . In the Taylor River sites, P:B ratios were higher and more variable ranging from 0.13 yr^{-1} (TS/Ph-7) to 0.17 yr^{-1} (TS/Ph-8) to 0.24 yr^{-1} (TS/Ph-6).

3.6. Multivariate and multi-dimensional scaling (MDS) analyses

Multiple regression analyses indicated that the best models explaining the variability in community structure and productivity across our sites included soil fertility, frequency and duration of inundation, and sulfide concentrations (Table 6). Best fitted models were highly significant ($p < 0.001$ and low $C(p)$ statistic), and showed high agreement ($r^2 > 0.9$) with no multicollinearity detected. Variance-inflation factors (VIF's) ranged from 1.2 to 3.2 and condition indices (CI) were < 30 for all fitted models, indicating that independent variables were not highly correlated (Table 6).

The MDS ordination showed a strong spatial variation in forest data (structure and productivity) and environmental factors across our sites (Figs. 9a and b). ANOSIM results revealed significant differences in forest data (global $R = 0.99$, $p = 0.02$) and environmental factors (global $R = 0.91$, $p = 0.02$) among sites resulting in two distinct site groups located in the two distinct experimental basins. The low stress value (0.01) for both MDS's provided a reliable two-dimensional representation of the relative groups separation in our study (Fig. 9a and b). The ordination analysis also indicated within-group differences in forest data and environmental factors,

Table 5

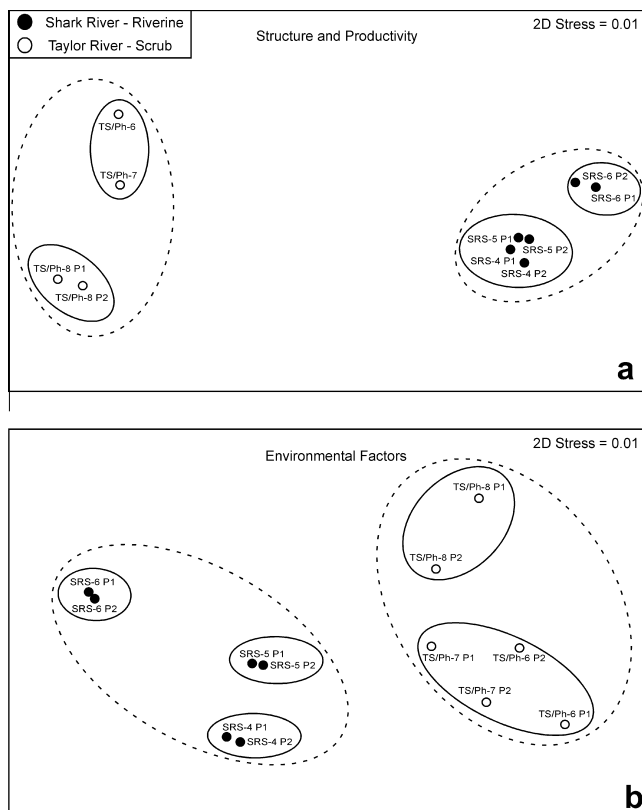
Statistical results for each component of annual ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) litterfall (plot data) in mangrove sites of the Florida Coastal Everglades. Means (± 1 SE) followed by different letters across each row are significantly different (Tukey HSD post hoc test, $p < 0.05$). ANOVA source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

Variable	Site				Year			
	SRS-4	SRS-5	SRS-6	TS/Ph-8	2001	2002	2003	2004
Total	8.11 ^b (0.75)	7.67 ^b (0.53)	10.14 ^a (0.74)	2.85 ^c (0.25)	5.05 ^c (0.87)	7.28 ^b (1.03)	8.04 ^{ab} (1.05)	8.40 ^a (1.29)
Leaves	5.35 ^b (0.39)	5.81 ^b (0.40)	7.41 ^a (0.48)	2.31 ^c (0.21)	3.70 ^b (0.57)	5.36 ^a (0.75)	5.94 ^a (0.72)	5.88 ^a (0.81)
Reproductive parts	1.96 ^a (0.24)	1.24 ^{ab} (0.11)	1.85 ^a (0.18)	0.45 ^b (0.05)	0.98 ^b (0.20)	1.44 ^a (0.23)	1.40 ^a (0.27)	1.68 ^a (0.33)
Wood	0.80 ^a (0.19)	0.62 ^a (0.14)	0.88 ^a (0.18)	0.09 ^b (0.03)	0.37 ^c (0.13)	0.48 ^b (0.15)	0.70 ^{ab} (0.20)	0.84 ^a (0.21)
ANOVA source ^a	Total				Leaves			
Site	$F_{3, 3.9} = 61.7^{***}$				$F_{3, 165} = 63.6^{***}$			
Year	$F_{3, 162} = 23.3^{***}$				$F_{3, 165} = 20.9^{***}$			
Site * year	$F_{9, 162} = 1.5^{ns}$				$F_{9, 165} = 0.7^{ns}$			
					Reproductive parts			
Site	$F_{3, 3.9} = 61.7^{***}$				$F_{3, 165} = 63.6^{***}$			
Year	$F_{3, 162} = 23.3^{***}$				$F_{3, 165} = 20.9^{***}$			
Site * year	$F_{9, 162} = 1.5^{ns}$				$F_{9, 165} = 0.7^{ns}$			
					Wood			
Site	$F_{3, 3.9} = 61.7^{***}$				$F_{3, 165} = 63.6^{***}$			
Year	$F_{3, 162} = 23.3^{***}$				$F_{3, 165} = 20.9^{***}$			
Site * year	$F_{9, 162} = 1.5^{ns}$				$F_{9, 165} = 0.7^{ns}$			

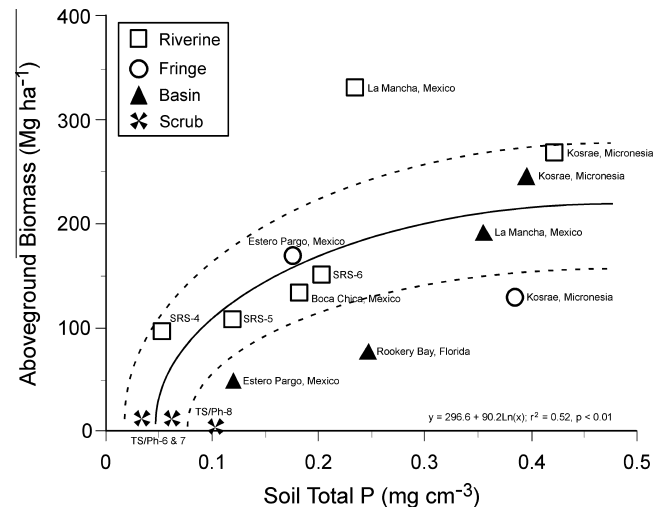
Table 6

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

Dependent variable independent variable	Anova source	p Model	r ² Model	C(p)	Variance inflation	Parameter estimates	p
Basal area	$F_{3, 4} = 33.7$	0.003	0.96	4.0	2.4		
Soil total P						26.78	0.037
Sulfide						−6.79	0.154
Frequency of inundation						0.08	0.042
Aboveground biomass	$F_{3, 8} = 46.7$	0.001	0.95	4.0	1.8		
Soil total P						243.19	0.071
Sulfide						−55.67	0.001
Frequency of inundation						13.50	0.039
Litterfall production	$F_{3, 8} = 60.2$	0.001	0.96	2.6	3.2		
Sulfide						−0.58	0.001
Flooding duration						6.2E−5	0.029
Frequency of inundation						0.001	0.033
Wood Production	$F_{4, 7} = 34.2$	0.001	0.95	1.9	2.2		
Soil total P						30.32	0.06
Sulfide						−0.77	0.01
Frequency of inundation						0.004	0.01
Soil N:P	$F_{3, 8} = 176.0$	0.001	0.98	−1.4	1.2	0.009	0.03
Root:shoot						5.83	<0.001
Sulfide						3.23	<0.001
Total N						−0.0004	<0.001
Flooding duration							

**Fig. 9.** Multi-dimensional scaling (MDS) ordination diagram of all replicates (plots 1 and 2) and sites showing variations in forest structure and productivity data (a) and environmental factors (b) in riverine and scrub mangrove forests in the Florida Coastal Everglades. Stress value for the MDS ordination is showed in each panel.

with SRS-6 and TS/Ph-8 showing higher dissimilarities compared to their group members (Fig. 9a and b). This observation is in agreement with our ANOVA results (Tables 1–3 and 5). The BIO-ENV procedure showed that variations in forest structure and productivity among sites were explained by a combination of P fertility, sulfide concentrations, and frequency and duration of

**Fig. 10.** Non-linear model between aboveground biomass and soil P density for different mangrove types. Standard parameters of the model and 95% confidence intervals are indicated. Data points include FCE mangrove sites (this study) and additional sites in Terminos Lagoon (Day et al., 1987, 1996), La Mancha Lagoon, Mexico (Twilley unpublished data), Kosrae Island, Micronesia (Cormier, 2003), and Rookery Bay, south Florida (Twilley, 1995; Krauss et al., 2006).

inundation (Spearman correlation = 0.92, $p = 0.01$), confirming the results obtained by the multiple regression analyses.

4. Discussion

Results from this study demonstrate that the degree of interaction among landscape features such as soil P fertility, sulfide concentrations, and hydroperiod control mangrove vegetation patterns in the FCE, which result in distinct riverine and scrub mangrove ecotypes across the coastal landscape (Twilley and Rivera-Monroy, 2005; Ewe et al., 2006; Mancera Pineda et al., 2009; Rivera-Monroy et al., 2011). Multiple regression and MDS ordination analyses confirm that the cumulative effect of those three environmental gradients explained more than 90% of the total variability in community structure and productivity across our

mangrove sites, as has been previously hypothesized (Table 6, Fig. 9; Koch, 1997; Koch and Snedaker, 1997; Chen and Twilley, 1999b; Krauss et al., 2006). Salinity has usually been considered an important factor in regulating community structure, productivity, and zonation of mangroves species, particularly in drier environmental settings where high salinities restrict 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) across our mangrove sites were below the critical value (65) that influences mangrove forest structure and mortality (Cintron et al., 1978), and thus could not explain the variability in forest structure and productivity between Shark River and Taylor River basins. In fact, a recent study suggests that 46% of the variation in C isotopic signature among FCE mangrove sites can be explained by changes in sulfide concentrations, but not salinity (Mancera Pineda et al., 2009).

Mangrove forests along Taylor River have lower P deposition during storm events due to the Buttonwood Ridge that isolates these scrub mangroves from the direct influence of Florida Bay (Fig. 1b; Davis et al., 2004; Castañeda-Moya et al., 2010). This ridge also affects the hydrology of this southeastern region of ENP, forming a barrier for water to export during the wet season, causing surface water to remain for most of the year (Michot et al., 2011). This distinct hydroperiod gradient along Taylor River was evident in this study where mangrove forests had no tidal influence and remain flooded almost 100% of the year, in contrast to mangroves along the southwestern coast of ENP in Shark River Estuary where tidal signatures were evident year round. At the most southeastern site of Taylor River, TS/Ph-8, hydroperiod was seasonally dynamic compared to the sites west in Taylor River behind Buttonwood Ridge. As a result of these distinct hydroperiods in these two regions, sulfide and porewater DIN concentrations were significantly higher in all Taylor River sites compared to Shark River sites, reflecting the lack of tides and lower water turnover in this region.

In addition to these regional gradients of resource, regulator, and hydroperiod associated with the presence and absence of a geologic barrier at the mouth of estuaries in southeastern ENP, there is also evidence of similar effects upstream of estuaries in the southwest ENP not impacted by this barrier. Mangrove forests along Shark River Estuary, to the southwest, are characterized by a distinct gradient in P fertility and corresponding shift in N:P ratios with distance inland from the mouth of the estuary (Chen and Twilley, 1999a,b; Chambers and Pederson, 2006; Mancera Pineda et al., 2009). These gradients in P density are associated with decreased mineral deposition (i.e., Ca-bound P) upstream of an estuary during hurricane events (Chen and Twilley, 1999a,b; Castañeda-Moya et al., 2010). Thus, the southwestern estuaries have regional P gradients, but less continuous flooding and lower sulfide stress, whereas southeastern estuaries inland of the Buttonwood Ridge have lower P input and higher flooding conditions and sulfide concentrations. The contrasting conditions in hydroperiod and P delivery between these two basins determine gradients in regulators (sulfide) and resources (P) and provide insights to interactive effects on allocations of biomass and net primary productivity (Mancera Pineda et al., 2009).

Patterns in aboveground wood biomass follow the soil P fertility gradient in both the regional and estuarine gradients of this landscape. Wood biomass estimates were 1.6 greater along the estuarine gradient in Shark River (Chen and Twilley, 1999b), compared to 12-fold reduction of biomass along regional gradients in mangroves between Shark River and Taylor River sites. Remote sensing analyses using RADAR and LIDAR confirm higher aboveground biomass (120–150 Mg ha⁻¹) in mangrove areas adjacent to the mouth of Shark River and other southwestern FCE estuaries including Harney River and Broad Creek, in contrast to lower estimates in

upstream areas of these estuaries (Rivera-Monroy et al., 2011). Mangrove biomass in estuaries southeastern of this region, along Taylor River, and regions behind Buttonwood Ridge, all have biomass <50 Mg ha⁻¹ and tree height <5 m (Simard et al., 2006; Rivera-Monroy et al., 2011). Estuarine gradients are also evident with the highest forest development in areas with lower soil N:P (28) at the mouth of Shark River Estuary relative to higher soil N:P ratios ranging from 46 to 105 in the upper estuary in southwest ENP. In contrast are the greater regional differences in N:P ratios reaching 109 in sites behind Buttonwood Ridge in southeastern ENP, where scrub mangrove forests dominate the landscape.

There is also a shift in community structure and species dominance along estuarine and regional environmental gradients, with *R. mangle* dominating sites with lower P concentrations. This pattern along with the higher growth rate of *L. racemosa* at sites with higher P concentrations suggests that P availability is a controlling factor on forest structure and productivity across FCE mangroves (Chen and Twilley, 1998, 1999b), as observed in other neotropical regions (McKee, 1995). Our results also suggest that P limitation (N:P = 102–109) along with permanent flooding conditions, as observed in Taylor River sites, may explain the scrub physiognomy of mangroves and the dominance of *R. mangle* in this basin (Koch, 1997). This species seems to perform well under these environmental conditions out competing *L. racemosa* and *A. germinans*. These latter two species are usually restricted to environments where flood duration is <50% of the year, as in the case of Shark River basin (Koch, 1996; Cardona-Olarte et al., 2006).

Biomass allocation patterns between above- and belowground components, along with NPP, were distinct between basins in the southwestern and southeastern region of ENP, with clear impacts from Buttonwood Ridge. Our results show that both litterfall and wood production significantly decreased with lower P availability and frequency of inundation in an estuarine basin inland of Buttonwood Ridge. Using the BGB data published by Castañeda-Moya et al. (2011), we determined that the proportion of belowground biomass allocation (BGB:AWB ratios) was 17 times higher in mangroves behind Buttonwood Ridge compared to those with daily tidal exchanges in estuaries to the southwest of ENP. Also, BGB:AWB ratios increased with increasing sulfide concentrations across our mangrove sites ($r^2 = 0.78$, $p < 0.001$) suggesting the regulatory effect of hydroperiod on root biomass allocation based on greenhouse experiments (Krauss et al., 2006). Indeed, fine root biomass relative to aboveground biomass significantly decreased with soil P availability and frequency of inundation in our study area (Castañeda-Moya et al., 2011). These findings are in accordance with resource limitation and biomass allocation theories for terrestrial forests (Chapin et al., 1987; Gleason and Tilman, 1992), and demonstrate that mangroves in ENP allocate a large proportion of their total biomass to belowground in response to P limitation and soil stress conditions (Lugo, 1990; Komiyama et al., 2000; Sherman et al., 2003; Lopez-Hoffman et al., 2007; Naidoo, 2009).

These observations are consistent with other mangrove studies in the neotropics where salinity is not a strong determining factor of forest development (Appendix). Differences in aboveground biomass allocation among mangrove ecotypes fit a significant ($r^2 = 0.52$, $p < 0.01$) non-linear relationship with total P density, suggesting that 52% of the variability in aboveground biomass allocation for mangroves can be explained by P availability (Fig. 10). This is comparable to the non-linear relationship found between basal area and P density based on the Monod model that explains P limitation constraint on biomass production of neotropical mangroves in sites with salinity <60 (Twilley and Rivera-Monroy, 2009). Thus, these models support the assumption that resource gradients such as soil P control mangrove forest development where salinity is not a determining constraint, and explain the

observed patterns (riverine > basin > scrub) of aboveground biomass allocation for mangrove wetlands in response to environmental gradients (Brown and Lugo, 1982).

The allocation of total production between above- and belowground components was distinct between basins, with riverine mangroves allocating most of the total NPP to aboveground (69%) while scrub mangroves showed the highest allocation to belowground (58%). These findings are consistent with global budget estimates of NPP_T for mangrove forests suggesting the significant contribution of NPP_B (38%) to the overall production (Bouillon et al., 2008). In addition, fine root production was a significant contributor (50%) to the total NPP_B allocation in our study sites. This is in agreement with previous studies showing that fine root production accounts for one-third of the total annual carbon allocation belowground in forest ecosystems (Nadelhoffer and Raich, 1992). The higher root biomass allocation, particularly coarse (5–20 mm diameter) roots (~70%; Castañeda-Moya et al., 2011) and substantial fine root production across our mangrove sites support the hypothesis that belowground allocation is a significant contribution to soil carbon storage in these forested wetlands (Chmura et al., 2003; Khan et al., 2007; Donato et al., 2011; Kauffman et al., 2011; McLeod et al., 2011).

The production to biomass (P:B) ratios also confirm patterns of carbon partitioning to biomass and productivity between riverine and scrub mangroves across the FCE landscape. The lower P:B ratios observed in all Shark River sites suggest that more of the energy flux from primary production is converted into plant biomass, in contrast to Taylor River sites where most of the available energy is used to offset the higher soil stress conditions (i.e., sulfide and permanent flooding) and lower P availability in these scrub forests. Similarly, lower P:B ratios have been reported for riverine mangroves in Terminos Lagoon, Mexico (0.18 yr^{-1} ; Day et al., 1987) compared to higher ratios for scrub forests in Biscayne Bay, Florida (0.36 yr^{-1} ; Ross et al., 2001). There is evidence that biomass production increases with increasing nutrient availability in mangroves (Lovelock et al., 2004, 2006; Feller et al., 2007; Naidoo, 2009) and terrestrial ecosystems (Litton et al., 2007; Vicca et al., 2012). For instance, higher wood production was observed in terrestrial forests with high-nutrient availability compared to forests of low-nutrient availability (Vicca et al., 2012). This is consistent with our findings, since we observed higher wood:litterfall production ratios in riverine mangroves (0.35 ± 0.08) along Shark River and considerably lower ratios in scrub mangroves (0.22 ± 0.03) in Taylor River. In addition, average aboveground P:B ratios were 4.4 times lower in Shark River relative to Taylor River (0.44 yr^{-1}). These results further support our hypothesis that scrub mangrove forests allocate more belowground biomass (i.e., high BGB:AWB ratios) and production relative to aboveground components (litterfall and wood) in response to P limitation and high soil stress conditions, at expenses of aboveground growth and development (Lovelock, 2008). These tradeoffs indicate a strong link between biomass and NPP allocation patterns and the phenotypic plasticity of mangrove species in response to environmental gradients to maximize efficiency of resource use and conserve the most limiting nutrient (Chapin et al., 1987). These distinct mangrove vegetation patterns add to our understanding of the environmental factors governing long-term biomass and productivity patterns of mangrove types across south Florida and prove to be critical to the accurate development of carbon budgets in neotropical mangroves.

4.1. Mangrove management

This study contributes to our understanding of how neotropical mangrove species spatial distribution and productivity patterns are regulated by environmental factors at large regional scales, particularly in karstic geomorphic settings. Many of the long-term

patterns observed across these landscape gradients are consistent with short-term patterns of biomass allocation observed in greenhouse studies of soil stress conditions. Validation of controlled experiments with landscape trajectory experiments such as this study improve global estimates of carbon sequestration in mangroves using classifications of coastal environmental settings. Scrub mangroves have a higher proportion of biomass and productivity in the soil and thus carbon estimates need to utilize different ratios compared to observations made on aboveground features of the forest. Changes in soil hydroperiod can have significant shifts in these biomass allocation patterns, along with the effects of salinity and soil fertility. Mangrove soils and standing wood biomass are significant sites of biomass accumulation that can be restored with particular focus on soil fertility and more frequent tidal inundation. Long hydroperiods and low soil fertility will reduce long-term biomass storage and production, thus affecting the provision of ecosystem services such as carbon sequestration in neotropical mangrove forests.

These results also have implications to large-scale mangrove restoration programs being implemented across the Americas, where these three species dominate (Zaldivar-Jimenez et al., 2010). Most of these restoration programs focus on replanting of single species (mainly *R. mangle*) in areas where massive diebacks have occurred, without taking into consideration the environmental soil conditions that can warrant species-specific seedling survival, and growth and forest development (Lewis, 2005; Bosire et al., 2008; Rovai et al., 2012). Most of these programs fail due to the lack of information about the relative importance of environmental variables, particularly soil fertility and hydroperiod, in regulating plant growth (Lewis, 2009). Our results provide quantitative evidence about critical variables such as hydroperiod and nutrient fertility that should be used to select performance measures for effective restoration efforts (Twilley and Rivera-Monroy, 2005). Indeed, our results provide baseline information to evaluate the impact of future increases in freshwater flow from the upper Taylor River and Shark River basins as part of the Comprehensive Everglades Restoration Plan (CERP, Rivera-Monroy et al., 2011). An increase in freshwater flow from the upper regions of these basins will restrict the inland migration of mangrove vegetation, particularly in Taylor River Slough where reductions in freshwater drainage during the past 100 years has facilitated the replacement of previous freshwater marshes dominated by *C. jamaicense* to brackish *R. mangle*-dominated scrub mangroves (Ross et al., 2000).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.07.011>.

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