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Monitoring of Tree Island Conditions in the Southern Everglades: The Effects of Hurricanes and Hydrology on the Status and Population Dynamics of Sixteen Tropical Hardwood Hammock Tree Islands

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Dynamics of Sixteen Tropical Hardwood Hammock Tree Islands**



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Executive Summary:

In 2005 we began a multi-year intensive monitoring and assessment study of tropical hardwood hammocks within two distinct hydrologic regions in Everglades National Park, under funding from the CERP Monitoring and Assessment Program. In serving as an Annual Report for 2010, this document, reports in detail on the population dynamics and status of tropical hardwood hammocks in Shark Slough and adjacent marl prairies during a 4-year period between 2005 and 2009. 2005-09 was a period that saw a marked drawdown in marsh water levels (July 2006 - July 2008), and an active hurricane season in 2005 with two hurricanes, Hurricane Katrina and Wilma, making landfall over south Florida. Thus much of our focus here is on the responses of these forests to annual variation in marsh water level, and on recovery from disturbance. Most of the data are from 16 rectangular permanent plots of 225-625 m², with all trees mapped and tagged, and bi-annual sampling of the tree, sapling, shrub, and herb layer in a nested design. At each visit, canopy photos were taken and later analyzed for determination of interannual variation in leaf area index and canopy openness. Three of the plots were sampled at 2-month intervals, in order to gain a better idea of seasonal dynamics in litterfall and litter turnover. Changes in canopy structure were monitored through a vertical line intercept method.

Our sampling protocols allowed us to trace effects of the 2005 hurricane(s), especially accelerated demographic turnover, i.e., coinciding increases in both mortality and ingrowth that peaked in 2008 in most stands. Following the hurricane, leaf area increased and canopy openness decreased for several years, then leveled off as stands approached or sometimes exceeded pre-hurricane fullness. More than anything, these tree islands displayed a strong resilience to the stresses asserted by hurricanes. The repeated sampling also revealed year-to-year vegetation dynamics that suggested responses to the relatively dry conditions that prevailed during 2006 to 2008. Perhaps more than anything else, our studies are demonstrating differences between hardwood hammocks embedded in the Ridge and Slough and Marl Prairie landscapes. These differences extend beyond their very different soils, forest structure, and composition, but also apply to dynamic processes observable within the context of a standard monitoring program, including demographic turnover, forest productivity, and litter dynamics.

The continued monitoring of tropical hardwood hammock tree islands is critical for Everglades restoration, since they provide ecological niches for a wide variety of plants and animals (including many migratory avian species) whose lifecycles are interdependent on the existence of these forested communities. Furthermore, tropical hardwood hammock tree islands can be thought of as indicator communities, i.e., one of several that may serve as “canaries-in-the-coal-mine” for the Everglades ecosystem as a whole. Significant losses in tropical hardwood hammock habitat, whether in the ridge and slough or the wet prairies, as a result of hydrologic fluxes that either directly, by flooding or extended hydroperiods, or indirectly, by drought conditions that increase and exacerbate the potential for a catastrophic fire, would be clear indicators of degradative environmental conditions within the Everglades. We need not look further than the Water Conservation Areas north of Everglades National Park or in the eastern wet prairies affected by the Mustang Corner Fire to see how hydrologic alterations and fluxes have adversely altered the landscape and led to significant losses in tropical hardwood hammock abundance and in their overall “health” or ecological function.

Introduction:

Tree islands are an integral part of the Everglades and the south Florida landscape. They are prominent features within the long-hydroperiod ridge and slough landscape of the Everglades as well as prevalent throughout the short-hydroperiod marl prairie grasslands at the peripheries (see Hanan et al. 2010; Ruiz et al. 2010). Within these two distinct landscapes, tree islands add structure and bio-topographic relief to a physiographically limited landscape. More importantly, however, they provide a network of refuges for forest-dwelling plants and animals and perform important biodiversity and nutrient cycling functions (Loveless 1959, Gaines et al. 2002, Meshaka et al. 2002, Jayachandran et al. 2004, Ruiz 2004, Hanan & Ross 2009)

Tree island morphology (i.e., their size, shape, composition, and structure), which is spatially variable throughout the Everglades, is influenced by several factors including: 1) the underlying bedrock topography or substrate, which determines elevation and the hydrologic conductivity of the soils, and thus the type of tree island (e.g., tropical hardwood hammock, bayhead, willowhead, or cypress dome) (Armentano et al. 2002); 2) surface water flow and nutrient transport dynamics, which has been hypothesized to drive tree island size and shape as well as species composition (Armentano et al. 2002, Givnish et al. 2008); and 3) the frequency and intensity of fires and windstorms, which can significantly impact the composition and structure of these forested patches by resetting the successional process within them (Wetzel 2002). The combined interactions of these exogenous factors as well as other abiotic and biotic drives, which themselves can be exogenous or endogenous, are responsible for the diverse assortment, distribution, and density of tree islands found throughout the Everglades.

Tropical hardwood hammocks, which are one of several distinct tree island types found within the Everglades, occur as either individual forested patches surrounded by marsh, or imbedded, usually at the head, of a larger forested tree patch/island (bayhead) that is hydrologically and compositionally different (**Figure 1**). In both cases, the location of these tropical hardwood hammocks appears to be predicated on the presence of a topographic high or bedrock outcrop that rises well above the marsh surface (Olmsted & Armentano 1997, Sah 2004, Hanan et al. 2010; **Figure 2**). Consequently, these forests are rarely, if ever, flooded and their soils are typically well drained but rarely xeric enough to affect plant growth (**Appendix 1**; Olmsted & Armentano 1997, Armentano et al. 2002, Sah 2004). Moreover, these soils are known to contain significant concentrations of phosphorus (**Appendix 1**; Oren et al. 2002, Jayachandran et al. 2004, Wetzel et al. 2005, Ross et al. 2006b, Wetzel et al. 2009). In general, these forest communities have inherently high productivity rates and well developed mixed-species canopies that tower over the surrounding vegetation (Olmsted & Armentano 1997). These conditions make tropical hardwood hammocks ecological hotspots of biodiversity for both native and exotics species of plants and animals and thus contribute significantly to the overall biodiversity of the Everglades (see Olmsted & Armentano 1997, Meshaka et al. 2002, Ruiz 2004).

These forest, however, are vulnerable to fires and windstorms as well as flooding and/or drought (Loveless 1959, Schortemeyer 1980, Patterson & Finck 1999), which can significantly change the environmental conditions and reset successional processes. These perturbations are temporally and spatially variable throughout the landscape and their impacts on biodiversity and ecosystem function are localized and often short-lived. However, prolonged flooding can have

significant repercussions across all trophic levels within these forests and, under extreme conditions, can lead to total ecosystem collapse.

Natural and management-related hydrologic changes are known to affect tree island vegetation and structure (see Reed & Ross 2004; Sah 2004). In northern portions of the Everglades, changes in tree island vegetation and structure have been attributed, in part, to management practices that have resulted in extreme and prolonged high water levels (Schortemeyer 1980, Wetzel 2002, Wetzel 2005). These non-natural and extended hydroperiods have resulted in the total loss of tree island habitat over large portions of the central and northern Everglades (Wetzel 2005). Unfortunately, in most cases, these losses appear irreversible unless drastic changes are made in hydrologic management.

As part of the ecological and social fabric of the Everglades, tree islands are focal ecosystems for Everglades restoration. Within the Comprehensive Everglades Restoration Plan (CERP), there is a need to formulate more meaningful tree island performance measures and monitor how restoration efforts affect them (RECOVER 2006). Changes in water management associated with the hydrologic restoration of the Everglades will result in changes in the internal water economy of tree islands. This, in turn, will lead to changes in plant function and species composition within these forests. Thus, it is as important to understand how these ecosystems function and respond to natural events, as it is to understand how the hydrologic restoration of the Everglades will affect the density, composition, and structure of these unique forested ecosystems.

Assessing the “performance” of these forested ecosystems, i.e., tropical hardwood hammocks, requires a better understanding of their reference condition, functioning, and ability to respond to and recover from periodic stresses (e.g., fire, windstorms, flooding, and/or drought), as well as their response to landscape level hydrologic modifications and management decisions. With this as the backdrop, we set forth on a multi-year intensive monitoring and assessment study of tropical hardwood hammocks within two distinct hydrologic regions in the southern Everglades (**Figure 3**). The document that follows reports on the population dynamics and status of 16 tropical hardwood hammocks during a 4-year period between 2005 and 2009: a period that saw a marked drawdown in marsh water levels between July 2006 and July 2008 and an active hurricane season in 2005 with two hurricanes, Hurricane Katrina and Wilma, making landfall over south Florida.

Methods:

Study Area:

This study was conducted within 16 tropical hardwood hammock tree islands located within the boundaries of Everglades National Park (ENP) and Big Cypress National Preserve (BCNP) in southern Florida (**Figure 1**). The climate of the region is similar to that of the tropics with daily maximum temperatures between April and October averaging above 27°C (Duever et al. 1994), while winters tend to be mild and usually free from freezes (Duever et al. 1994, Ross et al. 2009). As with most tropical regions, there is a distinct seasonal rainfall pattern with two discrete phases: an active rainy summer season, which parallels the Atlantic Hurricane season, and a relatively dry winter phase (see Duever et al. 1994). Longterm mean annual precipitation for the Everglades averages 138 cm yr⁻¹ but can vary both spatially and temporally in response to multi-scale, 5-6 year climate oscillations (Duever et al. 1994). Within the study region (**Figure 1**) precipitation between 2002 and 2009 averaged 129.4 cm yr⁻¹, which is well below the long-term 30-year average (1950-1980) for the Everglades, as a whole (see Duever et al. 1994). Between 2002 and 2009, annual precipitation ranged from a low of 115.2 cm yr⁻¹, in 2002, to as much as 141 cm yr⁻¹, in 2005 and 2008 (**Figure 4**). Moreover, only three years, 2005, 2006, & 2008, during this 8-year period, received precipitation near or above the long-term 30-year regional average (**Figure 4**). Evapotranspiration (ET) rates for the Everglades range between 88.9 cm yr⁻¹ and 139.7 cm yr⁻¹ (Jiang et al. 2009), and the balance between precipitation and ET is a critical determinant of ecosystem function during any given period.

Interannual variations in the mean monthly marsh water surface elevations within the study area, between 2000 and 2009, were uniform throughout the region and were affected by the rainfall pattern, particularly between July 2006 and July 2008 and in 2009 (**Figure 4 & 5**). During these two periods, mean monthly marsh water surface elevations were generally below the 10-year monthly marsh water surface elevation (**Figure 5**) in response to the lower than average amount of precipitation falling during those years (**Figure 4**). As a result, regional marsh water surface elevations, during the peak of our study (2006-2009), were at their lowest since 2001 (**Figure 5**).

2005 Hurricane Season:

In 2005, shortly after the initiation of this study, the south Florida region was impacted by two hurricanes: Hurricane Katrina and Hurricane Wilma. Hurricane Katrina made landfall in south Florida on the evening of August 25, 2005 as a Category 1 hurricane with maximum sustained winds of 70 knots (Knabb et al. 2006). Hurricane Wilma made landfall in southwest Florida, near Cape Romano, nearly two months later, during the early morning hours of October 24, 2005. Hurricane Wilma came onshore as a Category 3 hurricane with maximum sustained winds near 105 knots (Pasch et al. 2006). Both hurricanes traversed the southern tip of Florida and the Everglades (**Figure 6**). Hurricane Katrina came in from the Atlantic Ocean and exited to the Gulf of Mexico while Hurricane Wilma approached from the Gulf of Mexico and exited to the Atlantic Ocean (**Figure 6**). As a result, the leading edge or NE quadrant of each hurricane approached our study area from opposite directions. In

Hurricane Katrina, the NE quadrant was to the north of our study islands while in Hurricane Wilma the NE quadrant passed directly south and over most of the our tree islands. Wind field estimate data (**Figure 7**) shows that the maximum sustained winds over the Everglades were significantly less during Hurricane Katrina than Hurricane Wilma, 60 knots vs 95 knots, respectively (Knabb et al. 2006, Pasch et al. 2006). Observation of damaged sustained by our tree islands as a result of these two perturbation events were congruent with these wind speed values. Most tree islands visited after Hurricane Katrina revealed little to no damage while most tree islands (e.g., Satinleaf, Gumbo Limbo Hammock, Black Hammock, Chekika Island, and Grossman Hammock) visited after Hurricane Wilma showed significant amounts of tree damage, including windthrow.

Tree Island Selection & Plot Establishment:

Between 2005 and 2007, a network of 16 tree island plots was established within ENP & BCNP. All plots except for A4900 were located within the boundary of ENP (**Figure 1**). The tropical hardwood hammocks sampled in this study were selected from a pool of 62 tree islands previously sampled as part of an extensive survey of tree island resources within Shark River Slough in ENP (**Appendix 1**; Ross et al. 2005, Espinar et al. 2007), and from field observations made while working on two separate projects (Jones & Ross 2004, Ross et al. 2006a). The set of tree islands selected consisted of tropical hardwood hammocks from three geographic regions: Northeast Shark River Slough (NESS) – 3 islands, Shark Slough (SS) – 7 islands, & the peripheral Wet Prairies (WP) – 6 islands (**Table 1**; **Figure 1**).

The primary criterion for the selection of tree islands was to attain an accurate spatial representation of tropical hardwood hammocks within Shark River Slough and the peripheral wet prairies (**Figure 1**). Tree islands were not considered for selection, however, if their tropical hardwood hammock component was < 225 m² or if they were heavily disturbed or dominated by exotics species. Exceptions, however, were made for two tree islands: Irongrape & SS-81 (**Figure 1**). Irongrape was selected because it had recently been abandoned (*ca.* 2000) after many years of intensive recreational use and occupancy, and thus serves as a reference example of tropical hardwood hammock succession and recovery. SS-81 (**Figure 1**), on the other hand, was selected because of its close proximity, ~ 1 km south, to the Everglades skyway – a 1.6 km-long bridge along the Tamiami Trail being built to improve water flow between Water Conservation Area (WCA)-3B, to the north, and Northeast Shark River Slough in ENP, to the south. As a result, SS-81, became an ideal candidate for monitoring and assessing potential changes in tree island function brought about by the restored hydrologic connectivity between WCA-3B and NESS. Three other islands; Satinleaf, Gumbo Limbo Hammock, and Black Hammock (**Figure 1**), were selected because we had been monitoring these islands since 2001 (see Ross & Jones 2004) and thus could be used to access long-term changes in forest structure and species composition in response to hydrologic fluxes and perturbation events.

The size and shape of tropical hardwood hammocks vary dramatically throughout the Everglades. As a result, it was necessary to establish different sized plots to suit the dimensions of the hardwood hammocks on these islands (**Table 1**). Tree island plots ranged from 225 m² (15 x 15 m), for the smallest island (Ficus Pond), to 625 m² (25 x 25 m) for

Satinleaf and Gumbo Limbo Hammock (**Table 1**). In general, however, the average hardwood hammock plot established was 400 m² (20 x 20 m) (**Table 1**).

Table 1: Tree island plot attributes and their location. Tree islands denoted by superscript (a) were originally established in 2001/02 (see Ross & Jones 2004). Tree islands denoted by superscript (b) had data that preceded Hurricane Katrina & Wilma and were used in the pre & post-hurricane analysis.

Region	Tree Island	Date Established	Sampling Frequency	Plot Size (m ²)	Plot Dimensions (m)	Number of cells	Easting NAD83 (UTM_Z17N)	Northing NAD83 (UTM_Z17N)
NESS	Chekika Island ^b	Sep 2005	High	400	20 x 20	16	534372	2847485
NESS	Irongrape	Dec 2006	Low	400	20 x 20	16	533651	2836523
NESS	SS-81	Jun 2007	Low	300	15 x 20	12	547639	2848113
SS	Black Hammock ^{a,b}	May 2006	Low	400	20 x 20	16	531295	2832630
SS	Gumbo Limbo Hammock ^{a,b}	Jun 2006	Low	625	25 x 25	25	525999	2834793
SS	Manatee Hammock	Jul 2006	Low	400	20 x 20	16	518560	2820117
SS	Panther Mound	Jul 2006	Low	400	20 x 20	16	524189	2828472
SS	Satinleaf ^{a,b}	Sep 2005	High	625	25 x 25	25	524499	2838019
SS	SS-37	Jun 2007	Low	300	15 x 20	12	518488	2826245
SS	Vulture Hammock	Jun 2006	Low	400	20 x 20	16	528918	2841667
WP	A4900	Aug 2007	Low	400	20 x 20	16	512305	2841611
WP	E4200	Aug 2007	Low	400	20 x 20	16	529566	2819857
WP	Ficus Pond ^b	May 2005	Low	225	15 x 15	9	517701	2806030
WP	Grossman Hammock ^b	Jun 2005	High	400	20 x 20	16	541819	2833205
WP	Mosquito Hammock ^b	Mar 2005	Low	450	15 x 30	18	520271	2804429
WP	NP205	Jul 2007	Low	400	20 x 20	16	515279	2841219

Regardless of size, each plot, was gridded into 5 x 5 m (25 m²) cells, whose corners and midpoint were marked by 30 cm long ½” PVC stakes affixed to the ground. The center of each gridded cell was given a cell number while the cell corners were marked based on their relative location to the exterior SW corner (0,0) of the plot. The four exterior corners of the plot, e.g., the SW, NW, NE, and SE corners, were marked by a rebar driven to bedrock. In effect, this served two purposes: 1) it permanently fixed the tree plot boundary on each island, and 2) the rebars could then be used to establish four vertical control points to aid with the topographic survey of the plot. The cell network established in each island served as the framework for all monitoring activities within the islands. The plot and cells were set up using a compass, measuring tape, sighting pole(s), and right-angle prism.

The selected tree islands were organized into two sampling groups: **High** and **Low** frequency visits (**Table 1**). The sampling protocols for these two sampling regimes (i.e., the environmental and physical variables monitored and measured on each island) were generally identical, differing only with respect to sampling frequency and timing: **High** frequency islands (3) were visited bimonthly (i.e., Jan, Mar, May, Jul, Sep, & Nov) throughout the year while **Low** frequency islands (13) were visited biannually, usually in February and November of each year (**Table 2**). The **High** frequency islands included one island from each of the three geographic regions: NESS – Chekika Island; SS – Satinleaf;

and WP – Grossman Hammock (**Table 1**). The remaining 13 tree islands made up the **Low** frequency sampling group (**Table 1**).

Bimonthly sampling on the three **High** frequency islands included: 1) estimates of canopy openness based on densiometer reading; 2) census of understory shrub, seedlings, and herbaceous macrophytes; and 3) collection of litterfall and ground litter (**Table 2**). Twice each year, in February and November, hemispherical canopy photographs were taken in each cell to supplement the ongoing bimonthly densiometer based estimates of canopy openness and to monitor seasonal variations in leaf area (**Table 2**). During this same period, coarse woody debris measurements were taken. For the 13 **Low** frequency islands the biannual sampling included: 1) census of understory shrub, seedlings, and herbaceous macrophytes; 2) estimates of leaf area and two estimates of canopy openness based on hemispherical canopy photographs and densiometer readings; and 3) estimates of coarse woody debris (**Table 2**).

Table 2: Sampling activities and frequency (**High** and **Low**) for the 16 study tree islands. See vegetation sampling section for the details associated with these activities.

Sampling Frequency	Sampling Effort		
	Bimonthly (Jan, Mar, May, Jul, Sep, Nov)	Biannually (Nov & Feb)	Annually (Nov)
High			
Chekika Island Grossman Hammock Satinleaf	Seedlings & Understory Vegetation Litter Traps & Standing Litter Densiometer	Hemispherical Photographs Course Woody Debris	Tree Census Sapling Density Forest Canopy Structure
Low			
A4900 Black Hammock E-4200 Ficus Pond Gumbo Limbo Hammock Irongrape Manatee Hammock Mosquito Hammock NP205 Panther Mound SS-37 SS-81 Vulture Hammock	No Activities	Seedlings & Understory Vegetation Hemispherical Photographs Densiometer Course Woody Debris	Tree Census Sapling Density Forest Canopy Structure

On an annual basis, usually in November, all tree island plots were re-censused for changes in sapling densities and ingrowth into the tree stratum as well as tree growth (DBH) & mortality (**Table 2**). Ingrowth of new individuals or sprouts from existing trees were tagged and added to the plot’s tree database at this time as well. Furthermore, the structure of the canopy was assessed using a vertical line intercept method.

Topographic Survey, Soil Depth, & Tree Island Hydroperiod:

A detailed topographic survey of each tree island plot was conducted by surveying via auto-level from a 1st order vertical control monument (benchmark) to the top of the re-bars at the four corners of the plot. Because of the lack of nearby 1st-order USGS, NPS, or DOT vertical control monuments, reference benchmarks were established in the adjacent marsh at 11 tree islands (**Table 3**). The elevation of these benchmarks was determined either by differential GPS or by calculating the difference in elevation between the top of the reference benchmark and the EDEN (Telis 2005 & 2006) estimate of stage level at that location on the day of the survey. Once the elevations of the four plot corners (tops of re-bars) were determined, surface elevations of each cell's midpoint and corners were determined using the auto-level. At each surveyed location within the plot, a soil probe was used to measure depth to bedrock. These measurements allowed us to determine bedrock topography of each plot as well.

Table 3: Vertical datum used to determine tree island surface elevation.

Tree Island	Vertical Datum
A4900	EDEN stage data
Black Hammock	Benchmark (JBA219)
Chekika Island	EDEN stage data
E4200	EDEN stage data
Ficus Pond	EDEN stage data
Grossman Hammock	differential GPS
Gumbo Limbo Hammock	Benchmark (JBA94)
Irongrape	differential GPS
Manatee Hammock	differential GPS
Mosquito Hammock	Benchmark (A-433)
NP205	Benchmark (JBA191)
Panther Mound	differential GPS
Satinleaf	Benchmark (JBA47)
SS-37	EDEN stage data
SS-81	EDEN stage data
Vulture Hammock	differential GPS

Tree island hydroperiod was calculated by determining the number of days yr⁻¹ during 2000-2009, that marsh water levels exceeded the minimum plot elevation (meters above NAVD88) within each island.

Vegetation Sampling:

The vegetation census of each plot consisted of a nested sampling design that accounted for all the major vegetation strata (i.e., forest canopy, trees & saplings, shrubs, seedlings, and herbaceous macrophytes) present within the plots. The sampling method (described below in detail) parallels the methodology employed by Sah (2004) and addresses four major elements: 1) forest canopy structure and leaf area; 2) tree and sapling dynamics, 3) understory shrubs, seedlings, and herbaceous macrophyte dynamics; and 4) annual litter turnover rates (litterfall and ground litter biomass) and coarse woody debris dynamics.

1) *Forest Canopy Vertical Structure, Closure and Leaf Area:* The canopy's vertical structure or profile, including maximum canopy height, volume (m³ m⁻²), richness (S), and skewness, as well as the foliage height diversity (H') and evenness (J') (see MacArthur & MacArthur 1961), was determined, annually, using a vertical line intercept technique (Ross et al. 1998, Sah 2004). Starting at 1.5 m above the ground, we recorded the species and the height interval(s), in 1.0 m increments, of each tree crown that intercepted a vertical cylinder, 0.50 m in radius, centered on a level height pole that extended upwards through the canopy from the center of each cell. In the event that multiple conspecific

individuals intercepted the cylinder within the same height interval, the species was recorded only once.

Maximum canopy height was defined as the top-most 1-m interval occupied by the canopy during each census. Canopy volume ($\text{m}^3 \text{m}^{-2}$) was calculated as the mean number of 1-m strata occupied above each sampling point. Canopy richness (S) was defined as the total number of 1-m canopy strata occupied across all points. Canopy skewness characterizes the asymmetry of the canopy. The foliage height diversity (H') and evenness (J') follows the Shannon-Weiner diversity index (H') and evenness (J') where:

$$H' = - \sum_{i=1}^S (p_i \ln p_i) \text{ and,}$$

$$J' = H' / \ln (S)$$

During every sampling visit, the forest canopy closure of the plot was estimated by taking two densiometer readings, one facing north and one facing south, at the midpoint of each cell within the plot (Lemmon 1956). The densiometer estimates of forest canopy closure were supplemented biannually with hemispherical canopy photographs. At the midpoint of each cell, a hemispherical photo of the canopy directly overhead was taken using a Nikon 950 digital camera with a Nikon FC-E8 fisheye lens adapter (NIKON Inc., Melville, NY) placed and leveled 1.5 m above the ground. Tree island leaf area index (LAI) was calculated by processing the bi-annual hemispherical canopy photos taken using Gap Light Analyzer, GLA 2.0 (Frazer et al. 1999). For each hemispherical image taken, we calculated the percent canopy openness and the 4-ring leaf area index (LAI) – the ratio of the total one-sided leaf area to the projected ground area (Parker 1995).

- 2) *Trees and Saplings Dynamics*: Within each plot, trees (≥ 5 cm) were identified to species, tagged using numbered aluminum tags, and their diameter (cm) at breast height (DBH) and initial height (m) was measured. The location of each tagged tree was recorded to the nearest 0.5 meter using the SW corner of the plot as a reference (0,0). Furthermore, if a tree had multiple stems ≥ 5 cm DBH, each stem was tagged with a unique ID that allowed it to be cross referenced back to its “parent”. The DBH (cm) of these offshoot stems was measured as well. The density and species of all tree saplings (stems 1-5 cm in DBH) within each 5 x 5 m cell was recorded, and assigned to one of two DBH size classes: 1-3 cm or 3-5 cm.
- 3) *Understory Shrubs, Seedlings, and Herbaceous Macrophytes Dynamics*: At the midpoint of each cell, the density of woody seedlings (stems < 1 m) and shrubs (stems > 1 m and < 1 cm DBH) was estimated using nested circular plots of 1.0 m^2 and 3.14 m^2 , respectively. Seedlings present within the 1 m^2 (0.57 m radius) plots were counted and identified to species and assigned to one of three height categories (1-30, 30-60, & 60-100 cm). All shrubs rooted within the 3.14 m^2 (1 m radius) plots were counted and identified to species. The total cover of each shrub species was also estimated using a modified Braun-Blanquet scale based on the following six cover categories: Cat 1: $<1\%$; 2: 1-4%; 3: 4-16%; 4: 16-32%; 5: 32-66%; & 6: $>66\%$ (Sah 2004). The total cover of all herbaceous macrophytes, which includes seedlings, shrubs (< 1 m tall), epiphytes, vines

and lianas, within the 1 m radius plot was similarly estimated by species, using the same cover scale outlined above.

- 4) *Litterfall, Ground Litter Standing Biomass, and Coarse Woody Debris*: At the three high frequency sampling tree islands (Chekika Island, Satinleaf, and Grossman Hammock; **Table 1**) spatial and temporal variation in litter production was estimated by using epoxy-coated steel wire fine-mesh (52.70 x 52.70 x 18.42 cm) litter traps (8 traps per island) placed 0.20 m above the forest floor (**Plate 1**). Litter traps were placed in the SW corner of eight randomly selected cells within each of the three high frequency sampling tree islands. Litter traps were emptied bimonthly and their content, excluding coarse woody debris > 0.64 cm diameter, was dried (at 70° C for a minimum 96 hours or until each sample reached constant mass) and weighed. Standing litter biomass was estimated in the field by collecting *in situ* ground litter within a 0.25 m² quadrat placed 1.0 m north from the midpoint of four randomly selected cells within the plot. Litter within these quadrats, excluding coarse woody debris > 0.64 cm diameter, was collected to the intersection of the Oe horizon or (F) fermentation layer (a layer of partially decomposed litter with portions of plant structures still recognizable) and the Oa horizon (a layer of well-decomposed organic matter of unrecognizable origin) (**Plate 2**). On subsequent visits, the area of collection was rotated by 30° in order to avoid resampling the same location. As with the litter traps, these materials were also transported to the lab where they were dried and weighed.

Annual litter decomposition rates (k) for the three high frequency tree islands (**Table 2**) were calculated by the ratio of annual litter fall (kg ha⁻¹ yr⁻¹) to annual ground litter biomass (kg ha⁻¹) as outlined by Torti et al. (2001). The value k was then multiplied by 12, the number of months in a year, to obtain the mean turnover time for litter in each forest (Torti et al. 2001).

Fluxes in coarse woody debris (not reported here) were assessed biannually across all islands using the methodology developed by van Wagner (1968). Within each tree island, the density and diameter of coarse woody debris was sampled along a 7.07 m transects, extending from the SW to NE corner, of four randomly selected cells within the plot. Sampling along the transects consisted of removing and recording the diameter, of all woody material (> 0.64 cm in diameter) that intersected the transect. When objects of notable size, i.e., large branches or felled trees, could not be removed from the transect after having its diameter recorded, they were marked, with flagging, to ensure that they would not be resampled on future visits.

Data Analysis:

Plot establishment and sampling was initiated in May 2005 and continued through the summer of 2007 (**Table 1**). By 2007, all low frequency sampling tree island plots (**Table 2**) had been sampled, at least once, while the three high frequency sampling tree plots (e.g., Chekika Island, Satinleaf, & Grossman Hammock; **Table 2**) had been sampled bi-monthly since January 2006. As a result, complete datasets for all tree islands were not available until 2007. Consequently, tree island plots established and sampled in 2005 and 2006 (n=11; **Table 1**) were grouped and treated as one dataset (2005/06). Data from the three tree island

plots established and first time sampled in 2001 or 2002 (e.g., Satinleaf, Black Hammock, & Gumbo Limbo; **Table 2**) were similarly combined and used as reference datasets (2001/02) of pre-hurricane conditions for tree islands within Shark River Slough.

Initial exploratory data analysis revealed that NESS and SS tropical hardwood hammock tree islands did not differ enough from each other to warrant treatment as separate units for statistical analysis. As a result, the two groups were combined into a single unit representing all ridge and slough tropical hardwood hammock tree islands (RS). Consequently, statistical analyses were performed using two levels of the factor 'Region': ridge and slough (RS) and wet prairie (WP).

A multivariate technique, non-metric multidimensional scaling (NMDS) ordination, was used to examine the relationships among woody plant communities (saplings and trees) in hardwood hammocks of 16 tree islands. Sites were plotted as points in ordination space, with distance between points representing underlying similarity/dissimilarity in woody species composition among islands. Species abundance data used in the ordination was species' importance value (IV). Tree and sapling abundance (density and basal area) data were summed for each plot, relativized as a proportion of the plot total, and used to calculate Importance Value (IV) of species using the following equation

$$IV = 100 \bullet ((R_d + R_{ba}) / 2)$$

where R_d is the species relative density and R_{ba} is the species relative basal area. Importance value (IV) data of each species were standardized to species maxima and the Bray-Curtis dissimilarity index was used as a measure of dissimilarity in the ordination. The NMDS ordination based on only sapling density data, standardized to species maxima, was also used to analyze the temporal dynamics in species composition in the sapling stratum. Analysis of similarity (ANOSIM) was used to examine differences in woody vegetation composition between RS and WP islands, and among years.

The relationships between tree and sapling species composition and environmental variables: water-table depth (Dist_WT), Soil depth (SoilDep), pH, total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC) and non-carbon materials (Non-C) (**Appendix 1**), were examined using a vector-fitting procedure incorporated in the computer program DECODA (Minchin 1998). The fitted vectors represent direction and correlation of the variables with the ordination configuration. The significance of the environmental vectors was assessed using a Monte-Carlo procedure permutation test with 10,000 permutations of the species data (Minchin 1998).

Data obtained from the repeated measures of sapling and trees were used to examine the structural and compositional dynamics of woody stems. Several islands in our study area were impacted by two hurricanes (Hurricane Katrina and Hurricane Wilma) in 2005. However, visible impacts on tree layer were not uniform among all islands within any of two landscapes; Ridge and Slough (RS) and Wet Prairie (WP). Four Slough islands (Black

Hammock, Chekika Island, Gumbo Limbo Hammock and Satinleaf) and one Prairie island (Grossman Hammock) experienced considerable tree damage during Hurricane Wilma. Moreover, seven islands (Four RS islands: Black Hammock, Chekika Island, Gumbo Limbo Hammock and Satinleaf, and three WP islands: Ficus Pond, Grossman Hammock and Mosquito Hammock) were surveyed both prior to and after hurricane, and thus have pre- as well as post-hurricane tree and sapling data (**Table 1**). However, nine islands were surveyed for the first time after the hurricane (**Table 1**). Based on the assumption that tree mortality varied among islands depending on whether they were impacted by hurricane or not, we analyzed sapling and tree data in two steps: a) all 16 islands that had complete data for three years (2007-2009); and b) a sub-set of 7 islands that had pre- and post hurricane tree data (**Table 1**).

Repeated measures analysis of variance (Repeated measures ANOVA) was used to examine the differences in sapling and tree density, tree basal area, and tree mortality over time between two regions (RS and WP). Mauchly's sphericity test was used to check the assumptions of homogeneity of variance and co-variance. For the seven islands that had pre-hurricane data, Paired-test was also used to examine the differences in sapling and tree density and basal area between pre-hurricane and post-hurricane (after 2 years) measurements.

Woody plant seedling Importance Value (IV) was calculated for each species by dividing the sum of individual species seedling density within each island between 2007 and 2009 by the sum of seedling density for each tree island between 2007 and 2009, and then multiplying by 100.

Repeated measures-ANOVA was used to test differences in canopy height, volume, and closure, as well as richness, skewness and diversity in the occupancy of 1-m strata within the canopy of each tree island over time (2007-2009) between two regions. A similar analytical procedure was used to compare LAI, understory vegetation cover, seedling density, and species richness in the sapling and seedling stratum between the two regions. Regional differences in tree island soil depth, elevation, and depth to water-table were analyzed by one-way ANOVA. Paired *t*-tests were used to analyze temporal and spatial differences in tree island litterfall and ground litter biomass. All statistics were performed using Statistica v7.1 (StatSoft, Inc. 2006).

Results:

Tree Island Topography, Soil Depth, and Hydroperiod:

Summary statistics for the topographic survey of each tree island is presented in **Table 4**. Mean tree island elevation was spatially variable and ranged from a low of 0.491 m, at Ficus Pond, to as high as 2.663 m, at Vulture Hammock (**Table 4**). Plot elevations within individual islands were highly variable (**Table 4**). At Mosquito Hammock, because of karst topography (**Plate 3**), the range in elevation between the minimum and maximum values was about 1.740 m (**Table 4**). In contrast, at Chekika Island, the difference between the minimum and maximum elevation was < 20 cm (**Table 4**). Regionally, RS tree islands had the less within plot variability (Coefficient of Variation, COV= 5.7%) than WP islands (COV = 10.0%), with low spots frequently occupied by swamp forest trees. Mean tree island height above the marsh surface differed significantly between regions (ANOVA, $F_{1,14} = 28.397$, $P < 0.001$), with RS tree islands more elevated above the adjacent marsh (0.94 m) than WP tree islands (0.53 m).

On average, tree islands soils were 35.2 cm deep but ranged from 10 cm (E4200) to 105.4 cm deep (SS-81) (**Table 4**). Soil depths in RS tree islands average 0.46 m while in WP tree islands the soil depth averaged 0.17 m. This difference in mean regional soil depth was significant (ANOVA, $F_{1,14} = 7.122$, $P = 0.018$).

Table 4: Tree island topographic data (mean, minimum, and maximum), soil depth, mean annual water-table depth and hydroperiod.

Region	Tree Island	Mean (\pm 1 S.D.) Plot Elevation (m NAVD 83)	Minimum Plot Elevation (m NAVD 83)	Maximum Plot Elevation (m NAVD 83)	Mean (\pm 1 S.D.) Soil Depth (m)	Mean Annual Water-Table Depth (m)	Hydroperiod (days)
RS	Black Hammock	2.330 \pm 0.166	1.988	2.584	0.371 \pm 0.160	-0.80	0
RS	Chekika Island	2.624 \pm 0.035	2.545	2.712	0.323 \pm 0.086	-0.89	0
RS	Gumbo Limbo Hammock	2.059 \pm 0.071	1.916	2.24	0.345 \pm 0.053	-0.63	0
RS	Irongrape	2.240 \pm 0.050	2.092	2.345	0.322 \pm 0.072	-0.68	0
RS	Manatee Hammock	1.190 \pm 0.094	1.054	1.484	0.772 \pm 0.226	-0.64	0
RS	Panther Mound	1.789 \pm 0.047	1.687	1.89	0.300 \pm 0.069	-0.64	0
RS	Satinleaf	2.221 \pm 0.076	2.082	2.368	0.407 \pm 0.176	-0.64	0
RS	SS-37	1.279 \pm 0.104	0.979	1.444	0.240 \pm 0.136	-0.58	0
RS	SS-81	2.168 \pm 0.304	1.592	2.649	1.054 \pm 0.470	-0.55	0
RS	Vulture Hammock	2.663 \pm 0.191	2.338	2.977	0.465 \pm 0.265	-0.94	0
WP	A4900	1.767 \pm 0.142	1.487	2.2	0.134 \pm 0.131	-0.41	3
WP	E4200	1.535 \pm 0.122	1.284	1.725	0.101 \pm 0.062	-0.63	0
WP	Ficus Pond	0.491 \pm 0.016	0.188	0.734	0.207 \pm 0.106	-0.42	1
WP	Grossman Hammock	2.042 \pm 0.144	1.386	2.238	0.143 \pm 0.171	-0.77	0
WP	Mosquito Hammock	0.892 \pm 0.265	-0.428	1.312	0.141 \pm 0.053	-0.79	0
WP	NP205	1.994 \pm 0.118	1.615	2.221	0.304 \pm 0.170	-0.57	0

Between 2000 and 2009, the mean annual water-table depth across all islands was approximately 66 cm below the top surface of each island (**Table 4**). As a result, during this 10-year period (2000-2009), the mean annual water-table depth was usually found well below the soil horizon in the bedrock (**Figure 8**). However, on rare occasions, usually as a result of heavy rains associated with tropical storms or hurricanes, the water-table rose enough to saturate the surface soils of several tree islands, mostly in WP (**Figure 9**). The duration of these flooding events was usually short-lived and did not change the annual hydroperiod of most tree islands during the 2000-2009 period (**Table 4**). Two WP islands, Ficus Pond and A4900, were exceptions, with calculated hydroperiods of 1 and 3 days, respectively (**Table 4**). No regional difference in the location of the water-table (**Figure 8**) was found, however (ANOVA, $F_{1,14} = 1.810$, $P = 0.200$).

Trees & Saplings Dynamics:

A total of 42 different tree and sapling species were identified and recorded across all 16 tree islands (**Table 5**). The total number of woody species (≥ 1 cm DBH) per island ranged from, as few as 5 at SS-81 to as high as 17 at Grossman Hammock (**Table 5**). Tree and sapling species richness was significantly higher in WP tree islands (13.2 ± 1.3 (SE)) than in RS tree islands (7.4 ± 0.7 (SE)); repeated measure ANOVA $F_{1,13} = 14.4$, $P = 0.002$).

Tree and sapling importance values (IV) for all tree islands are shown in **Table 5**. Across all islands the most dominant species ($IV \geq 40\%$) were *Bursera simaruba* (BURSIM), *Celtis laevigata* (CELLAE), *Chrysobalanus icaco* (CHRICA), *Eugenia axillaris* (EUGAXI), *Myrsine floridana* (MYRFLO), *Nectandra coriacea* (NECCOR), & *Sideroxylon foetidissimum* (SIDFOE) (**Table 5**). For most RS tree islands, *E. axillaris* was the most dominant species with IV exceeding 45%. At SS-81, however, *C. laevigata* was the dominant species with an IV of 86% (**Table 5**). Within WP tree islands, no single species was dominant throughout the region but codominance between two species was observed at E4200 (*Sideroxylon salicifolium* (SIDSAL) & *M. floridana*) and at Mosquito Hammock (*Myrcianthes fragrans* (MYRFRA) & *Quercus virginiana* (QUEVIR); **Table 5**). In most cases, the IV of the dominant species in WP hammocks was well below 50% (**Table 5**). *E. axillaris*, the dominant species in RS tree islands, had an IV below 12% in all WP islands except Ficus Pond, where it dominated with an IV of 46% (**Table 5**).

A nonparametric multi-dimensional scaling (NMDS) ordination, based on importance value (IV) of woody species in tree and sapling strata, revealed that RS and WP tropical hardwood hammocks were somewhat different in plant community composition (**Figure 10**); in one year (2009), ANOSIM indicated significantly different forest composition between the two regions (ANOSIM; $R=0.561$; $P < 0.001$). In general, WP tree islands were richer in tree species than RS tree islands (**Figure 11**). The mean annual numbers of species per plot in WP and RS tree islands during 2007- 2009 were 13.2 and 7.4 species plot⁻¹, respectively. The size of plots might have influenced the number of species recorded in each tree island, but average plot size was about 400 m² in both regions (**Table 1**), suggesting little regional bias. The vectors representing soil depth (SoilDep), pH, total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), and non-C materials (Non-C) were all significantly

Table 5: Importance values (IV) for trees and saplings species. See **Appendix 2** for species code names.

Species Code	RS										WP					
	Black Hammock	Chekika Island	Gumbo Limbo Hammock	Irongrape	Manatee Hammock	Panther Mound	Satinleaf	SS-37	SS-81	Vulture Hammock	A4900	E4200	Ficus Pond	Grossman Hammock	Mosquito Hammock	NP205
ANNGLA	-	-	-	-	-	-	-	1.3	2.7	-	-	-	-	-	0.7	0.5
ARDESC	-	-	-	-	-	-	-	-	-	-	15.6	0.5	2.2	9.2	1.0	5.9
BURSIM	32.5	-	30.5	5.8	2.6	41.8	37.8	14.7	-	18.3	19.3	2.9	12.2	26.5	3.0	16.5
CAEBON	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-
CALPAL	-	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-
CARPAP	5.5	-	0.1	5.3	2.4	-	-	-	-	-	-	-	-	-	-	-
CELLAE	3.9	5.5	10.8	2.9	18.0	34.7	2.1	21.9	68.6	12.1	-	-	-	0.4	-	-
CHRIKA	3.5	-	0.1	-	0.5	-	3.3	3.4	-	1.8	1.9	-	6.2	0.3	1.0	4.7
CHROLI	-	-	-	-	-	-	7.2	-	-	0.1	-	-	0.2	1.0	-	-
CITAU	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
COCDIV	-	-	-	-	-	2.4	1.1	14.6	-	0.2	14.6	11.8	1.2	36.1	-	35.9
DIOVIR	-	-	-	-	-	-	-	-	-	-	3.5	-	-	-	-	-
ERYHER	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
EUGAXI	45.3	50.0	51.6	52.9	59.9	7.0	45.4	24.9	-	45.1	3.2	2.2	46.3	4.2	-	11.8
EXOPAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.7	-
FICAUR	5.3	-	-	-	-	4.5	1.6	0.7	27.6	-	0.9	0.6	-	1.9	0.8	7.9
FICCIT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2	1.0
ILEKRU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-
LYSLAT	-	-	-	-	-	-	-	-	-	-	28.3	-	-	-	-	2.5
MAGVIR	-	-	-	-	-	-	-	0.3	-	-	1.4	-	-	-	-	-
METTOX	-	-	-	-	-	-	-	-	-	-	-	1.4	6.4	-	12.6	-
MYRCER	-	-	-	-	-	-	-	0.3	-	-	1.7	-	-	-	2.2	-
MYRFLO	-	3.3	0.3	-	0.2	1.0	0.2	7.7	-	1.4	7.4	19.8	2.4	1.6	6.1	0.2
MYRFRA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	29.0	-
NECCOR	-	-	0.2	-	-	-	-	-	-	-	-	-	0.9	8.0	0.3	3.6
PERBOR	-	-	-	-	-	-	-	0.5	1.1	-	1.5	-	1.1	-	-	-
PRUMYR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6	-
PSIGUA	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-
QUEVIR	-	-	-	-	-	-	-	-	-	-	-	15.6	-	-	26.1	-
SABPAL	-	-	-	-	-	4.7	-	-	-	-	-	17.6	-	-	-	-
SALCAR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.1	-
SAMCAN	-	-	0.3	-	-	-	-	-	0.6	-	-	-	-	-	-	-
SAPSAP	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-
SCHCHR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5	-
SCHTER	-	-	0.1	-	-	-	-	-	-	0.1	-	5.8	-	2.7	-	-
SIDFOE	6.2	40.6	4.9	33.1	18.2	-	0.1	-	-	18.3	-	-	-	0.9	-	9.2
SIDSAL	-	-	-	-	-	-	-	-	-	-	0.3	22.0	23.5	1.4	5.9	-
SIMGLA	-	-	-	-	-	-	-	1.1	-	-	0.8	-	-	1.4	-	-
SOLERI	-	0.5	1.8	-	-	5.3	2.2	-	-	0.3	-	-	-	-	-	-
THRRAD	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
TREMIC	-	0.2	-	-	-	-	0.7	-	-	-	-	-	-	-	-	-
ZANFAG	-	0.1	-	-	-	-	-	9.5	-	-	-	-	-	1.9	-	0.5
Total # Species	7	8	11	6	7	8	11	13	5	12	16	11	11	17	18	13

correlated with the configuration scores in the ordination. Water-table depth was not significant, however (**Table 6**). The primary gradient along which RS and WP sites were separated was represented by increasing soil nitrogen and total organic matter toward the WP tree islands, and increasing soil depth, pH and total phosphorus toward the RS tree islands (**Figure 10**). In general, WP tree islands were richer in nitrogen and organic matter, whereas soil in RS tree islands were deeper, alkaline and rich in total phosphorus and non-C materials.

Table 6: List of variables for which vectors were fitted in the 2-dimensional NMDS ordination. For each variable, 'r' is the correlation between values of that variable and site scores on its fitted vector and p-value is from the permutation test for statistical significance of the correlation.

Variable	r	p-value	NMDS Axis-1	NMDS AXIS-2
Tree island height (IslandHt)	0.775	0.001	-0.622	0.783
Water-table Depth (Dist_WT)	0.337	0.265	-0.069	0.998
Soil depth (SoilDep)	0.794	0.001	-0.935	0.355
Soil nitrogen (TN)	0.718	0.008	0.949	-0.316
Soil phosphorus (TP)	0.709	0.009	-0.909	0.417
Soil pH (pH)	0.643	0.003	-0.977	0.213
Soil organic carbon (TOC)	0.687	0.015	0.928	-0.373
Soil Non-Carbon materials (Non-C)	0.634	0.026	-0.605	0.796
Species richness (SppRich)	0.830	0.000	0.817	-0.577
Shannon diversity (ShanDiv)	0.931	0.000	0.828	-0.560

During the sampling period (2001/02-2009), the relative abundance (species' importance value) of tree species (trees and saplings) in individual tree island plots did not vary significantly. Analysis of similarity (ANOSIM) also showed no significant differences in species composition between the five sampling events (2001/02, 2005/06, 2007, 2008 and 2009) ($R = 0.059$; $p > 0.05$). However, a change in *sapling* species composition in some RS tree islands, such as Black Hammock, Gumbo Limbo Hammock, Satinleaf, Chekika Island, and Panther Mound, was observed in post-hurricane years (**Figure 12**). In four RS tree islands for which pre-hurricane estimates of sapling density were available, there were more species in the sapling layer 1-2 years post-hurricane than before the hurricane (**Appendix 3**). In these islands, the mean number of sapling species were 3.8 and 6.5 species per plot in the pre-hurricane sampling year and in 2007 (2 years after the hurricane), respectively (**Figure 13**). However, across all six tree islands for which pre- and post hurricane sapling data were available,, representing both RS (4) and WP (2) landscapes, the effects of year on species richness and species diversity was not statistically significant (Repeated measure ANOVA). Nonetheless, several species that were newly present or in increasing abundance 1-2 years after hurricane were absent or in low abundance in the following years. For instance, *Carica papaya* (CARPAP) in Black Hammock, and *Solanum erianthum* (SOLERI) in Stainleaf were abundant in sapling layer in one or two post-hurricane years, but was subsequently rare. Similarly, *S. erianthum* and *Trema micranthum* (TREMIC) in Chekika, and *Myrsine floridana* in Satinleaf were present in the sapling layer only in the first two years after the hurricane (**Appendix 3**).

For the 3-year sampling period (2007-2009), the mean woody stem (≥ 1 cm dbh) density and basal area were $7,933 \pm 3,823$ (SE) stems ha^{-1} and 33.3 ± 15.8 (SE) $\text{m}^2 \text{ha}^{-1}$, respectively. While mean woody stem density did not significantly differ (Paired t -test; $P > 0.05$) between years, mean woody stem basal area was significantly higher in 2009 than in 2007 (Paired t -test; $df = 14$, $t = 2.8$, $P = 0.015$) and also 2008 (Paired t -test, $df = 15$, $t = 5.9$, $P < 0.001$) (**Figure 14**). Trees (≥ 5 cm dbh) constituted 18.0% of total stem density, but they contained 89.3% of total basal area. Mean tree density was lowest in Panther Mound (500 ± 25 (SE) trees ha^{-1}) and highest in Mosquito hammock ($2,242 \pm 80$ (SE) trees ha^{-1}). Mean tree (DBH ≥ 5 cm) basal area also varied greatly among islands, ranging from $4.9 \text{ m}^2 \text{ha}^{-1}$ in E4200 to $72.6 \text{ m}^2 \text{ha}^{-1}$ in Black Hammock (**Figure 15**).

WP tree islands had more trees (≥ 5 cm DBH) than RS tree islands during 2007-09 (**Figure 16**), while the latter had larger trees (**Figure 17**). However, differences in mean tree density and basal area between the regions over the three years (2007-2009) were not statistically significant (**Table 7**), in part because of among-year variability; the effects of Year on both tree density and basal area were significant (Repeated measures ANOVA; $F_{2,28} = 19.9$; $p < 0.001$; and $F_{2,28} = 6.7$; $p = 0.004$, respectively). Mean tree density in WP and RS tree islands, and basal area in WP tree islands were significantly higher in 2009 than in 2007 (Repeated ANOVA: Bonferroni test; Figure 16 and 17). Sapling density also exhibited temporal and spatial variation (**Figure 18**), but neither differences between regions nor between years were statistically significant (**Table 7**).

Table 7: Repeated measures analysis of variance (ANOVA) for tree density, tree basal area, and sapling density on tree islands in two regions sampled for three years (2007-2009).

Effects	Tree density				Tree basal area				Sapling density			
	df	F	<i>p</i>	Observed power	df	F	<i>p</i>	Observed power	df	F	<i>p</i>	Observed power
<i>Between-subjects Effects</i>												
Intercept	1	115.6	<0.001	1.000	1	53.6	<0.001	1.000	1	38.1	<0.001	1.000
Region	1	2.3	0.151	0.292	1	2.0	0.182	0.257	1	0.4	0.551	0.088
Error	14				14				13			
<i>Within-subjects Effects</i>												
Year	2	19.9	<0.001	0.999	2	6.7	0.004	0.885	2	0.3	0.744	0.093
Year • Region	2	1.3	0.288	0.258	2	1.4	0.265	0.274	4	1.2	0.322	0.236
Error	28				28				24			

Four RS tree islands and three WP tree islands had pre-hurricane sapling and tree data (**Table 1**). Three of the RS tree islands (Black Hammock, Gumbo Limbo Hammock, and Satinleaf) had pre-hurricane sapling and tree data, dating back to 2001/02, whereas pre-hurricane data was collected one to six months prior to Hurricane Wilma (2005) in the 4th RS tree island (Chekika Island) and all three WP tree islands (Ficus Pond, Grossman Hammock, and Mosquito Hammock). Likewise, the post-hurricane data on those islands were not from the

same year. For instance, RS tree islands were sampled from several months to one year after the hurricane, whereas WP tree islands were sampled in 2007, 2 years after Hurricane Wilma. Therefore, hurricane impacts on sapling and tree density and basal area in these islands were analyzed using pre-hurricane data, dating back to 2001/02 or collected 1-6 months prior to the hurricane, and post-hurricane data collected in 2007, 2008, & 2009.

In general, hurricane impacts on woody stem (i.e., trees and saplings) density and basal area were minimal. Although the WP tree islands had more trees than RS tree islands during both pre-hurricane and post-hurricane sampling years (**Figure 19**), differences in mean tree density and basal area between regions were not statistically significant (**Table 8**). However, there was a significant year effect on tree density ($F_{3, 15} = 5.6$; $P = 0.009$) and basal area ($F_{3, 15} = 3.76$; $P = 0.34$). Overall mean tree density on those islands in 2009 ($1,742 \pm 165$ (SE) trees ha^{-1}), four years after hurricane, was significantly (Repeated measures ANOVA; Bonferroni test) higher than in the pre-hurricane sampling year ($1,571 \pm 121$ (SE) trees ha^{-1}) and in 2007 ($1,561 \pm 149$ (SE) trees ha^{-1}). Likewise, mean basal area in 2009 (36.4 ± 7.1 (SE) $m^2 ha^{-1}$) was significantly higher than in the pre-hurricane sampling year (32.3 ± 7.4 (SE) $m^2 ha^{-1}$). On islands with pre- and post hurricane data, differences in mean sapling density between pre- and post-hurricane years were not statistically significant (**Table 8**).

Table 8: Repeated measures analysis of variance (ANOVA) for tree density, tree basal area, and sapling density on tree islands in two regions sampled in both pre- and post-hurricane years. Pre-hurricane data on three RS islands dated back to 2001/2002 and on 1 RS and 3 WP islands were from 1-6 months prior to the Hurricane Wilma. Post-hurricane data were from 2, 3 and 4 years after the hurricane.

Effects	Tree density				Tree basal area				Sapling density			
	df	F	<i>p</i>	Observed power	df	F	<i>P</i>	Observed power	df	F	<i>p</i>	Observed power
<i>Between-subjects Effects</i>												
Intercept	1	173.0	<0.001	1.000	1	25.9	0.004	0.838	1	60.2	0.001	1.000
Region	1	3.2	0.135	0.305	1	2.7	0.163	0.348	1	0.4	0.540	0.082
Error	5				5				4			
<i>Within-subjects Effects</i>												
Year	3	5.60	0.009	0.867	2	3.76	0.034	0.694	3	0.02	0.995	0.053
Year • Region	3	1.39	0.283	0.218	2	0.05	0.984	0.057	3	0.31	0.820	0.093
Error	15				15				12			

Tree density and basal area on any island are functions of tree mortality and in-growth during the preceding period. Mean annual tree mortality on our 16 tree islands during 2001/02-2009 was 3.1%. In the two years between 2007 and 2009, the annual mean percent tree mortality in RS tree islands was significantly higher (One way ANOVA: $F_{1,14}=27.3$; $P < 0.001$) than in WP tree islands (**Figure 20**). These results were not unexpected, as several RS islands exhibited visible damage from Hurricane Wilma in 2005. In the three RS tree islands (Black Hammock, Gumbo Limbo, and Satinleaf) for which pre-hurricane data was available, the mean annual tree mortality between 2001/02 and 2005/06 was 4.6 %, with Gumbo Limbo Hammock experiencing higher mortality rates than Black Hammock or Satinleaf (**Figure 21**). However, it should be noted that the cumulative mortality on these tree islands over the period in question was confounded, as it included both background mortality from the four year period prior to the hurricanes, and hurricane-caused mortality. In post-hurricane years,

tree mortality varied among islands over the sampling years (**Table 9**). On several islands (Black Hammock, Chekika Island, Gumbo Limbo Hammock, and Satinleaf) that experienced significant hurricane damage, tree mortality was especially high in 2008 (**Table 9**). Moreover, the other six RS islands (Irongrape, Manatee Hammock, Panther Mound, SS-37, SS-81 and Vulture Hammock) which exhibited varying impacts from the hurricane, mortality was highest in 2009. Elevated rates of mortality on these islands 3-4 years after a hurricane suggest delayed, hurricane-related mortality, perhaps accentuated by the effects of drought that prevailed between 2006 and 2008 (**Figures 4 & 5**).

Table 9: Annual tree mortality (%) on 16 islands sampled between 2001 and 2009.

Island	Annual tree mortality (%)			
	2001/02 - 2005/06	2005/06 - 2007	2007 - 2008	2008 - 2009
A4900			0.0	0.0
Black Hammock	3.5	0.0	6.2	1.4
Chekika Island		5.6	10.9	1.6
E4200			0.0	0.0
Ficus Pond		2.6	0.0	2.6
Grossman Hammock		0.0	1.6	0.0
Gumbo Limbo Hammock	6.8	3.8	13.7	0.0
Irongrape			4.5	4.8
Manatee Hammock		7.1	1.8	5.5
Mosquito Hammock		1.1	2.1	1.0
NP205			0.0	2.4
Panther Mound		0.0	4.8	5.0
Satinleaf	3.4	0.0	5.4	1.0
SS-37			0.0	6.7
SS-81			0.0	4.3
Vulture Hammock		0.0	0.0	6.2

In both 2008 and 2009 sampling years, mean tree ingrowth was significantly higher (paired t -test, $P < 0.001$) than mean tree mortality (**Figure 22**). During this period mean tree mortality also differed significantly between the RS and WP landscapes (**Table 10**). Mean tree mortality on RS and WP islands were 48 and 16 trees $\text{ha}^{-1} \text{yr}^{-1}$, respectively. Mean annual tree ingrowth, however, did not differ between regions. Likewise, the effects of Year on both mortality and ingrowth were not statistically significant. However, there was an increasing trend in mean ingrowth in 2007-08 and 2008-09 (**Figure 23**).

Both mortality and ingrowth were inversely related to water-table depth. Considering all 16 tree islands, mean annual mortality averaged over the two-year period 2007-09) significantly decreased ($r = -0.59$; $p = 0.01$) with increasing mean water-table depth, i.e., mortality was highest on islands where the mean water-table was far below the ground (**Figure 24a**). Tree ingrowth showed a similar trend, though the relationship between ingrowth and water-table depth was not significant ($r = -0.30$, $p = 0.255$) (**Figure 24b**). Thus, demographic turnover in the tree community was highest in RS islands in which the water table was recessed farthest from the surface.

Table 10: Repeated measures analysis of variance (ANOVA) for tree mortality (number of dead trees $\text{ha}^{-1} \text{yr}^{-1}$) and ingrowth (the number of new trees of $\text{dbh} \geq 5 \text{ cm} \text{ ha}^{-1} \text{yr}^{-1}$) on 16 tree islands in RS and WP landscapes sampled in 2008 and 2009.

Effects	Tree mortality				Tree ingrowths			
	df	F	<i>p</i>	Observed power	df	F	<i>p</i>	Observed power
Intercept	1	39.49	<0.001	1.000	1	44.06	<0.001	1.000
Region	1	10.43	0.006	0.851	1	0.05	0.830	0.055
Error	14				14			
Year	1	0.01	0.916	0.051	1	1.56	0.233	0.213
Year • Region	1	0.29	0.599	0.079	1	0.09	0.764	0.059
Error	14				14			

Forest Canopy Dynamics:

Maximum Canopy Height & Volume:

Between 2007 and 2009, the mean maximum canopy height for the 16 study tree islands was approximately $11.5 \text{ m} \pm 1.53 \text{ (SD)}$. Within the RS landscape, mean maximum canopy height averaged $12.8 \text{ m} \pm 0.32 \text{ (SE)}$ while in adjacent wet prairies (WP tree islands) mean maximum canopy height averaged $10.1 \text{ m} \pm 0.45 \text{ (SE)}$. This difference in mean maximum canopy height between regions was significant (repeated measures ANOVA, $F_{1,14} = 9.187$, $P = 0.009$ after Bonferroni correction). Interannual variation in mean maximum canopy height between 2007 and 2009 were uniform and showed similar patterning within years (**Figure 25**). These interannual oscillations in the mean maximum canopy height within regions are the result of natural variations in yearly tree heights within individual stands (**Table 11**). Maximum canopy heights within individual tree islands, in general, do not appear to have been significantly affected by either Hurricane Katrina or Wilma (**Table 11**). However, maximum canopy height did decrease slightly in three tree islands following the hurricanes. Two tree islands, Gumbo Limbo Hammock and SS-37, showed a slight decrease in maximum canopy height two and three years after Hurricanes Katrina and Wilma (**Table 11**) but, given the timing, it is unlikely that this change in mean maximum canopy height was a direct effect of the hurricanes (**Table 11**). On the other hand, the change in maximum canopy height observed between 2005/06 and 2007 (12 m vs 9 m, respectively) at Grossman Hammock (WP tree island) does appear to be hurricane related (**Table 11**).

Between 2007 and 2009, mean canopy volume per square meter of ground surface for the 16 study tree islands was approximately $4.92 \pm 1.54 \text{ m}^3 \text{ m}^{-2} \text{ (SD)}$. During this period, the mean canopy volume of RS tree islands was $4.96 \pm 0.27 \text{ m}^3 \text{ m}^{-2} \text{ (SE)}$ while WP tree islands averaged $4.87 \pm 0.24 \text{ m}^3 \text{ m}^{-2} \text{ (SE)}$. This difference in mean canopy volume between regions was not significant at $P > 0.05$. However, overall yearly canopy volume for all tree islands was significantly higher in 2009 than in 2007 (repeated measures ANOVA, $F_{2,14} = 0.006$ $P = 0.009$ after Bonferroni correction). Interannual variation in mean canopy volume was evident (**Figure 26**). In general, mean canopy volume increased yearly for RS tree islands. However, for WP tree islands, mean canopy volume decreased slightly between 2007 and 2008 (**Figure 26**). However, by 2009 mean canopy volume in both regions were higher than they had been originally in 2007 (**Figure 26**).

Table 11: Tree island canopy structure in ridge and slough (RS) & wet prairie (WP) tree islands. Parameters include the canopy volume ($\text{m}^3 \text{m}^{-2}$), leaf area index (LAI), maximum canopy height (m), skewness of the canopy height distribution, the number of 1-meter height intervals occupied from 2-16 m (richness), and the foliage height diversity (H') & evenness (J') of the canopy height distribution.

Group	Year	Tree Island	Canopy Volume $\text{m}^3 \text{m}^{-2}$	LAI	Maximum Canopy Height (m)	Canopy Skewness	Canopy Richness	Foliage Height Diversity (H')	Foliage Height Evenness (J')
RS	2002	Black Hammock	5.24	-----	12	-0.02	10	2.20	0.96
	2005/06	Black Hammock	4.31	2.39	11	-0.09	9	2.13	0.97
	2007	Black Hammock	4.75	2.65	13	-0.29	11	2.24	0.93
	2008	Black Hammock	5.13	2.82	13	-0.16	11	2.28	0.95
	2009	Black Hammock	5.44	2.71	13	-0.06	11	2.25	0.94
	2005/06	Chekika Island	6.56	0.86	14	-0.80	12	2.42	0.97
	2007	Chekika Island	6.06	2.35	15	-0.61	13	2.46	0.96
	2008	Chekika Island	5.94	2.56	14	-1.04	12	2.43	0.98
	2009	Chekika Island	6.56	2.10	15	-1.25	13	2.49	0.97
	2002	Gumbo Limbo Hammock	6.78	-----	12	-0.52	10	2.23	0.97
	2005/06	Gumbo Limbo Hammock	4.44	1.72	15	0.44	13	2.36	0.92
	2007	Gumbo Limbo Hammock	3.64	1.97	13	-0.62	11	2.31	0.97
	2008	Gumbo Limbo Hammock	5.92	2.70	14	0.18	12	2.30	0.93
	2009	Gumbo Limbo Hammock	5.48	2.61	13	-0.40	11	2.31	0.96
	2007	Irongrape	4.13	-----	13	0.66	11	2.25	0.94
	2008	Irongrape	2.93	2.32	12	-0.15	10	2.22	0.97
	2009	Irongrape	3.50	2.56	13	-0.31	11	2.30	0.96
	2006	Manatee Hammock	5.19	2.69	12	0.39	10	2.03	0.88
	2007	Manatee Hammock	4.63	3.06	12	-0.05	10	2.23	0.97
	2008	Manatee Hammock	6.00	2.64	14	-0.68	12	2.37	0.95
	2009	Manatee Hammock	8.00	2.24	14	-0.50	12	2.36	0.95
	2005/06	Panther Mound	4.19	1.29	14	0.15	12	2.26	0.91
	2007	Panther Mound	4.00	2.09	12	-0.87	10	2.29	1.00
	2008	Panther Mound	4.06	-----	14	-0.19	12	2.38	0.96
	2009	Panther Mound	5.06	2.26	13	0.15	11	2.27	0.95
	2001	Satinleaf	4.63	-----	11	0.55	9	2.02	0.92
	2005	Satinleaf	4.20	1.10	13	0.66	11	2.21	0.92
	2007	Satinleaf	5.72	3.26	13	-0.20	11	2.23	0.93
	2008	Satinleaf	7.04	3.22	13	-0.36	11	2.27	0.95
	2009	Satinleaf	6.48	2.92	13	-0.35	11	2.30	0.96
	2007	SS-37	2.73	2.21	10	1.25	7	1.81	0.93
	2008	SS-37	2.25	3.01	8	0.83	6	1.73	0.97
	2009	SS-37	3.67	2.56	8	1.16	6	1.67	0.93
	2007	SS-81	2.91	2.24	11	1.30	9	1.94	0.88
	2008	SS-81	3.50	2.76	12	1.29	10	1.95	0.85
	2009	SS-81	4.50	1.95	12	0.61	10	2.05	0.89
	2005/06	Vulture Hammock	6.94	-----	14	-0.76	12	2.37	0.95
	2007	Vulture Hammock	5.31	2.90	14	-0.71	12	2.44	0.98
	2008	Vulture Hammock	5.31	3.01	15	-0.87	13	2.48	0.97
	2009	Vulture Hammock	8.00	2.53	16	-0.70	14	2.53	0.96
	2007	A4900	5.25	3.16	10	0.04	8	2.04	0.98
	2008	A4900	5.00	3.02	11	-0.06	9	2.12	0.96
	2009	A4900	6.19	2.57	11	0.17	9	2.06	0.94
	2007	E4200	1.22	0.83	7	1.12	5	1.55	0.96
	2008	E4200	2.40	0.87	6	2.40	4	1.22	0.88
2009	E4200	1.51	0.74	7	1.51	5	1.49	0.93	
2005/06	Ficus Pond	4.82	2.87	11	0.56	9	2.05	0.93	
2007	Ficus Pond	6.56	3.47	11	0.10	9	2.07	0.94	
2008	Ficus Pond	4.78	3.39	8	0.60	6	1.76	0.98	
2009	Ficus Pond	6.78	2.74	13	0.21	11	2.18	0.91	
2005/06	Grossman Hammock	5.00	2.35	12	0.49	7	1.82	0.93	
2007	Grossman Hammock	4.88	3.07	9	0.33	7	1.91	0.98	
2008	Grossman Hammock	5.88	3.31	11	0.25	9	2.01	0.92	
2009	Grossman Hammock	6.13	2.22	10	0.24	8	1.99	0.96	
2005/06	Mosquito Hammock	5.34	2.11	11	0.11	9	2.05	0.93	
2007	Mosquito Hammock	6.12	2.54	12	0.04	10	2.13	0.93	
2008	Mosquito Hammock	5.06	2.81	11	0.14	9	2.04	0.93	
2009	Mosquito Hammock	4.78	2.06	11	0.19	9	2.10	0.96	
2007	NP205	4.56	2.81	11	-0.04	9	2.10	0.96	
2008	NP205	4.00	2.90	11	0.00	9	2.14	0.97	
2009	NP205	6.50	2.68	12	0.04	10	2.13	0.93	

Canopy Closure & Leaf Area Index (LAI):

Between 2007 and 2009, mean canopy closure and LAI were $87.2\% \pm 1.94(\text{SD})$ and $2.56 \pm 0.21 (\text{SD})$, respectively. Forest canopy closure within RS tree islands averaged $88.7\% \pm 1.07 (\text{SE})$ and were slightly higher than those of WP tree islands, which averaged $85.3\% \pm 1.26 (\text{SE})$. Similarly to the observed pattern in forest canopy closure, LAI, was on average, lower in WP tree islands than RS tree islands; $2.51 \pm 0.17 (\text{SE})$ & $2.59 \pm 0.10 (\text{SE})$, respectively. These differences in both canopy closure and LAI between regions were not significant $P > 0.05$ (repeated measures ANOVA). Interannual variations between 2007 and 2009 in the hemispherical photograph-derived estimates of tree island forest canopy closure and LAI are shown in **Figure 27** & **Figure 28**. RS & WP tree islands saw a yearly increase in mean canopy closure and LAI between 2007 and 2008 (**Figure 27** & **28**). However, between 2008 and 2009, mean canopy closure and LAI decreased within both regions (**Figure 27** & **28**) and were either similar to or lower than they had been originally in 2007 (**Figure 27** & **28**), two years post Hurricane Katrina and Wilma.

Between 2005 and 2008, forest canopy closure for individual tree islands increased as function of time since Hurricane Katrina and Wilma (**Figure 29**). However, between 2008 and 2009, forest canopy closure decreased slightly across all islands, except for Irongrape in RS (**Figure 29**). Unequivocally, E4200 had the lowest forest canopy closure value of all tree island plots regardless of region or year (**Figure 29**). This marked contrast in forest canopy closure between E4200 and the rest of the tree islands in this study is a result of a significant portion of the plot in E4200 lying within a forest/canopy gap. These forest gaps are not uncommon in WP tree islands, since they are very susceptible to fires. Fires within this pyrogenic landscape can consume significant portions of forest biomass and oxidize what little soil may exist (see **Table 4**), which ultimately affects the amount of rooting medium or suitable substrate available for the recruitment, growth, and survival of new individuals following a fire. As a result, many tree islands within the WP landscape have canopy forest gaps characterized by shallow soils and exposed bedrock.

Densiometer estimates of forest canopy closure in the two intensive sampling tree islands plots, Grossman Hammock (WP) and Satinleaf (RS), established prior to or just shortly after the 2005 hurricanes, show a substantial hurricane effect on canopy closure (**Figure 30**). Prior to Hurricane Katrina, forest canopy closure at Grossman Hammock was estimated at 89%, a value slightly lower than the 3-year mean for this tree island between Jan 2007 and Nov 2009 (**Figure 30**). A month after Hurricane Katrina, however, forest canopy closure had decreased slightly to 85%. A month later, following Hurricane Wilma, forest canopy closure at Grossman Hammock decreased considerably to 67% while at Satinleaf the estimated canopy closure was 48% (**Figure 30**). By March 2007, forest canopy closure increased above 90% in both islands, which have remained close to that value ever since (**Figure 30**).

Vertical Canopy Profile –Richness, Skewness, Diversity, and Evenness:

Between 2006 and 2009, the vertical canopy profile of all 16 tree island plots displayed distinct interannual and regional variations in the vertical distribution of foliage within the

canopy (**Figure 31 & 32a & 32b**), leading to notable difference in canopy richness, skewness, diversity (H'), & evenness (J') (**Table 11**). Tree island canopy richness, which represents the total number of 1-m vertical intervals occupied by the canopy, was, with one exception, (SS-37) higher in RS tree islands than in WP tree islands (**Figure 33a**), paralleling the results reported above for mean canopy height. Mean canopy richness was significantly different (repeated measures ANOVA, $F_{1,14} = 7.070$, $P = 0.019$) and higher in RS tree islands (10.5) than in WP tree islands (8). Vulture Hammock, in RS, had the highest canopy richness value of all tree islands with 14 1-m intervals of canopy occupancy while E4200, a WP tree island, had the lowest canopy richness with 4 1-m intervals of canopy occupancy (**Table 11**). Canopy skewness, which is a measure of canopy asymmetry, varied within and across regions (**Figure 33b**) and is indicative of the high variability in tree island canopy structure within the Everglades as a result of divergent histories and successional age or stage. Most often, canopy skewness of RS tree islands were negatively skewed (mean = -0.098) while canopy skewness for WP tree islands were positively skewed (mean = 0.404). This difference between regions was not significant at $P > 0.05$ (repeated measures ANOVA) but is indicative of a higher percentage of canopy occupancy within the lower forest stratum in WP tree islands than in RS tree islands (**Figure 31, 32a, 32b, & 33**). Canopy diversity (H'), which incorporates richness and evenness components in the vertical canopy profile, was significantly different (repeated measures ANOVA, $F_{1,14} = 5.605$, $P = 0.033$) and higher in RS tree islands (2.24) than in WP tree islands (1.95) and reflect the same pattern observed for mean canopy richness (**Figure 33a & 33c**). Canopy evenness (J'), which quantifies the variability in stratum occupancy for the entire vertical canopy profile of each tree island, on the other hand, was nearly identical for both RS and WP tree islands, 0.948 and 0.945, respectively, and showed very little variation among islands except for SS-81, where mean canopy evenness averaged 0.87 (**Figure 33d**).

Pre- and post-hurricane differences in the vertical canopy profiles for the three RS tree islands with data extending back to 2001/02 (Black Hammock, Gumbo Limbo Hammock, and Satinleaf) show differentiating temporal patterns between 2001/02 and 2005/06 and between 2005/06 and 2009 (**Figure 34**). Between the pre (2001/02) and immediate post-hurricane phase (2005/06), canopy volume for all three tree islands decreased from an average of $5.55 \text{ m}^3 \text{ m}^{-2}$ to $4.31 \text{ m}^3 \text{ m}^{-2}$. However, by 2009, average canopy volume for all three tree islands had increased to $5.80 \text{ m}^3 \text{ m}^{-2}$. Canopy skewness varied as well during this period (**Table 11**). In Black Hammock and Gumbo Limbo Hammock, the pre-hurricane vertical canopy profile was negatively skewed while in Satinleaf the skew was positive. Following the hurricanes, however, canopy skewness at Black Hammock became slightly more negative while at Gumbo Limbo Hammock and Satinleaf it became positive. By 2009, 4-years post-hurricane Katrina and Wilma, the canopy skewness for all three tree islands had become negative in response to a general increase in the total number of upper canopy strata occupied as the canopies in these three tree islands recovered, developed and reorganized following hurricanes Katrina and Wilma. In contrast, the vertical canopy profile for the three WP tree islands plots (Ficus Pond, Grossman Hammock, & Mosquito Hammock), which were established and sampled in 2005, prior to Hurricane Katrina and Wilma, showed no significant visual change in structure between 2005/06 and 2007 and between 2007 and 2009 (**Figure 34**). Canopy volume, however, at Ficus Pond and Mosquito Hammock increased substantially between 2005/06 and 2007 from $4.82 \text{ m}^3 \text{ m}^{-2}$ to $6.56 \text{ m}^3 \text{ m}^{-2}$ and from 5.34 m^3

m⁻² to 6.12 m³ m⁻², respectively, while canopy volume at Grossman Hammock decreased slightly from 5.00 m³ m⁻² to 4.88 m³ m⁻², paralleling the post-hurricane decrease observed in the three RS tree islands (**Table 11**). Between 2007 and 2009, canopy volume at Ficus Pond and Grossman Hammock increased to 6.78 m³ m⁻² and 6.13 m³ m⁻², respectively, while the canopy volume in Mosquito Hammock decreased to 4.78 m³ m⁻² (**Table 11**). Unlike the three RS tree islands, the canopy skewness of all tree WP tree islands did not change much as a result of the 2005 hurricane season and remained positive throughout the 4-year period (**Table 11**).

Understory Vegetation – understory vegetation cover (shrubs & herbs) and tree seedlings:

Understory Vegetation Cover (shrubs and herbs):

Regional and yearly differences in mean understory vegetation cover between 2007 and 2009 in RS and WP tree islands were not statistically significant (repeated measures ANOVA, $F_{1,14} = 1.210$, $P = 0.290$; $F_{2,28} = 0.981$, $P = 0.386$). Furthermore, regional differences in mean understory vegetation cover between years (2007-09) were also not significant (repeated measures ANOVA, $F_{2,28} = 2.023$, $P = 0.151$). On average, however, mean understory vegetation cover for RS tree islands were slightly higher than that of WP tree islands, with yearly averages 1.8X, 1.1X, and 1.3X greater in RS tree islands than in WP tree islands for 2007, 2008, & 2009, respectively (**Figure 35**).

Bi-monthly understory vegetation cover for the three high frequency sampling islands, i.e., Chekika Island, Grossman Hammock, and Satinleaf, paralleled each other between Jul 2007 and May 2009 (**Figure 36**). During this period, mean understory vegetation cover for the three tree islands decrease from a combined average of 32%, at the beginning of the period, to approximately 13% at the end (**Figure 36**). However, during the last six-months of 2009, total understory vegetation cover at Chekika Island and Grossman Hammock increased from 14% and 9% to 65% and 56%, respectively, while understory vegetation cover at Satinleaf Hammock remained stable at about 13% (**Figure 36**).

Tree Seedlings:

Across all 16 tree islands, a total of 36 different species of tree seedlings were observed in our network of 1 m² sub-plots (**Table 12**). The total number of tree seedling species per island ranged from five at SS-81 to 17 at Grossman Hammock (**Table 12**). Seedling species richness was significantly higher in WP tree islands (11.1 ± 0.7 (SE)) than in RS tree islands (8.1 ± 0.4 (SE)); repeated measure ANOVA $F_{1,14} = 7.471$, $P = 0.016$).

Table 12: Tree seedling importance values (IV) and total number of species. See **Appendix 2** for species code names.

Species Code	RS										WP					
	Black Hammock	Chekika Island	Gumbo Limbo Hammock	Irongrape	Manatee Hammock	Panther Mound	Satinleaf	SS-37	SS-81	Vulture Hammock	A4900	E4200	Ficus Pond	Grossman Hammock	Mosquito Hammock	NP205
ANGLA	-	-	< 0.1	-	-	0.4	-	-	2.3	-	-	-	-	-	-	-
ARDESC	-	-	-	-	0.4	-	-	-	-	-	37.4	0.3	0.1	3.2	4.7	9.4
BURSIM	1.3	-	0.2	-	11.2	4.1	2.4	2.9	-	0.2	1.5	0.4	-	0.2	0.1	1.2
CAEBON	0.1	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
CALPAL	-	-	-	-	-	-	-	-	-	-	-	-	-	2.3	-	-
CARPAP	-	-	-	-	0.5	-	0.1	-	-	-	-	-	-	-	-	-
CELLAE	0.3	20.4	1.3	1.9	24.8	5.1	1.6	5.8	88.2	3.4	-	-	-	-	-	-
CHRICA	2.3	0.1	0.1	0.2	5.0	0.8	2.2	26.9	-	5.4	2.9	-	58.6	0.2	2.0	15.1
CHROLI	-	-	-	-	-	-	3.1	-	-	0.3	-	-	-	0.1	-	-
COCDIV	-	-	-	-	-	-	< 0.1	2.5	-	-	4.4	18.0	2.9	2.0	-	1.7
DIOVIR	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-
EUGAXI	87.0	68.6	98.1	85.3	53.8	87.2	90.3	49.9	-	84.2	29.1	8.6	34.5	13.4	-	44.9
EXOPAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23.7	-
FICAUR	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
HAMPAT	-	-	-	-	-	-	-	-	-	-	-	-	-	< 0.1	-	-
ILECAS	-	-	-	-	-	-	-	-	-	-	1.3	-	-	-	-	-
LYSLAT	-	-	-	-	-	-	-	-	-	-	2.2	-	-	-	-	1.5
MAGVIR	-	-	-	-	-	-	< 0.1	-	-	-	-	-	-	-	-	-
METTOX	-	-	-	-	-	-	-	-	-	-	0.5	6.3	0.3	-	8.2	2.0
MYRCER	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-	2.3	-
MYRFLO	0.1	6.8	< 0.1	-	0.7	-	< 0.1	9.1	-	0.9	12.2	45.9	0.4	2.6	8.7	0.5
MYRFRA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.7	-
NECCOR	0.3	-	-	-	-	-	-	-	-	0.2	-	-	0.4	71.7	3.0	19.5
PERBOR	-	-	< 0.1	-	-	-	0.1	0.7	2.0	-	5.6	0.3	-	-	0.1	0.2
QUEVIR	-	-	-	-	-	-	-	-	-	-	-	4.9	-	0.1	34.7	-
SABPAL	0.4	-	-	-	1.1	1.3	-	0.1	-	-	-	-	-	-	0.1	-
SAMCAN	-	-	< 0.1	-	-	-	-	-	1.1	-	-	-	-	-	-	-
SAPSAP	-	-	-	-	-	-	-	-	-	-	-	-	-	< 0.1	-	-
SCHACT	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-
SCHCHR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.6	-
SCHTER	-	0.1	-	-	-	-	-	-	6.5	-	-	7.0	-	3.1	-	-
SIDFOE	8.1	0.5	0.1	12.3	2.0	-	-	-	-	5.3	-	-	-	< 0.1	-	3.5
SIDSAL	-	-	-	-	-	-	-	-	-	-	0.2	8.3	2.8	-	0.9	0.7
SIMGLA	-	-	-	-	-	-	-	1.4	-	-	1.2	-	-	0.2	-	-
SOLERI	-	3.5	0.1	-	0.3	1.2	0.2	-	-	-	-	-	-	-	-	-
ZANFAG	-	-	-	-	-	-	-	0.7	-	-	0.2	-	-	0.4	-	-
Total # Species	9	7	10	6	10	7	11	10	5	8	15	10	8	17	14	12

Species importance values (IV) based on seedling densities are presented for all islands in **Table 12**. Within RS tree islands, *E. axillaris* (EUGAXI) was by far the most important tree seedling with average IV of 70.4. At Gumbo Limbo Hammock and Satinleaf, *E. axillaris* seedling densities dwarfed all other species with IVs of 98.1 and 90.3, respectively. However, at SS-81, where *E. axillaris* was never observed, *C. laevigata* (CELLAE) was the

dominant seedling with an IV of 88.2. In contrast, for all other RS tree islands, the average IV of *C. laevigata* was 7.2. Within WP tree islands, no single species was dominant throughout the region. With the exception of *Nectandra coriacea* (NECCOR) in Grossman Hammock (IV = 71.7), the IV value of the dominant tree seedling species within this region were below 60. *E. axillaris*, which was present in all WP tree islands except Mosquito Hammock, was the dominant tree seedling species at NP205 with an IV of 44.9. At A4900, *Ardisia escallonioides* (ARDESC) and *E. axillaris* were co-dominant with IVs of 37.4 and 29.1, respectively. At Ficus Pond, *Chrysobalanus icaco* (CHRICA) was the dominant tree seedling species with an IV of 58.6, while at Mosquito Hammock *Quercus virginiana* (QUEVIR) was the dominant tree seedling (IV = 34.7). At E4200, *Myrsine floridana* (MYRFLO) was the dominant tree seedling species with an IV of 45.9 (**Table 12**).

Total tree seedling densities were greater in 2008 ($328,673 \pm 80,275$ (SE) stems ha⁻¹) than in 2007 ($236,674 \pm 70,953$ (SE) stems ha⁻¹) or 2009 ($265,698 \pm 94,190$ (SE) stems ha⁻¹), but the effect of Year was not significant (repeated measures ANOVA, $F_{2,28} = 1.150$, $P = 0.331$). Moreover, in the effect of Region on tree seedling density was also not significant (repeated measures ANOVA, $F_{2,28} = 0.884$, $P = 0.424$), even though seedlings densities were 2.9X, 3.9X, & 5.1X greater in RS tree islands than in WP tree islands in 2007, 2008, & 2009, respectively (**Figure 37**).

Independent of region, between 2007 and 2009, mean seedling densities varied from a mean low of 30,386 stems ha⁻¹ at E4200 to as high as 1,161,000 stems ha⁻¹ at Gumbo Limbo Hammock (**Figure 38**). Within regions, Gumbo Limbo Hammock had the highest mean seedling densities of all RS tree islands, while Grossman Hammock topped the list for all WP tree islands with a mean seedling density of 174,400 stems ha⁻¹. In contrast, SS-81 (49,306 stems ha⁻¹) and E4200 had the lowest seedling densities for RS and WP tree islands, respectively.

The three stands sampled at bimonthly intervals displayed marked differences in trend over time (**Figure 39**). In each island, densities remained relatively constant between Jan 2006 and Jul 2007, with little seasonal variations. However, starting in May 2007, seedling densities at Chekika Island and Satinleaf increased while at Grossman Hammock the opposite trend was observed. At Chekika Island, seedling densities increased by nearly 5X between May 2007 (87,500 stems ha⁻¹) and March 2008 (405,000 stems ha⁻¹) but since then have decreased gradually to densities similar to their initial level in 2006. Seedling densities at Satinleaf increased by 11X between May 2007 and Jan 2008, when they peaked at 850,000 stems ha⁻¹ and have remained relatively high ever since. In contrast, seedling densities at Grossman hammock have gradually decreased over time and are now much lower than they were at the start of the census period in Jan 2006 (**Figure 39**).

Predictive Models: understory vegetation cover and seedling densities

Predictive models (multiple regression) for understory vegetation cover and seedling densities using LAI yielded mixed results (**Figure 40**). LAI failed to predict understory

seedling densities (**Figure 40a**). However, understory vegetation cover was negatively correlated to LAI (**Figure 40b**).

Litterfall & Ground Litter Biomass:

Between 2007 and 2009, mean litterfall production for the three high frequency sampling islands averaged $6,630 \text{ kg ha}^{-1} \text{ yr}^{-1}$. During this 3-year period, mean annual litterfall production was significantly lower in 2007 ($5319 \pm 537 \text{ (SE) kg ha}^{-1} \text{ yr}^{-1}$) than in 2008 ($7,179 \pm 724 \text{ (SE) kg ha}^{-1} \text{ yr}^{-1}$; paired t -test(2) = -8.449, $P = 0.014$) or 2009 ($7,392 \pm 561 \text{ (SE) kg ha}^{-1} \text{ yr}^{-1}$; paired t -test(2) = -83.303, $P < 0.001$) (**Table 13**). Mean tree island litterfall production increased monotonically in all tree islands, except for Satinleaf in 2009 ($8,072 \text{ kg ha}^{-1} \text{ yr}^{-1}$) when litterfall production was slightly less than it had been in 2008 ($8,263 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (**Table 13**). Between islands, mean litterfall production was significantly lower at Chekika Island than at Grossman Hammock (paired t -test(2) = -27.7, $P = 0.001$) or Satinleaf (paired t -test(2) = -8.5, $P < 0.014$) (**Table 13**).

Table 13: Mean litterfall production, ground litter biomass, and litter turnover rates for Chekika Island, Grossman Hammock, and Satinleaf between 2007 and 2009. Mean with same superscripts do not differ at $P > 0.05$.

Tree Island	Mean Litterfall Production ($\text{kg ha}^{-1} \text{ yr}^{-1}$)			
	2007	2008	2009	Mean
Chekika Island	4256.0	5806.3	6279.1	$5447 \pm 611 \text{ (SE)}^a$
Grossman Hammock	5725.1	7469.4	7825.3	$7007 \pm 649 \text{ (SE)}^b$
Satinleaf	5977.3	8263.3	8072.2	$7437 \pm 732 \text{ (SE)}^b$
Mean	$5319 \pm 537 \text{ (SE)}^a$	$7179 \pm 724 \text{ (SE)}^b$	$7392 \pm 561 \text{ (SE)}^b$	6630
	Mean Ground Litter Biomass (kg ha^{-1})			
	2007	2008	2009	Mean
Chekika Island	5843.1	4239.7	6630.2	$5571 \pm 703 \text{ (SE)}^{ab}$
Grossman Hammock	3849.9	4754.3	6575.5	$5060 \pm 802 \text{ (SE)}^a$
Satinleaf	5495.1	5669.2	7980.6	$6382 \pm 801 \text{ (SE)}^b$
Mean	$5062 \pm 615 \text{ (SE)}^{ab}$	$4888 \pm 418 \text{ (SE)}^a$	$7062 \pm 460 \text{ (SE)}^b$	5671
	Mean Litter Turnover Time (months)			
	2007	2008	2009	Mean
Chekika Island	16.4	8.8	12.6	$12.6 \pm 2.2 \text{ (SE)}^a$
Grossman Hammock	8.1	7.6	10.1	$8.6 \pm 0.8 \text{ (SE)}^a$
Satinleaf	11.0	8.2	11.9	$10.4 \pm 1.1 \text{ (SE)}^a$
Mean	$11.8 \pm 2.5 \text{ (SE)}^{ab}$	$8.2 \pm 0.3 \text{ (SE)}^a$	$11.5 \pm 0.8 \text{ (SE)}^b$	10.5

Between 2007 and 2009, mean ground litter biomass, at the three high frequency sampling islands averaged $5,671 \text{ kg ha}^{-1}$ (**Table 13**). Mean annual ground litter biomass was significantly lower in 2008 ($4,888 \pm 418 \text{ (SE) kg ha}^{-1}$) than in 2009 ($7,062 \pm 460 \text{ (SE) kg ha}^{-1}$) (paired t -test(2) = -12.2, $P < 0.007$) while annual differences between 2007 and 2008 and between 2007 and 2009 were not significant at $P > 0.05$. During this 3-year period, mean

ground litter biomass increased yearly at Grossman Hammock and Satinleaf while, decreasing at Chekika Island between 2007 and 2008. Between islands, mean annual ground litter biomass was highest at Satinleaf (6,382 kg ha⁻¹) followed by Chekika Island (5,571 kg ha⁻¹) and then Grossman Hammock (5,060 kg ha⁻¹). Differences in mean annual ground litter biomass between Chekika Island and Grossman Hammock and between Chekika Island and Satinleaf were not significant at $P > 0.05$. However, during the 3-year period, mean annual ground litter biomass differed significantly between Satinleaf and Grossman Hammock (paired t -test(2) = -6.150, $P = 0.025$) (**Table 13**).

Mean annual litter turnover times (months) ranged between 8 to 12 months with an averaged residency of 10.5 months (**Table 13**). For all years (2007-09), Grossman Hammock had the shortest annual litter turnover times at 8.1, 7.6, & 10.1 months, while Chekika Island had the longest at 16.4, 8.8, & 12.6 months. However, during this period, mean litter turnover rates did not differ significantly. For all tree islands, the highest litter turnover times occurred in 2008 while turnover rates in 2007 and 2009 were lower than 2008 and very similar to each other, about 12 months (**Table 13**). Differences in mean annual litter turnover times between 2008 and 2009 were significant (paired t -test(2) = -7.450 $P = 0.018$) and appear to be correlated to differences in annual precipitation (**Figure 13**). However, rainfall alone does not explain the observed difference in mean litter turnover times between years, since mean litter turnover times between 2007 and 2008 were not significantly different, at $P > 0.05$ (**Table 13**), even though annual precipitation was less in 2007 than in 2008 and similar to that of 2009 (**Figure 4 & 41**).

Discussion:

Tropical hardwood hammock tree islands in the southern Everglades show remarkable resiliency even under the effects of extreme environmental stressors like hurricanes. These stressors generally cause extensive defoliation, stem breakage, windthrow, tree mortality and in extreme cases can adversely impact the physical structure of these forests (Brokaw & Walker 1991, Tanner et al. 1991, Whingham et al. 1991, Loope et al. 1994, Turner et al. 1997). The biological inertia or ecological resilience of these forests, i.e., the amount of disturbance that they can withstand before changing stable states or being significantly altered (Gunderson 2000), ensures that natural or anthropogenic disturbances will result in community reorganization and reemergence with very little change in composition or structure within relatively short temporal scales, as long as the physical environment is not substantially altered. This scenario is exemplified at Satinleaf, Black Hammock, and Gumbo Limbo Hammocks, where forest structure and species composition have remained relatively stable since 2001/02 (see Ross & Jones 2004). These tree islands were directly impacted by Hurricanes Katrina and Wilma in 2005 and were, in 2001/02, 10-years removed from a previous catastrophic windstorm event, Hurricane Andrew, in 1992 (see Loope et al. 1994, Olmsted & Armentano 1997). Community dynamics within these islands demonstrate that, in general, tropical hardwood hammock tree islands within the southern Everglades have a propensity to withstand changes to their stable state even under repeated disturbance events. As a general rule, these tree islands have a high degree of ecological resilience which maintains community entropy, or fragmentation, at relatively low levels. At the same time, however, biological inertia may prevent a highly degraded tree island from naturally reorganizing and reemerging back to its pre-disturbance native state. Furthermore, repeated perturbation events, like hurricanes or fires, are likely to further increase community degradation and entropy and thus shift the community further and further away from its original native stable state. This appears to be the situation at Irongrape and SS-81 and possibly at E4200 as well. The physical environment within these three hammocks has been significantly altered by both anthropogenic and natural perturbation events including fire (in the case of E4200), such that a shift towards the original native plant community will require a significant shift in the current physical environment present within these tree islands. This is particularly true for Irongrape. After several decades of intense anthropogenic recreational use, the current macrophyte community present is not much different than what was there after abandonment nearly a decade ago. Currently most species at Irongrape tend to be ephemeral in response to competition from early successional species like *Caesalpinia bonduc* and *Verbesina virginica*. These shrubs tend to preclude tree species from becoming established and thus thwart the successional process, even though part of the forest at Irongrape is still intact and quite capable of restocking itself.

Furthermore, these communities exhibited high variability in species composition and stand level structural characteristics, including tree density, basal area, canopy structure, and understory vegetation composition. Much of this variation was associated with the two distinct wetland landscapes in the study area, the ridge and slough (RS) and wet prairie (WP) regions. In general, tree island plant community structure and composition are manifestations of species' sensitivity to hydrology, available nutrient resources, and disturbance regimes (Armentano et al. 2002; Wetzel 2002; Sah 2004; Ross et al. 2006, Ross et al. *in press*). Hydrology is the major driver of marked species differences along topographic gradient within a tree island or among various types of tree islands, such as willow heads, bayhead swamps, bayheads, and hardwood

hammocks that differ in the extent of inundation from none (hardwood hammocks) to 10 months yr^{-1} (bayhead swamps) (Armentano et al. 2002; Ross and Jones 2004; Sah 2004). However, in the hardwood hammocks which seldom get flooded, and where a decade long mean annual water table is below 40 cm (**Table 4**), present tree species composition is probably more the legacy of long-term interaction between hydrology and edaphic and other physical processes (D'Odorico et al. *in press*), and recurrent disturbances. In this study, the ordination results also revealed that regional differences in tree species composition in hardwood hammocks were not correlated with hydrologic variable (water-table depth), but were strongly correlated with tree island height and measured soil variables, including soil nitrogen and phosphorus (**Table 6**). Though there is obviously a strong correlation between tree island height and water table depth, these two variables express different characters, due to natural or management-related differences in water level. The absence of a stronger relationship between water depth and plant composition was a surprise, but the effect may have been obscured by variability in soil depth and type, as well as the relatively narrow range of water depths we encountered in our well-drained sites. It should also be noted that our estimates of water depth assume a flat water table between marsh and tree island, which can in some situations represent a rather crude approximation of reality. On the other hand, tree island height does have ecological effects independent of its association with water depth. For instance, low height above marsh in WP islands make them more vulnerable to fire that originate in the surrounding marsh, and also to short-term flooding that may occur in response to upward shifts in water table caused by storm events, rainfall, or water management activities. For instance, hundreds if not thousands of wet prairie islands were burned in 2008 as the result of the Mustang Corner fire (see Ruiz et al. 2010), which will leave its imprint on the species composition on those islands in the years to come. Nutrient availability is also considered one of the most important factors affecting competition among species and determining plant community composition (Tilman 1985). Hammocks in RS and WP regions did differ sharply in soil characteristics. RS islands had higher total soil phosphorus (TP) and non-carbon minerals (Non-C), and lower total nitrogen (TN) than their WP counterparts (**Appendix 1**). Moreover, plant community composition is also influenced by spatial and temporal heterogeneity of available resources. In general, plant species diversity is positively related to heterogeneity of available resources (Ricklefs 1977, Huston 1979). In our study area, within plot variation (Coefficient of Variation) in mean surface elevation was higher in WP islands (10.0%) than in RS islands (5.7%). The within plot topographic variation possibly have created higher heterogeneity in soil water and other below ground resources on WP islands, resulting in higher species richness on those islands than in RS hammocks.

Disturbances also affect resource availability and heterogeneity in forest ecosystems (Carlton and Bazaz 1998). In the hardwood hammocks, major disturbances include infrequent wildfires, and more frequent hurricanes and tropical storms. We don't know the fire history of these islands, but given the likelihood of more frequent fires in WP than RS landscape, WP communities which have relatively high tree density and low basal area resulted from high number of small trees, might be recovering from past severe fire events, and still far from being matured. Alternatively, on these low productive islands that are characterized by the thin and low P soils, less intense self-thinning may facilitate small trees to co-exist with the larger trees (Ross et al. 2010). Other disturbances such as hurricanes that affect forest structure by causing extensive defoliation, stem breakage, and uprooting of trees not only increase tree mortality (Ross et al. 2003), but also increase light availability in the understory. Increased level of

available light in the understory in 1-2 post-hurricane years was possibly the reason for increase in the number of species in the sapling stratum (**Figure 13**). In the hardwood hammocks, we did not have a multiple year pre-hurricane survey-based estimate of background mortality. At this time, our best guess of background mortality is somewhere between the 1.5% annual rate observed in the Big Pine Key pine forest over a 10 year period without any major disturbance (Sah et al. 2010), and the 4.8% observed during this study on three islands (Black Hammock, Gumbo Limbo and Satinleaf) which also included mortality within the first year after the Hurricane Wilma. In several RS hardwood hammocks, higher mortality in the 3rd and 4th post-hurricane years than in the 1st and 2nd years post-hurricane (**Table 9**) could be the result of interaction of multiple disturbances, e.g., hurricane and drought. Trees stressed by the hurricane were likely to be hard hit by the drought that prevailed for two years between 2006 and 2008. In these years, particularly in the dry season when hammock plants use regional ground water (Saha et al. 2010), it is likely that ground water became less accessible, resulting in permanent wilting of the already hurricane-stressed trees.

Ridge and slough tropical hardwood hammock tree islands have significantly higher soil bulk density and lower soil organic content than their WP counterparts (**Appendix 1**, Jayachandran et al. 2004, Wang et al. 2010). Soil phosphorus (P) and nitrogen (N) concentrations show an inverse relationship in RS and WP tropical hardwood hammock soils, with higher P and lower N in the former (**Appendix 1**; Wang et al. 2010). This difference in soil nutrient concentration is reflected in the foliar N:P ratio of these forests, with leaf N:P generally lower in RS trees than in WP trees. These regional differences in tropical hardwood hammock soil bulk density, total organic matter, P & N concentrations, and foliar N:P ratio suggest that there are intrinsic differences in the way and rate in which organic matter and nutrients are cycled through these forests and in the type and quality of soils found within RS and WP tree islands

Litterfall, which is only one facet of nutrient cycling in forested communities, represents a major pathway by which aboveground nutrients are transferred and incorporated into the soil through decomposition (Melillo et al. 1982, Vitousek & Sanford 1986, Karberg et al. 2008). The process and rate by which litterfall decomposes within a forest determines how much carbon (C) is stored in the soil or released into the atmosphere as carbon dioxide (CO₂) as well as how much N, P, and calcium (Ca) is available for plant and microbial uptake (Karberg et al. 2008). Litter decomposition or litter turnover rates at the soil surface are subject to several factors, including temperature and precipitation, the chemical composition of the litter (“litter quality”), and the heterotrophic fauna found within the forest floor (Melillo et al. 1982, González & Seastedt 2001, Hobbie et al. 2006, Karberg et al. 2008). Rates and fluxes in litter decomposition regulate the accumulation of nutrients and organic matter in the soil horizon (Melillo et al. 1982).

Our estimates of litterfall for southern Everglades tropical hardwood hammocks (6,630 kg ha⁻¹ yr⁻¹) fall within the range reported by Ross et al. (2003) & Sah (2004) for tropical hardwood hammocks in the Florida Keys & topical hardwood hammock tree islands in Shark River Slough, respectively, as well as estimates for other dry tropical forests worldwide (Martínez-Yrizar 1995). Litter decomposition rates or turnover, for the three high frequency sampled tree islands averaged about 10.5 months and were also within the range of values reported for other dry tropical forests (Martínez-Yrizar 1995). Within the southern Everglades, litter turnover rates were faster at Grossman Hammock (10.1 months), a WP tree island, than at the two RS tree

islands, Satinleaf Hammock (11.9 months) and Chekika Island (12.6 months). This difference in regional litter turnover rate may be related to differences in foliar N concentration, which decrease in the order Grossman Hammock, Satinleaf, and Chekika Island (Saha et al. 2010). N concentration or the C:N ratio of plant matter has been linked to higher litter decomposition rates in other forests (Melillo et al. 1982, Wedderburn & Carter 1999). In other words, leaves rich in the growth-limiting nutrient decompose faster than more nutrient-deficient leaves. Within the context of the P-limited WP tree islands (Wang et al. 2010), phosphorus is much more likely to be translocated back into other plant tissues during the early stages of leaf senescence. Consequently, these senesced leaves may have higher N:P ratios than the non P-limited RS tree islands and could result in the observed difference in litter turnover rates between these two regions. Furthermore, since soil P-concentrations are much higher in RS tree islands than WP tree islands, N is likely to be translocated back into other tissues while P remains in the senescent leaves and, through decomposition, would ultimately end up incorporated back into the soil. This process of differentiating nutrient translocation between regions provides, in theory, another pathway besides the transpiration driven chemohydrodynamic nutrient loading model (Wetzel et al. 2005, Ross et al. 2006b) and the guano deposition model (Givnish et al. 2008) for explaining the observed high concentrations of P in the soils of RS tree island. These three processes are not mutually exclusive, so their combined effects could result in the surprisingly high concentration of P found in the soils of RS tree islands.

Hydroperiods for the 16 tropical hardwood hammock tree islands were surprisingly similar even though they were embedded in two distinct marsh assemblages with contrasting and significantly different hydroperiods (Lockwood et al. 2003, King et al. 2010). On average, the annual water-table depth within these 16 tree islands was found well below the soil surface in the underlying bedrock. As a result, fluxes in marsh water levels and in the water-table depth within these tropical hardwood hammock tree islands could play a major role in the water budget of these forested communities particularly during the winter dry months when marsh water levels are at their lowest and precipitation is minimal or during periods of drought. Some support may be derived from our finding of low tree mortality during periods of a relatively high water-table. However, the lack of precipitation during dry spells might be more of a limiting factor than the actual water-table depth. The tiniest amount of precipitation during periods of drought could sustain and maintain soil moisture within these forests at levels just above the wilting point (i.e., the minimal amount of soil moisture that a plant can withstand before wilting begins, ultimately resulting in desiccation and death) even though marsh water levels and water-table depth continues to decline in response to the imbalance between precipitation and ET.

Slight increases in marsh hydroperiod or water depth in Everglades National Park are likely to have little impact on tropical hardwood hammock tree island resources in either the ridge and slough or the wet prairies. However, wet prairie tree islands, because of their karst topography and shallow, organic soils, might respond more quickly than ridge and slough tree islands to any system wide modification of marsh water depth and/or hydroperiods. A small incremental upward shift in the water-table depth within the wet prairie landscape has the potential to partially flood these tree islands and increase soil moisture. These changes to the physical environment of wet prairie tree islands could precipitate further changes to the physical and chemical properties of the soils as well as lead to shifts in species composition, nutrient cycling, and productivity.

Conclusion:

Southern Everglades ridge and slough and wet prairie tropical hardwood hammock tree islands are biological focal points within a physiographically limited landscape that attract and provide refuges for forest-dwelling plants and animals and perform important nutrient cycling functions. Differences in community structure, composition, and function within these hammocks are marked by a high degree of within-region variability that masks most regional differences within these forested communities. However, regional differences between these forested communities are evident particularly with respect to species composition and richness, the physical and chemical properties of their soils, and overall community productivity. Their responses to exogenous factors, i.e., perturbation events like hurricanes and fires or hydrologic stress in the form of flooding or drought, tend to be very similar with very little discrimination between regions. In general, tropical hardwood hammock tree islands are capable of recovering quickly from most perturbation events that do not change the overall physical environment that they occupy. The built in biological inertia within these communities ensures that the effects of most perturbations will be ephemeral. This is not to say, however, that these forested communities are static; nothing could be further from the truth. Natural long-term changes in forest structure and composition do occur within these communities in response to successional processes by which early successional species (e.g., *Carica papaya*, *Sambucus nigra* subsp. *canadensis*, *Solanum erianthum*, & *Trema micrantha*) give way to later successional ones (e.g., *Sideroxylon foetidissimum*, *Simarouba glauca*, and others).

The continued monitoring of tropical hardwood hammock tree islands is critical for Everglades restoration, since they provide ecological niches for a wide variety of plants and animals (including many migratory avian species) whose lifecycles are interdependent on the existence of these forested communities. Furthermore, tropical hardwood hammock tree islands can be thought of as keystone communities or the “canary-in-the-coal-mine” of the Everglades, as a whole. Significant losses in tropical hardwood hammock habitat, whether in the ridge and slough or the wet prairies, as a result of hydrologic fluxes that either directly, by flooding or extended hydroperiods, or indirectly, by drought conditions that increase and exacerbate the potential for a catastrophic fire, would be clear indicators of degradative environmental conditions within the Everglades. We need not look further than the Water Conservation Areas north of Everglades National Park or in the eastern wet prairies affected by the Mustang Corner Fire to see how hydrologic alterations and fluxes have adversely altered the landscape and led to significant losses in tropical hardwood hammock abundance and in their overall “health” or ecological function.

Continued monitoring efforts should focus on: 1) monitoring changes in water table depth and hydroperiod in response to Everglades restoration efforts; 2) understanding how hydrologic fluxes, flooding and drought, affect tree species composition, abundance, and productivity; and 3) understanding the successional pathways by which these forested communities recover from perturbation events that significantly alter their physical environment, particularly fires, which can consume the entire standing biomass within a tree island as well as oxidize soils, leading to lowered surface elevations and increases in hydroperiod and flooding potential within these forested communities.

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Plate 1: Epoxy-coated steel wire fine-mesh (52.70 x 52.70 x 18.42 cm) litter traps used in the three high frequency sampling tree islands.



Plate 2: Ground litter collection plots (0.25m²) before (top) and after (bottom) litter collection.

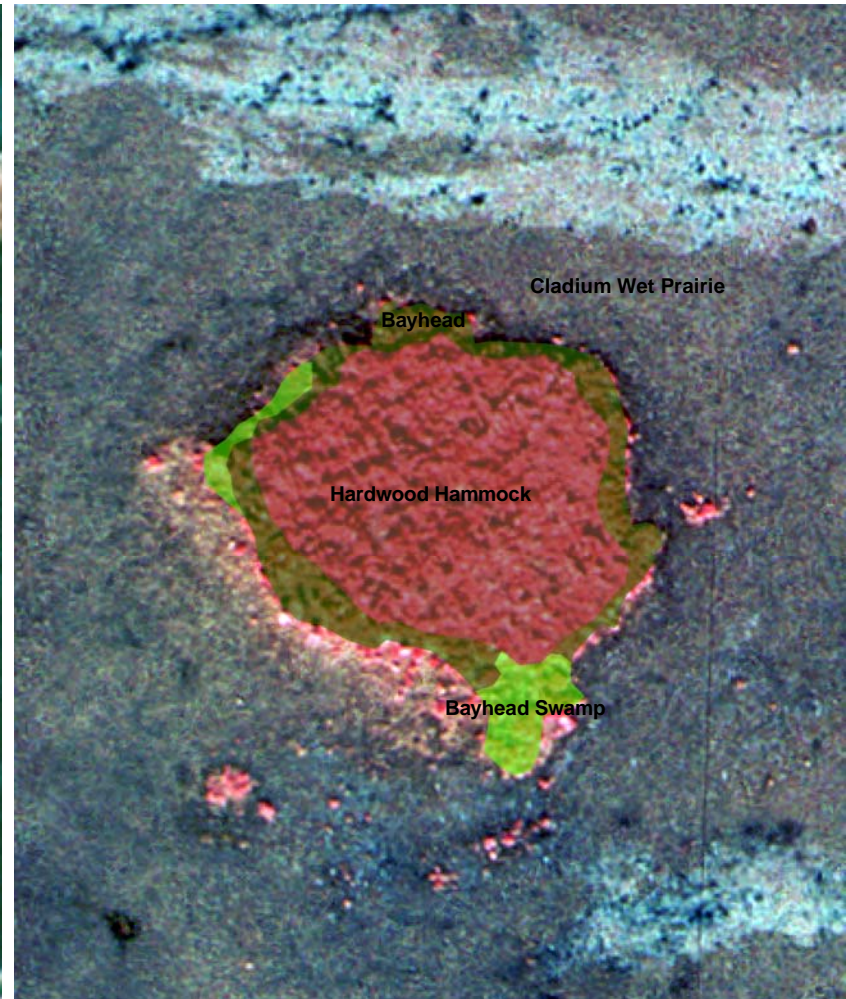


Plate 3: Krast topography at Mosquito Hammock and typical of many wet prairie (WP) tree islands within the southern Everglades.

a: Ridge & Slough (RS) Tree Island (Satinleaf Hammock)



b: Wet Prairie (WP) Tree Island (Mosquito Hammock)



0 25 50 100 Meters



Figure 1: 1994 NAPP aerial photographs overtopped with community zones associated with (a) ridge and slough and (b) wet prairie tree islands.

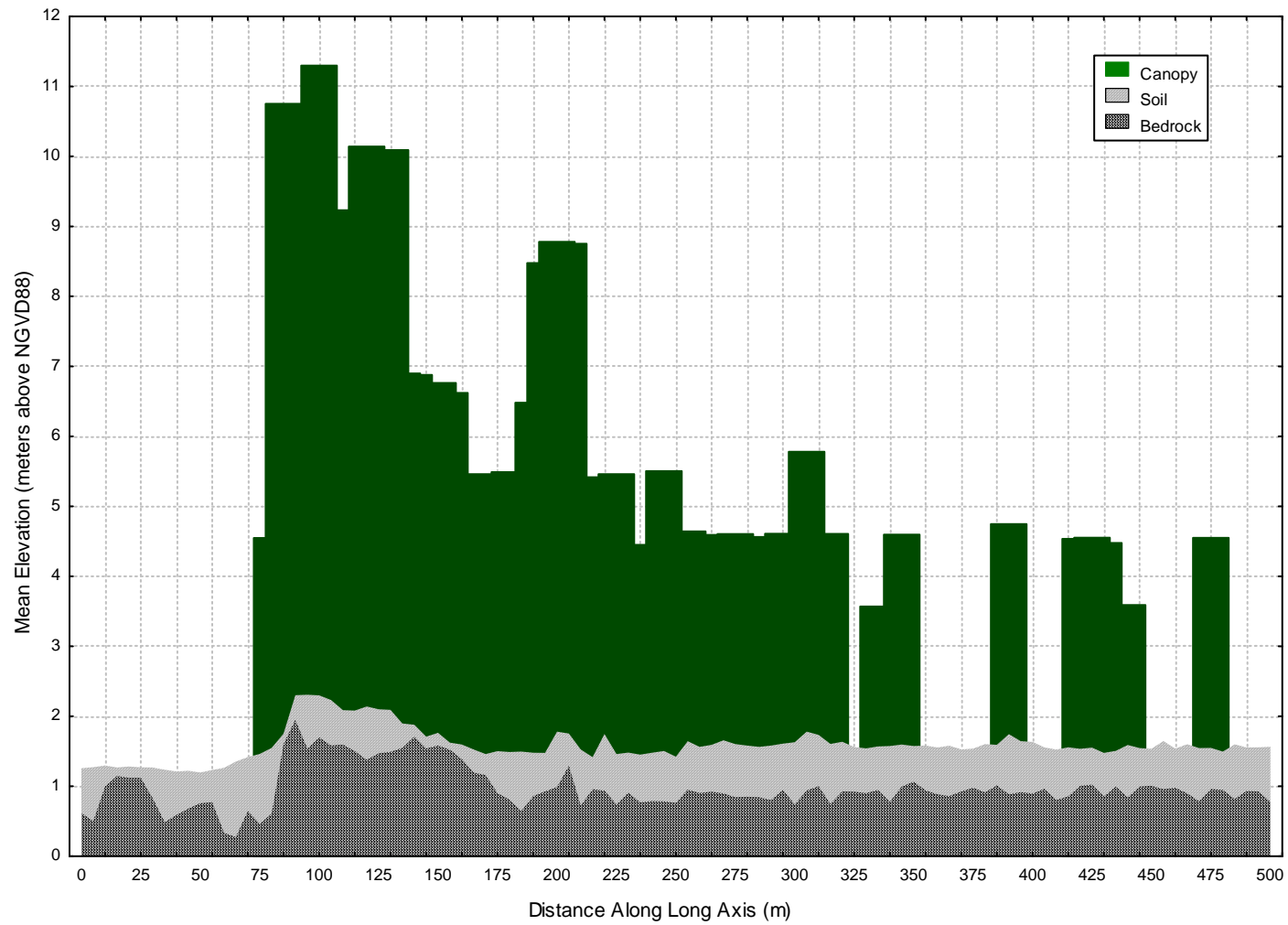


Figure 2: Canopy height, soil depth, and bedrock elevation along the long axis of Satinleaf Hammock.

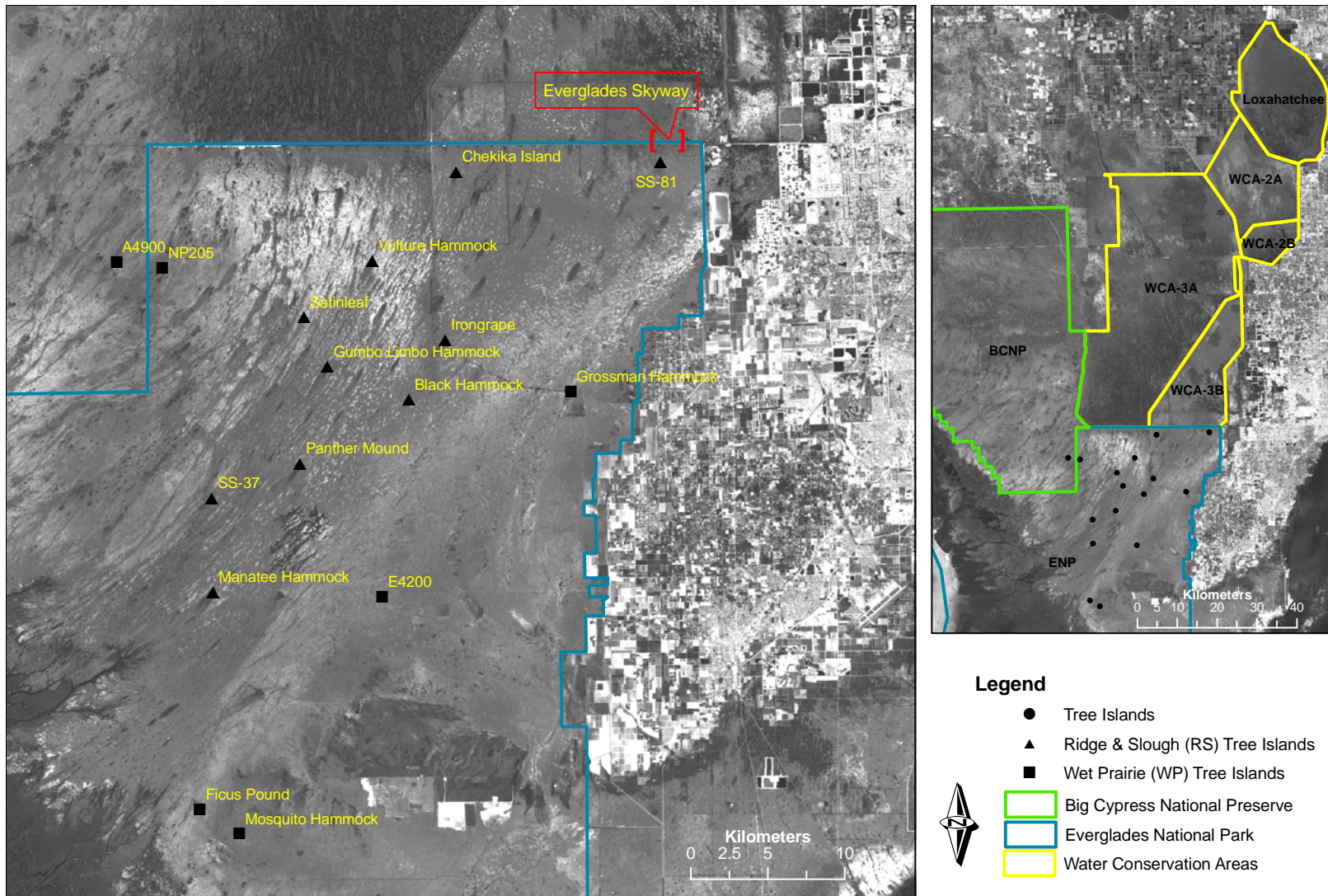


Figure 3: Location of study islands within the southern Everglades.

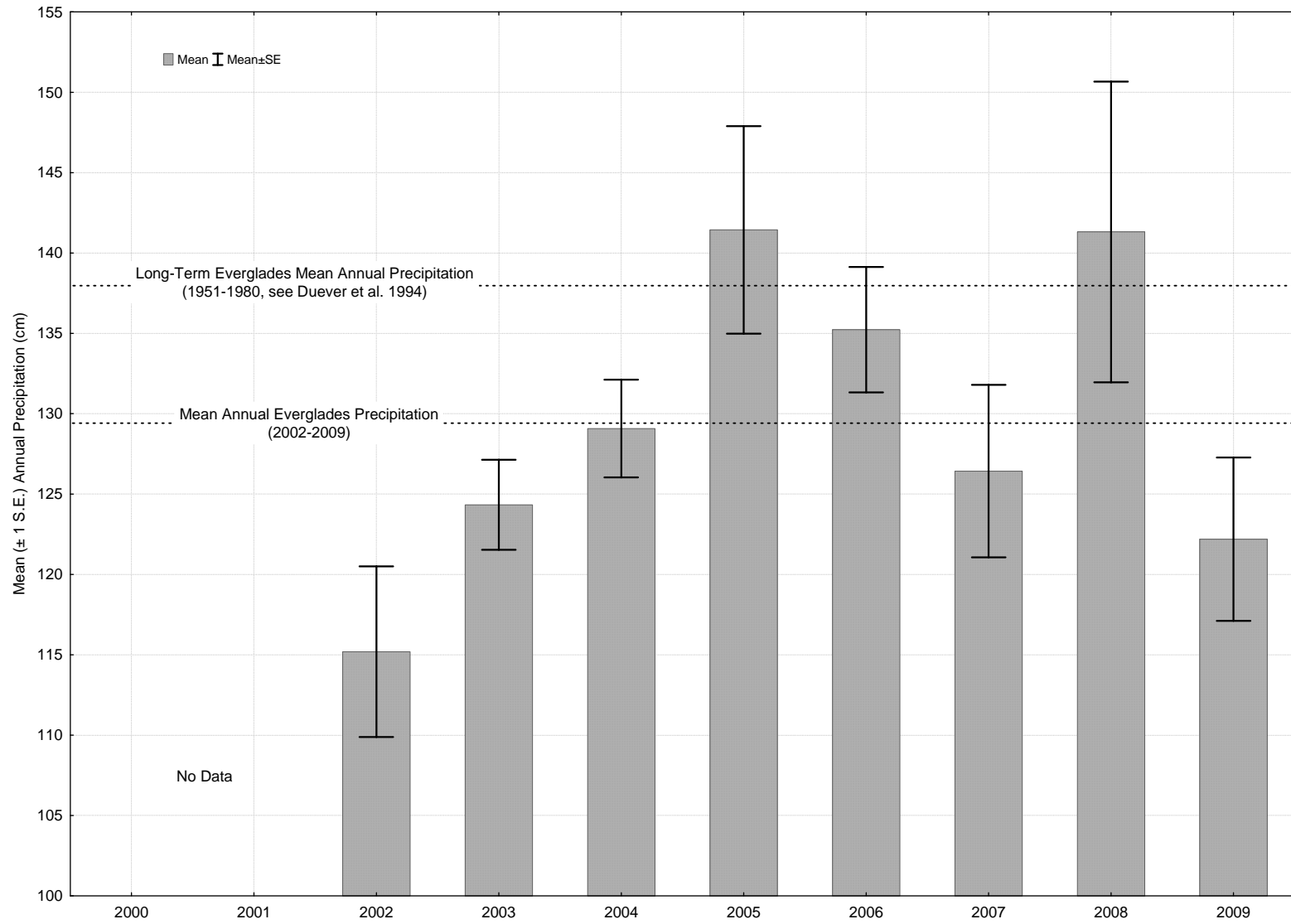


Figure 4: Mean (± 1 S.E.) annual precipitation (cm) for the southern Everglades between 2002-2009.

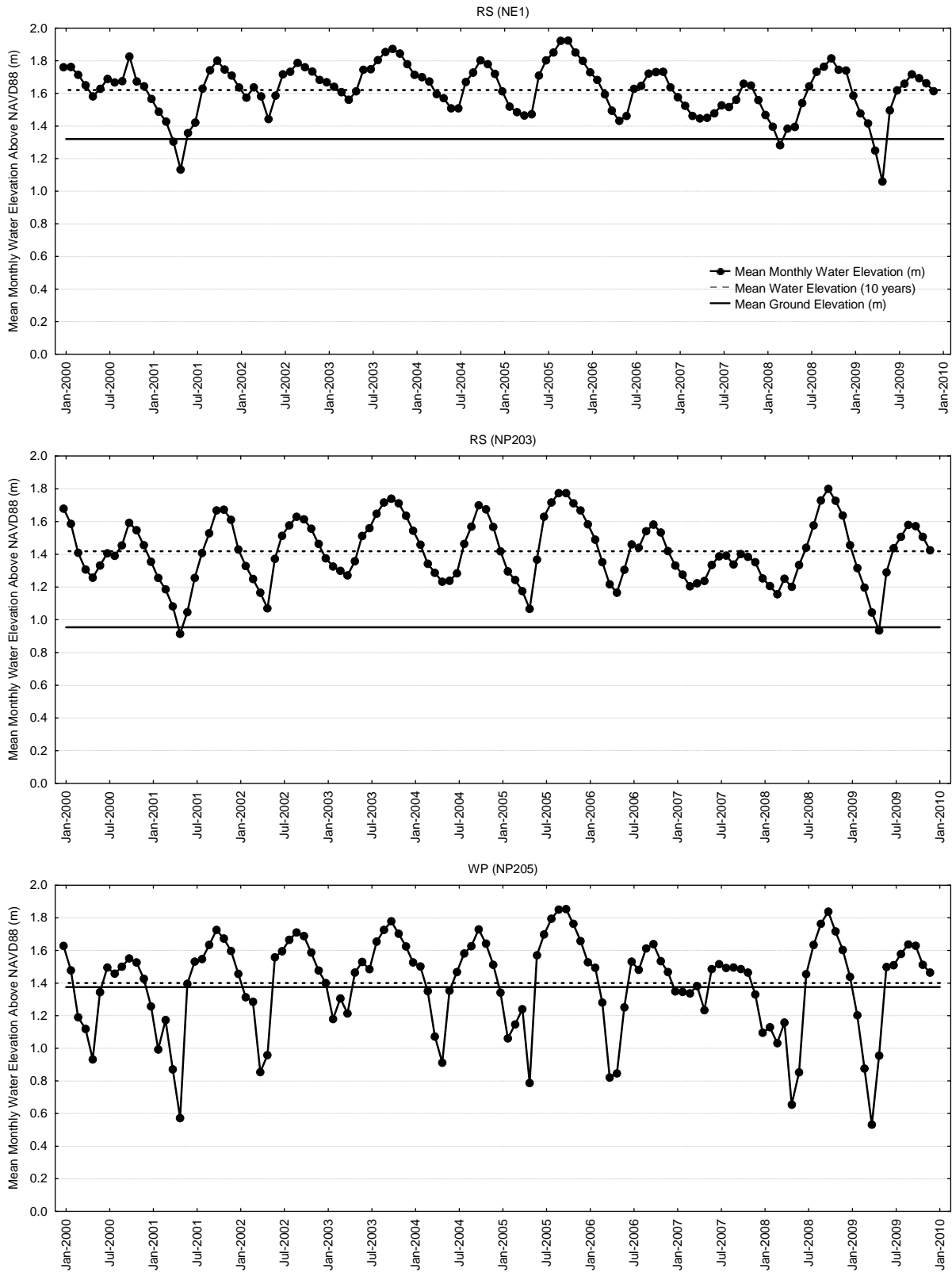


Figure 5: Hydrograph of mean monthly marsh surface elevations at three hydrostation located within the study area.

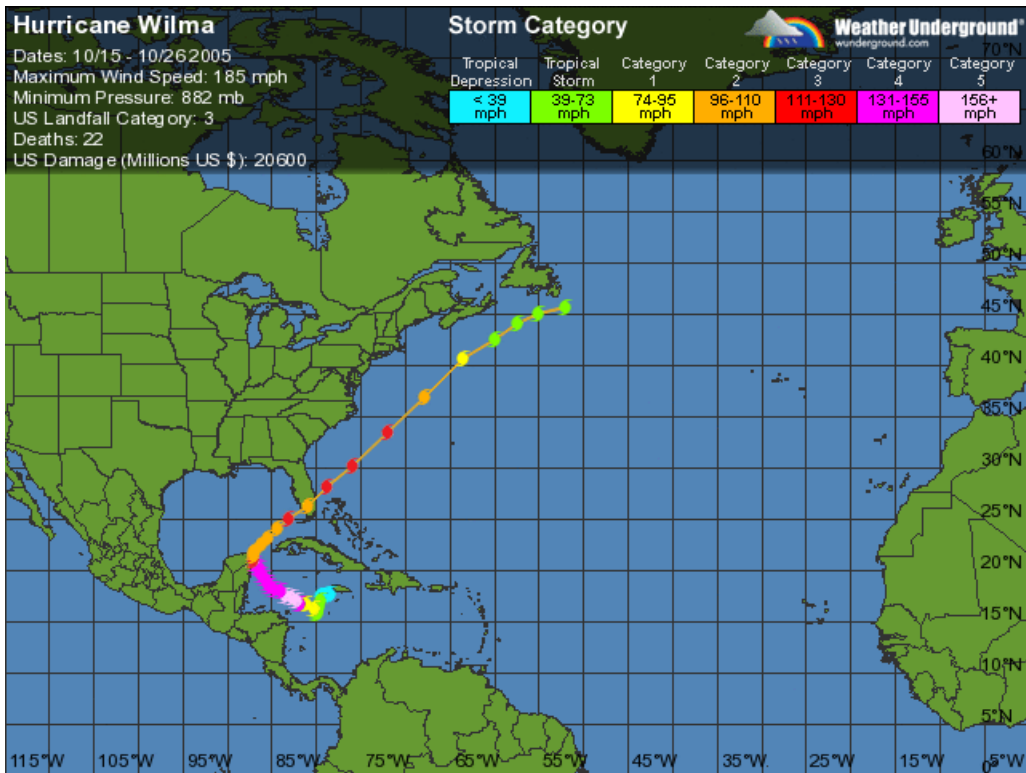
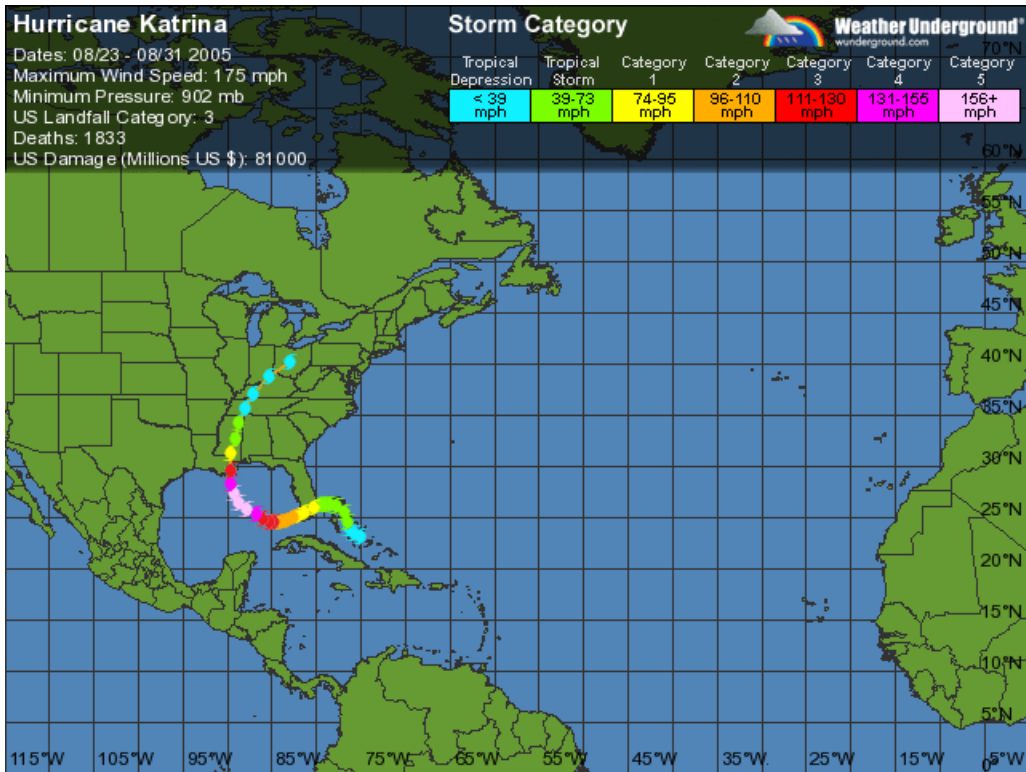
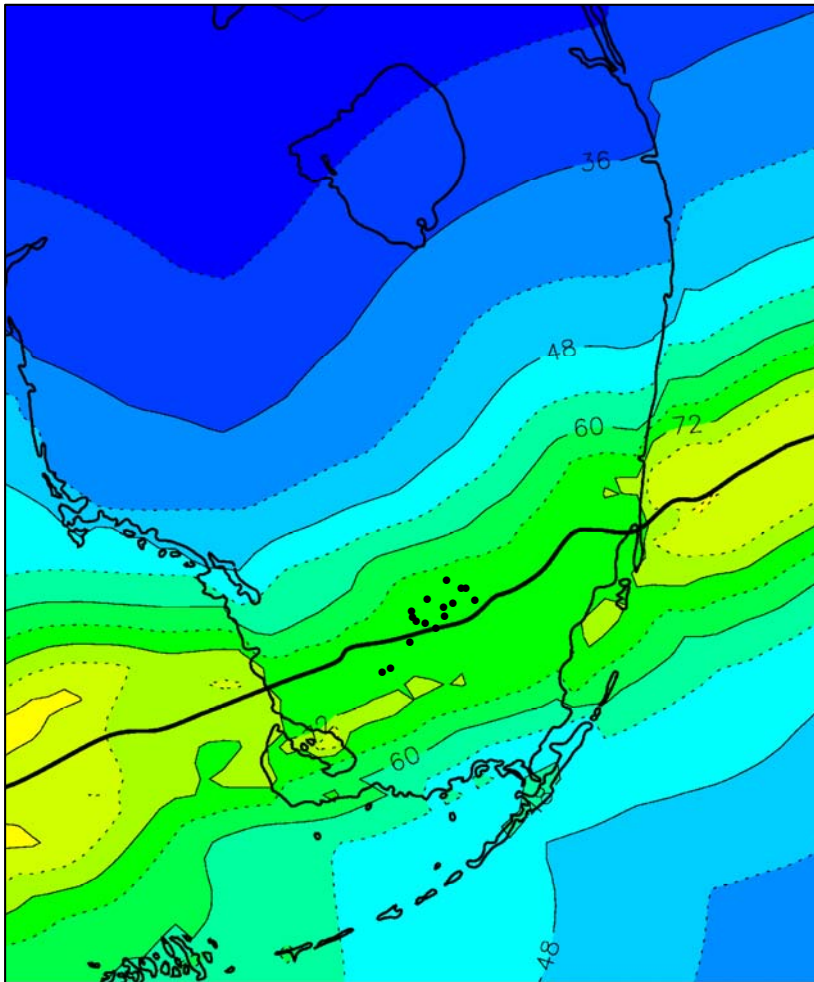


Figure 6: Intensity track for Hurricane Katrina and Wilma over south Florida.

a) Hurricane Katrina



b) Hurricane Wilma

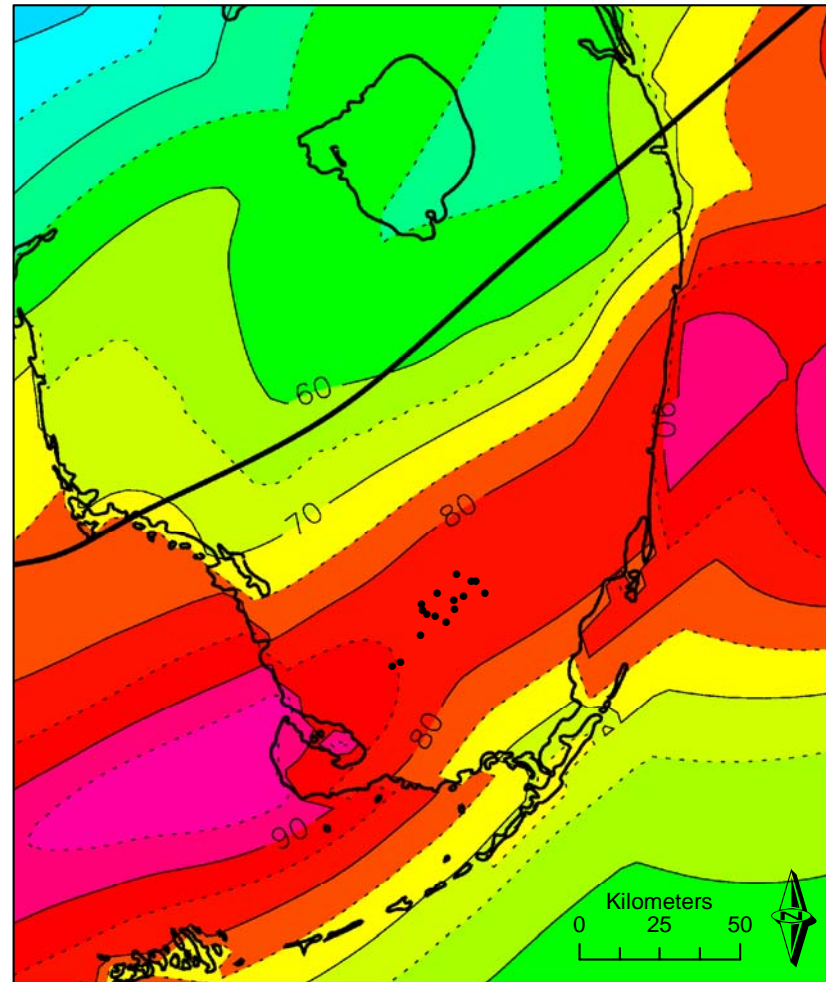


Figure 7: Maximum wind contours in mph for Hurricane a) Katrina and b) Wilma. Tree islands are denoted by black dots. Contours maps & data available from the Atlantic Oceanographic and Meteorological Laboratory – Hurricane Research Division (http://www.oaml.gov/hrd/data_sub/wind2005.html).

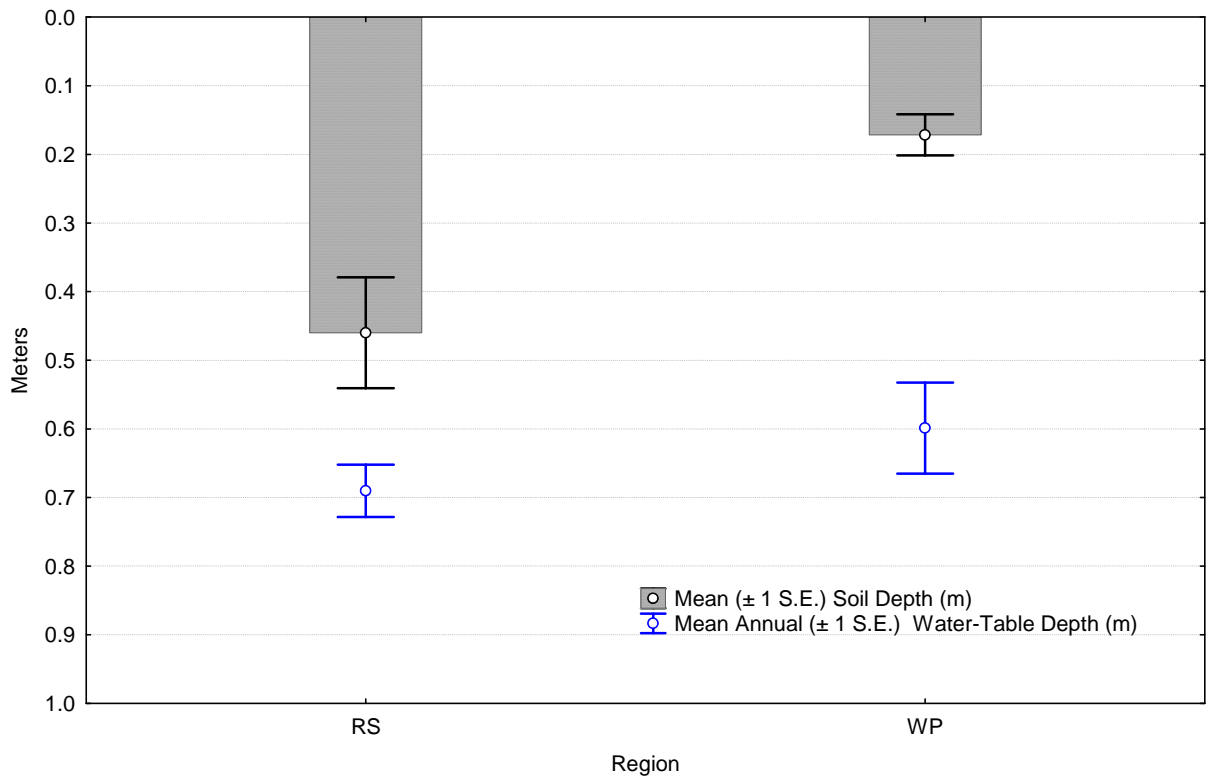


Figure 8: Regional differences in tree island mean soil depth (m) and water-table depth (m)

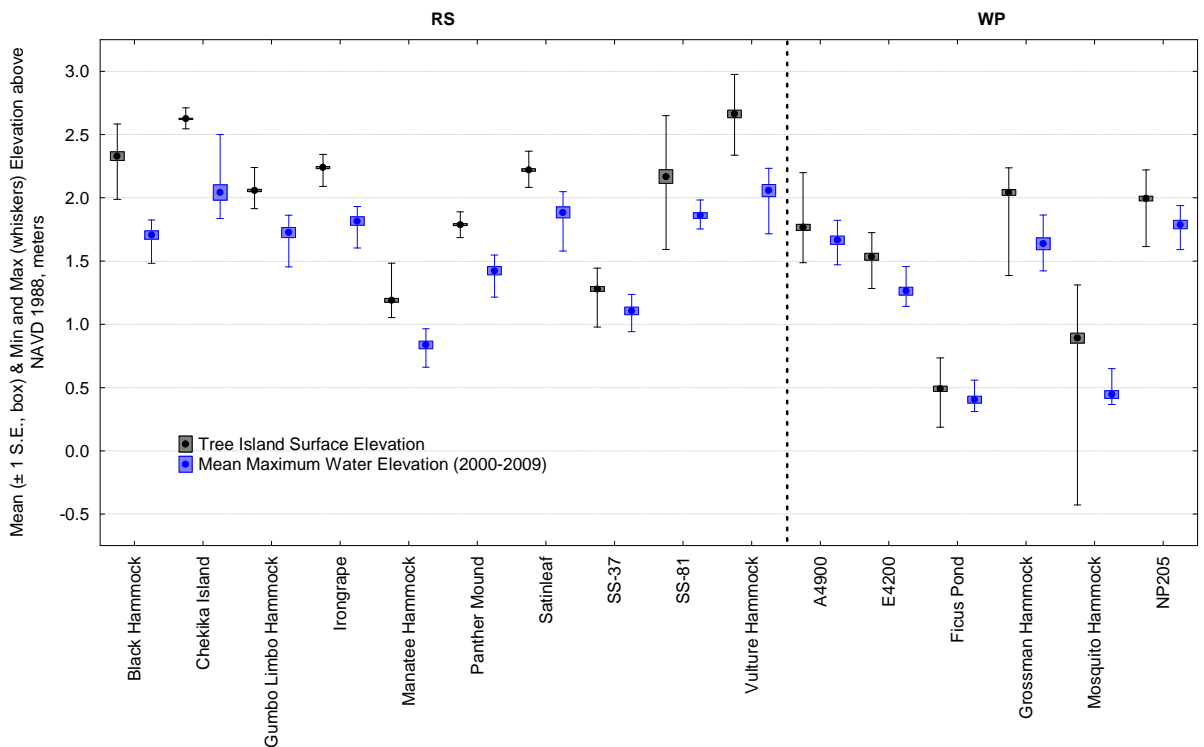


Figure 9: Tree Island surface elevation and mean maximum water elevation above NAVD 1988 (m) between 2000 and 2009.

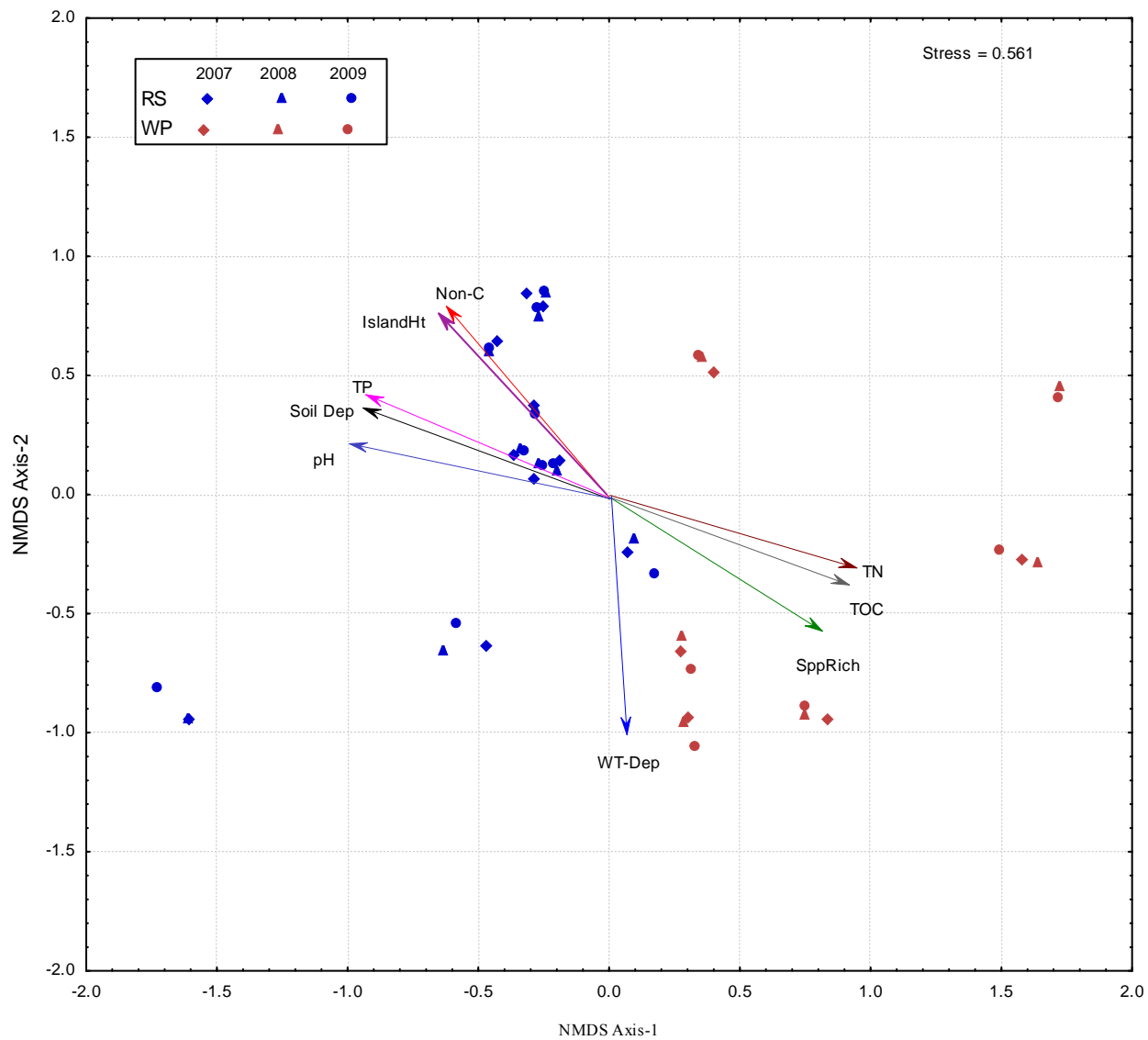


Figure 10: 2-D scatter-plot of NMDS ordination based on Sapling and trees IVI on 16 tree island hammocks sampled between 2007 and 2009. Fitted vectors are, Distance to water level (Dist_WT), Soil depth (SoilDep), Soil nitrogen (TN), phosphorus (TP), total organic carbon (TOC), pH, and non-carbon materials (Non-C), and Species richness (SppRich).

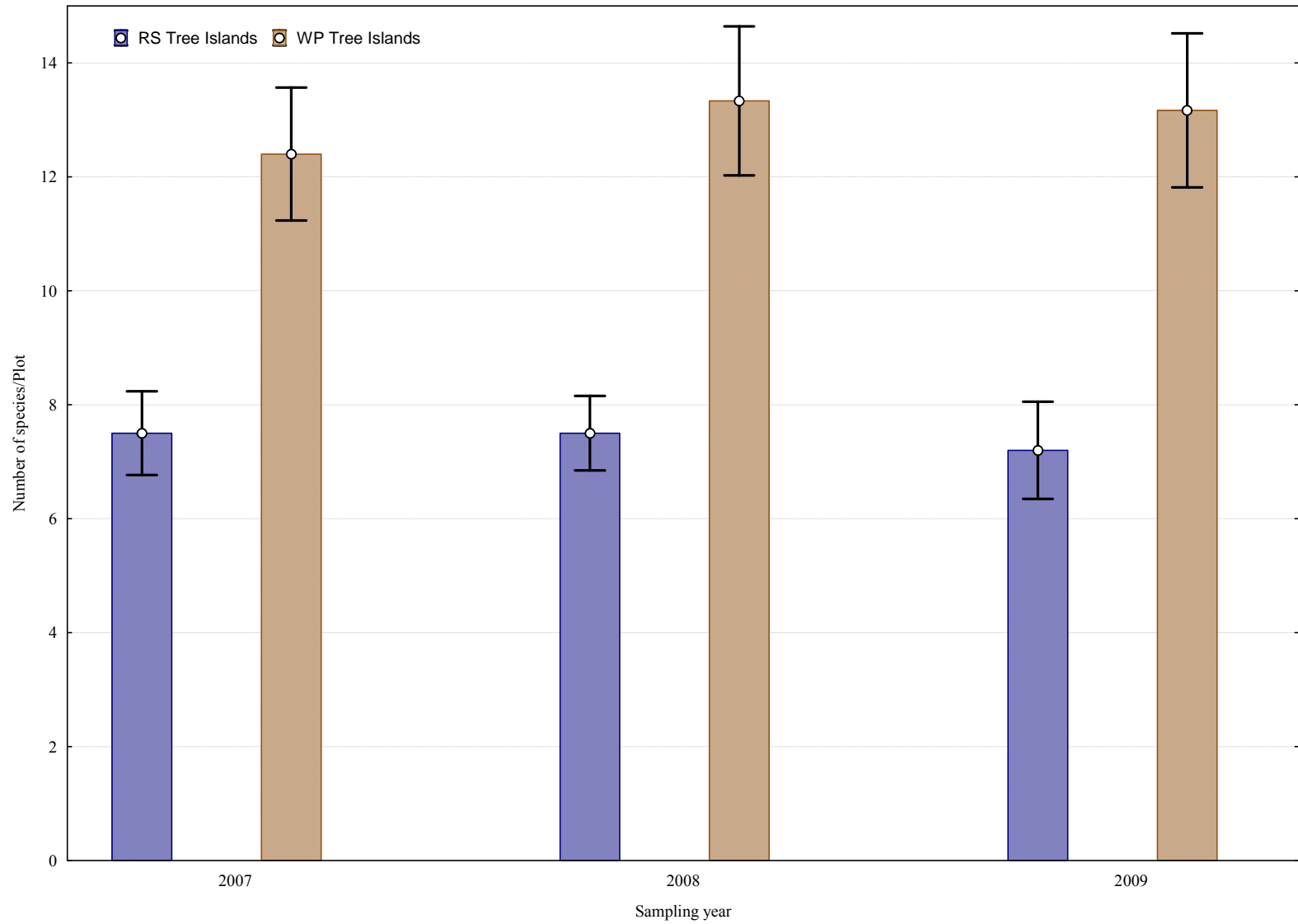


Figure 11: Tree species richness (species/plot) in the sapling and tree strata in hardwood hammocks on tree islands in 2 regions.

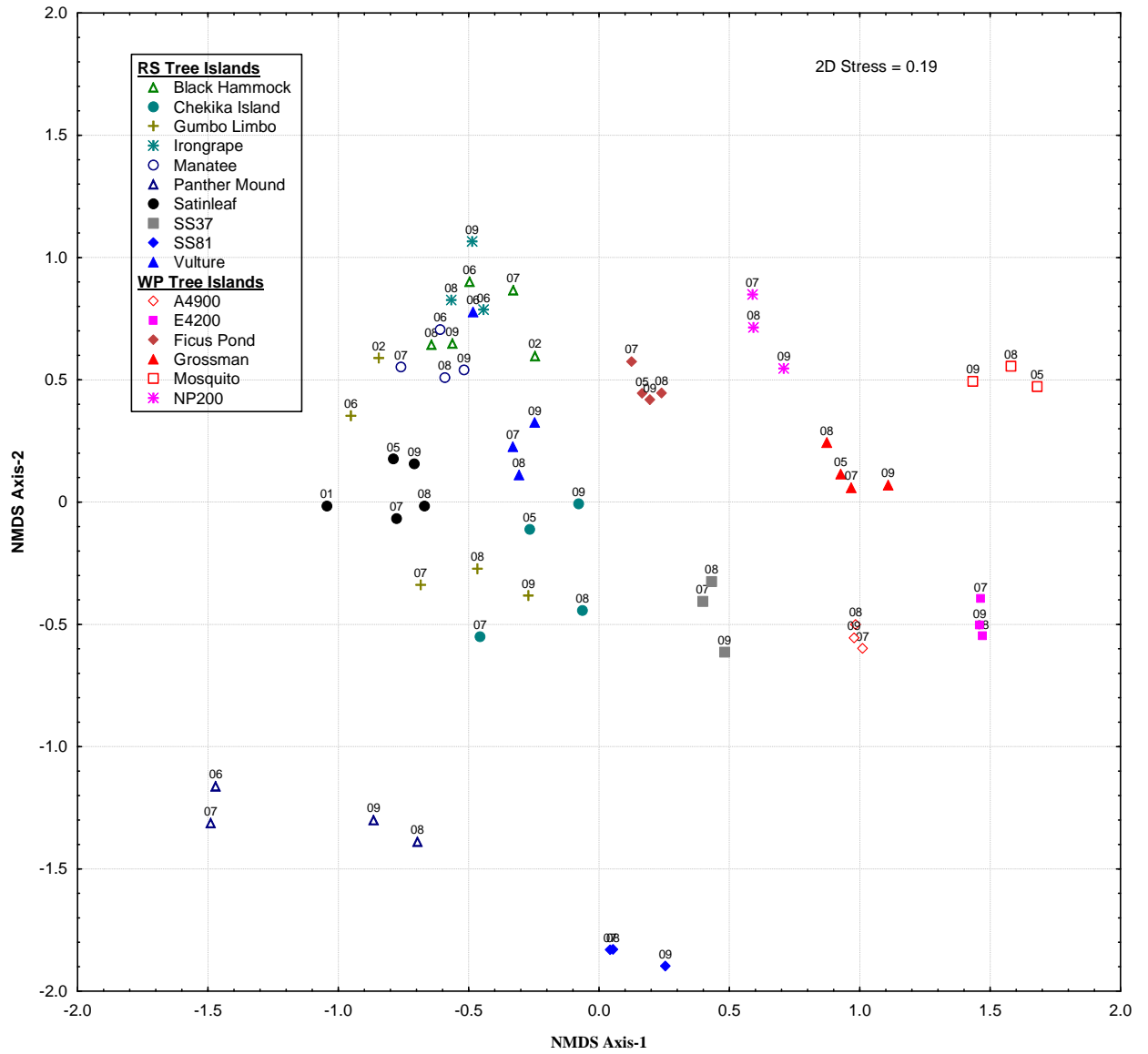


Figure 12: 2-D scatter-plot of NMDS ordination based on Sapling density on 16 tree island hammocks sampled between 2001 and 2009.

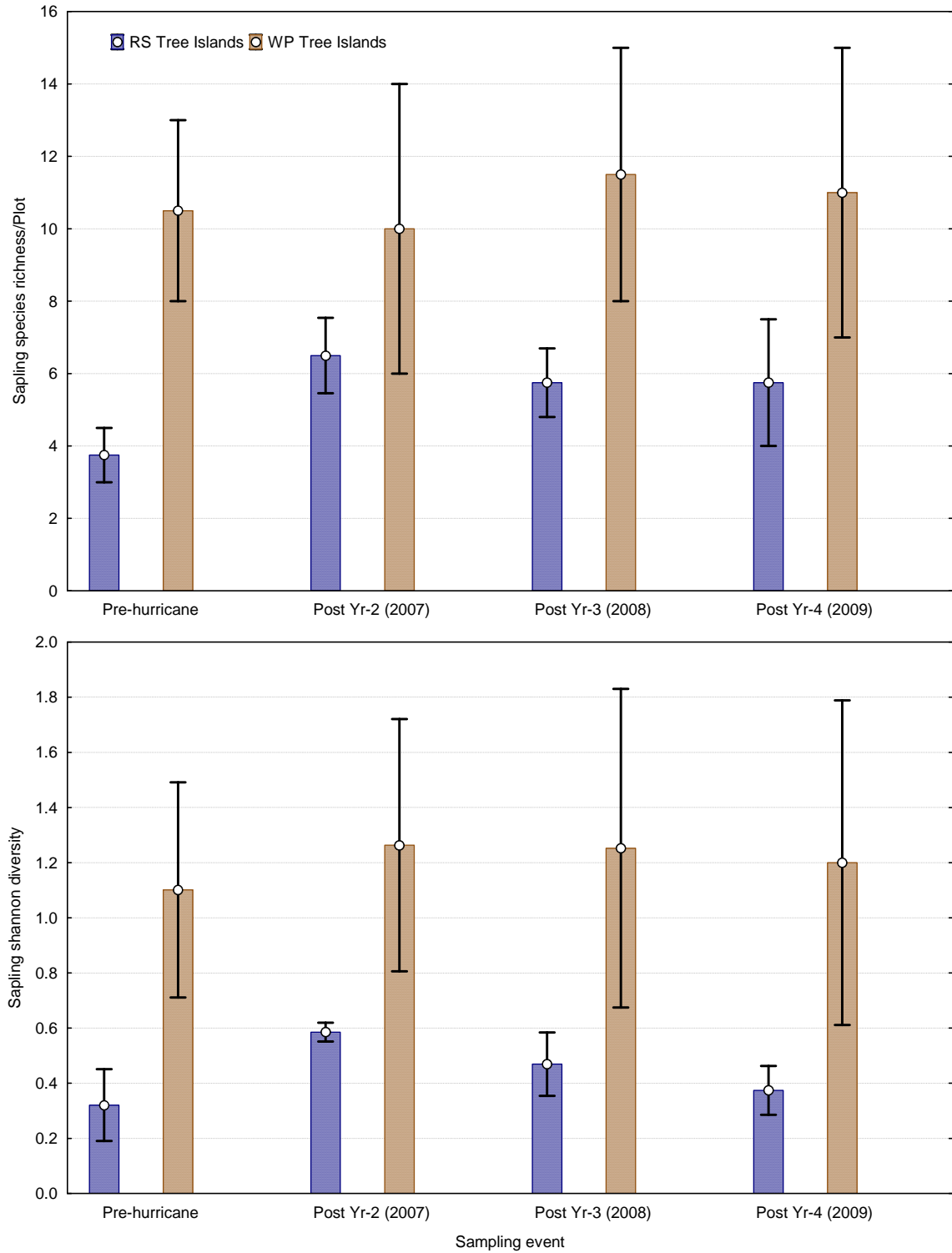


Figure 13: Mean (\pm SE) species richness and Shannon species diversity in 6 hardwood hammocks in RS and WP landscapes periodically sampled in pre-hurricane year (2001/2002 or 2005/2006) and 2, 3 and 4 years after hurricane.

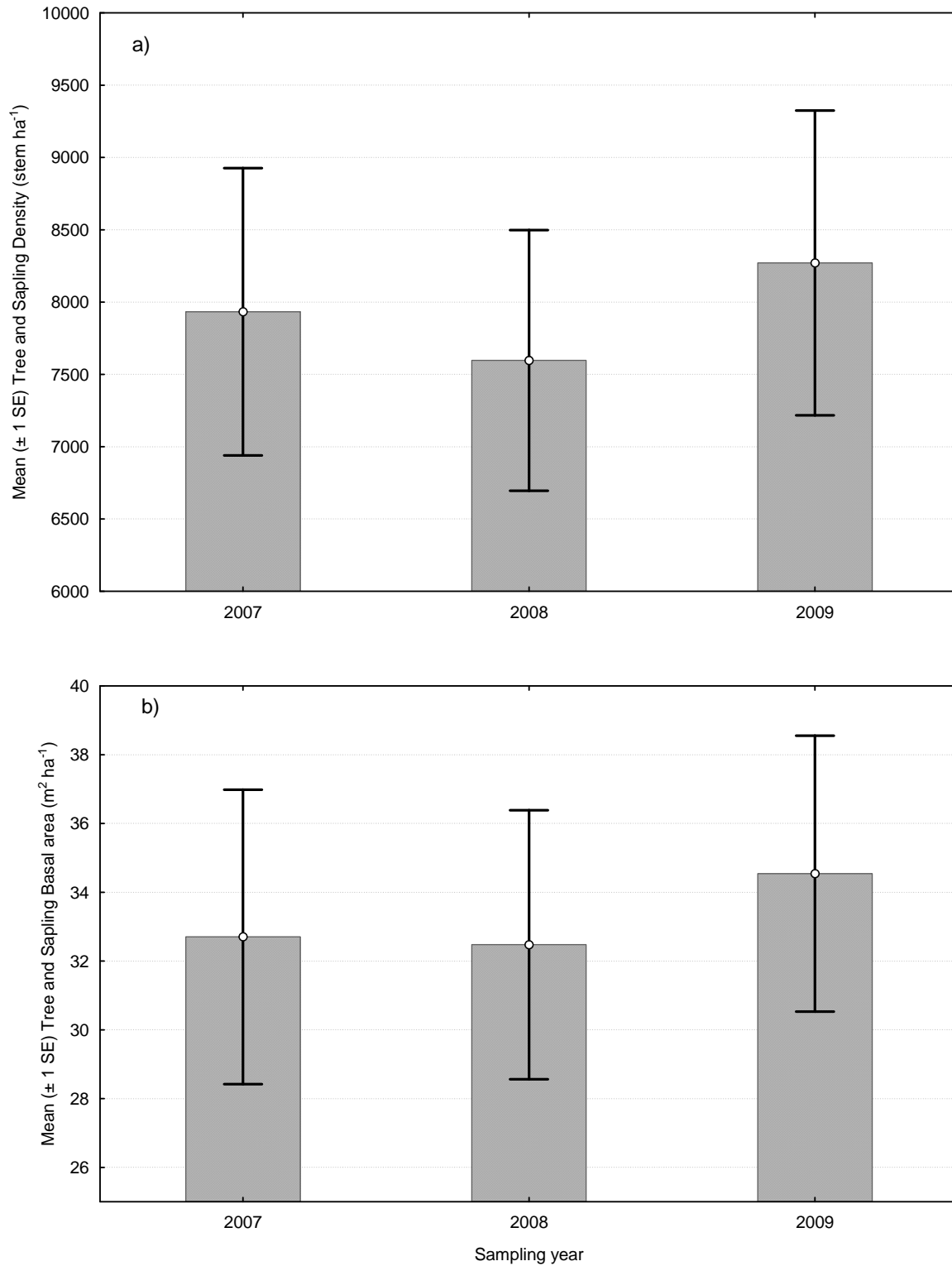


Figure 14: Annual mean (± 1 SE) woody stem ($>1\text{cm}$ dbh) density (a) and basal area (b) in tropical hardwood hammock tree islands sampled between 2007 and 2009.

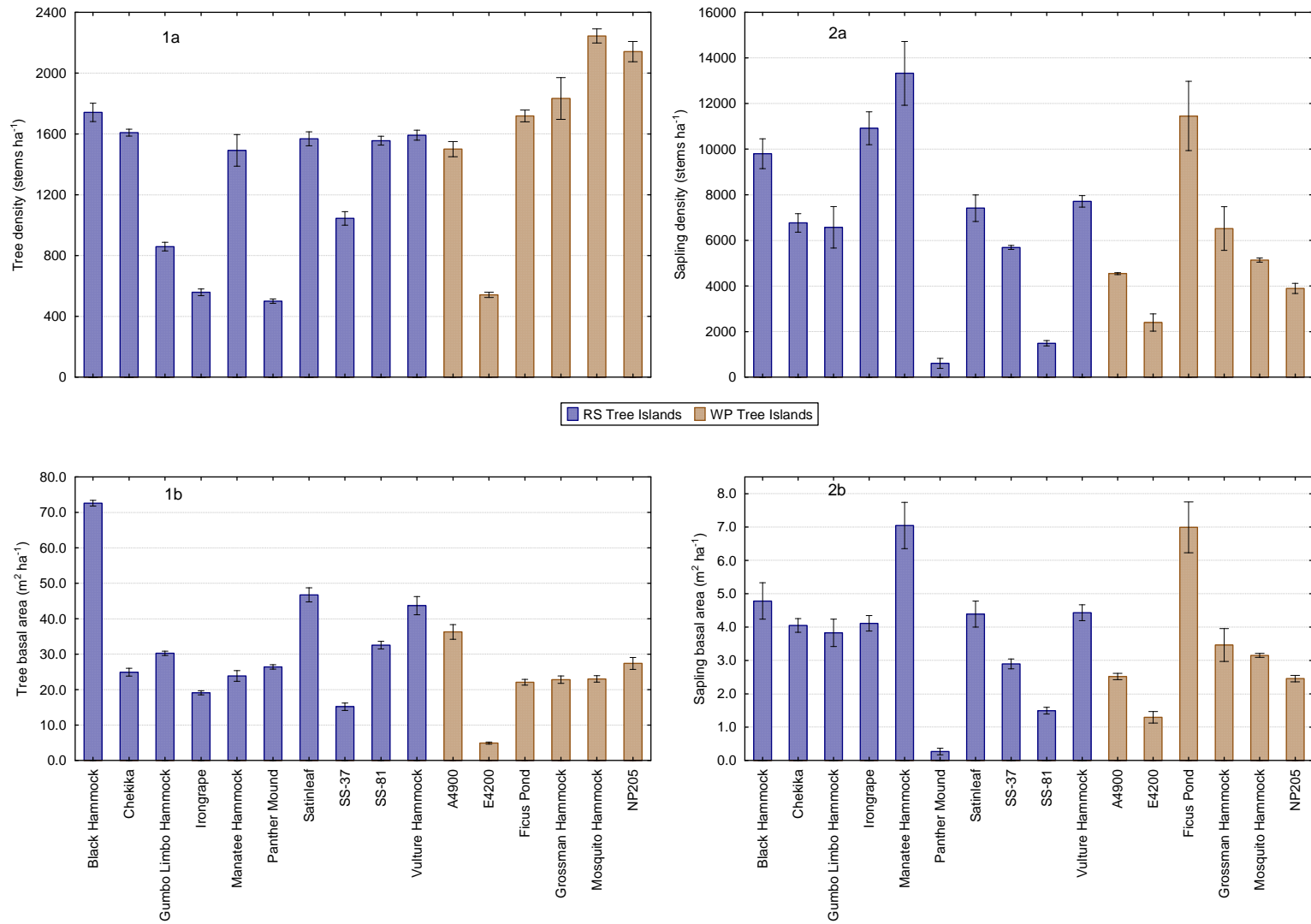


Figure 15: Annual mean (± 1 SE) tree and sapling density and basal area in 16 tree island hammocks sampled between 2007 and 2009. (1a) Tree density, (1b) Tree basal area, (2a) Sapling density, and (2b) Sapling basal area.

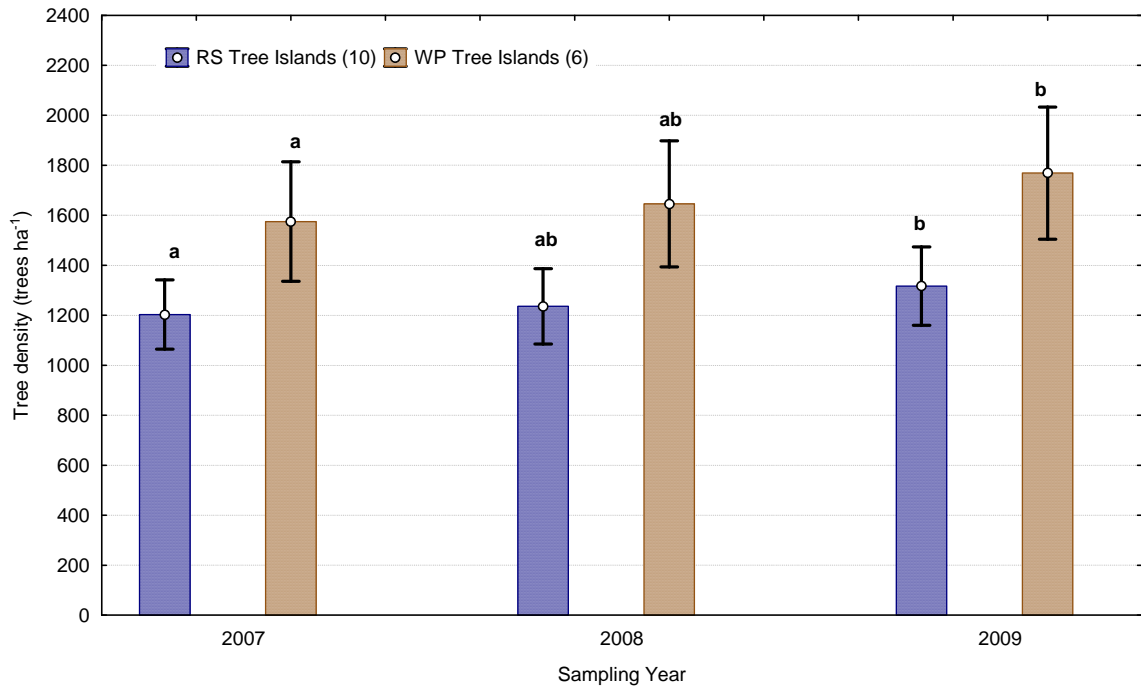


Figure 16: Mean (\pm 1 SE) tree density on tree islands in 2 regions sampled annually for 3 years (2007-2009). Different letters above the bars represent significant differences (Bonferroni test) between years within a region (Repeated measures analysis of variance; Within-subjects effect).

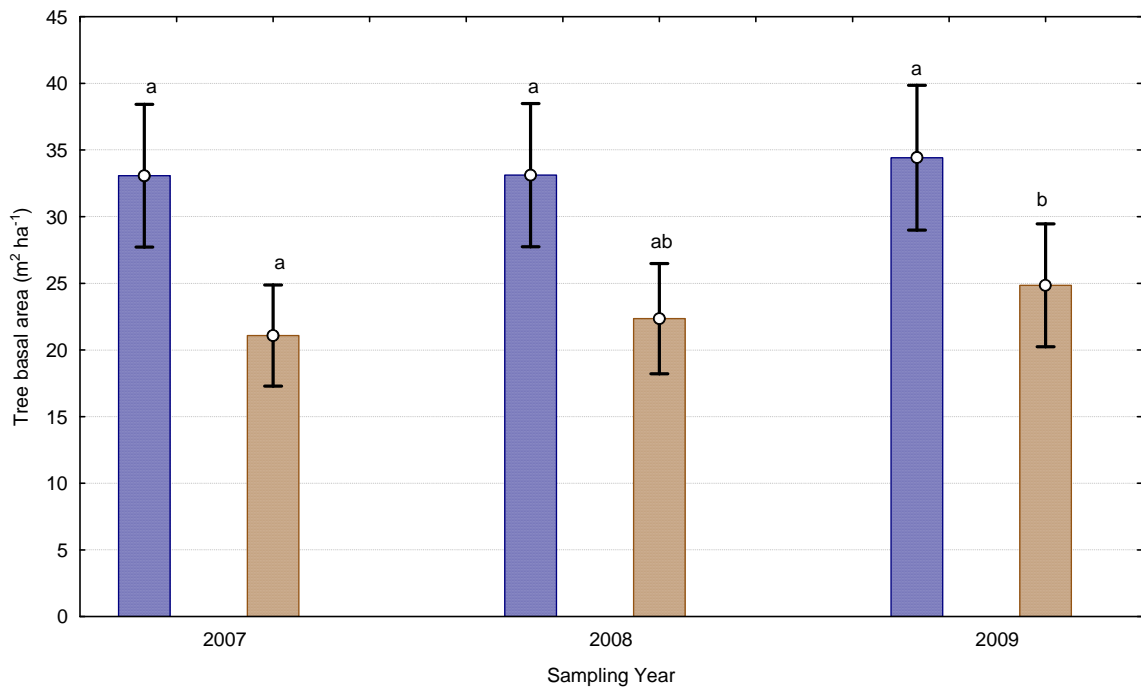


Figure 17: Mean (\pm SE) tree basal area on tree islands in 2 regions sampled annually for 3 years (2007-2009). Different letters above the boxes represent significant differences (Bonferroni test) between years within a region (Repeated measures analysis of variance; Within-subjects effect).

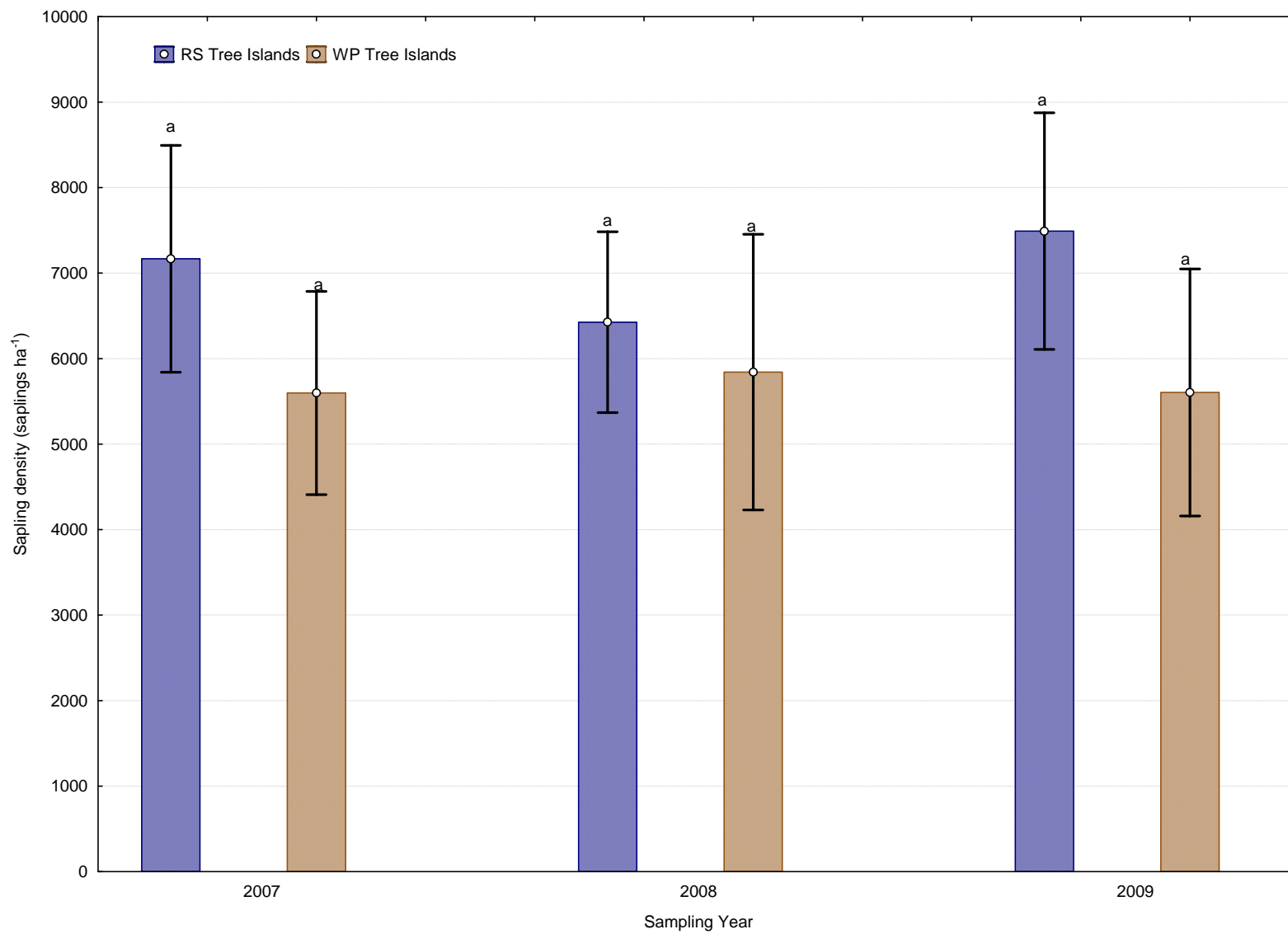


Figure 18: Mean (\pm SE) sapling density on tree islands in 2 regions sampled annually for 3 years (2007-2009).

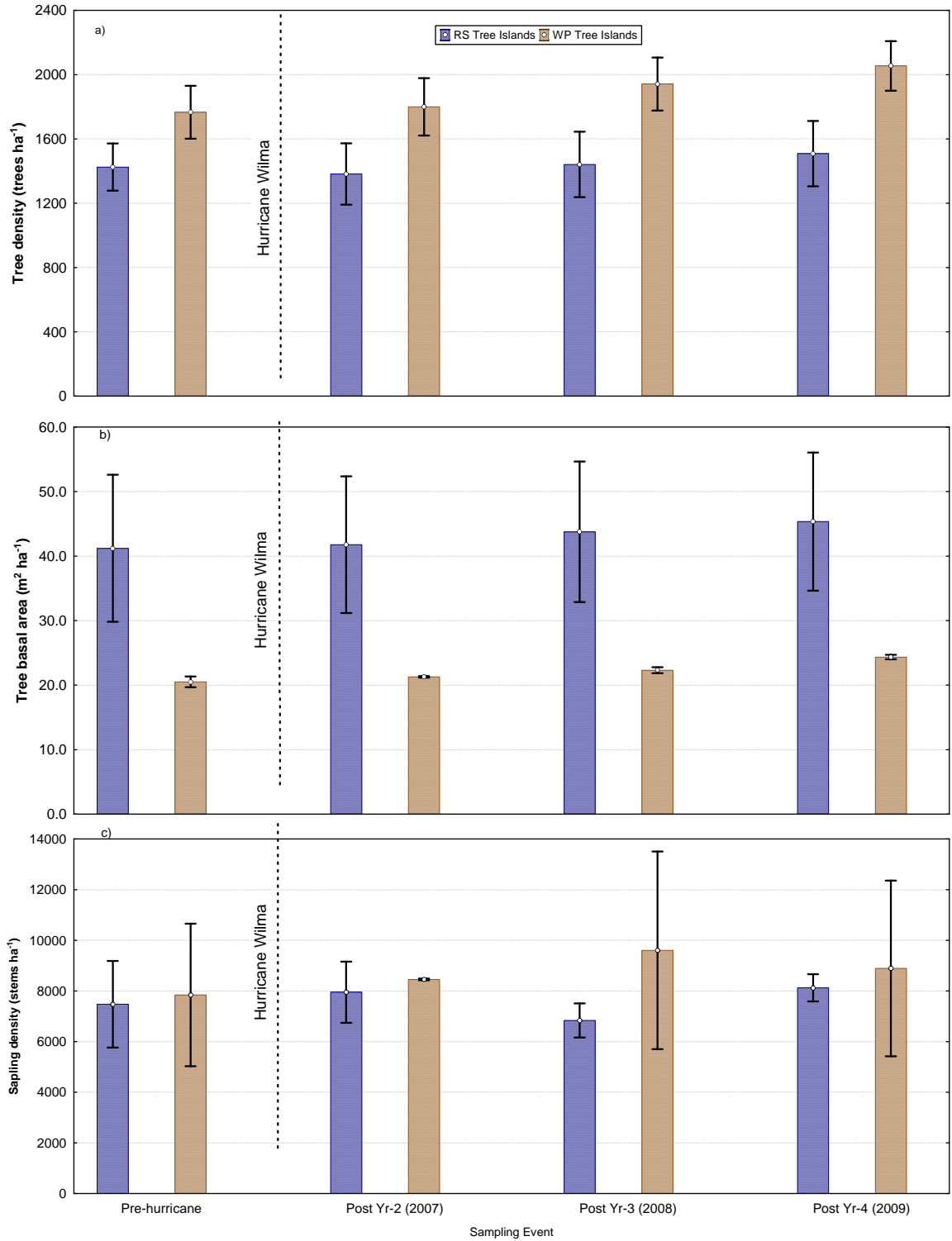


Figure 19: Mean (\pm SE) tree density (a) and tree basal area (b), and sapling density (c) on seven tree islands; four in RS and three in WP regions. Pre-hurricane data on three RS islands dated back to 2001/2002 and on 1 RS and 3 WP islands were from 1-6 months prior to the hurricane.

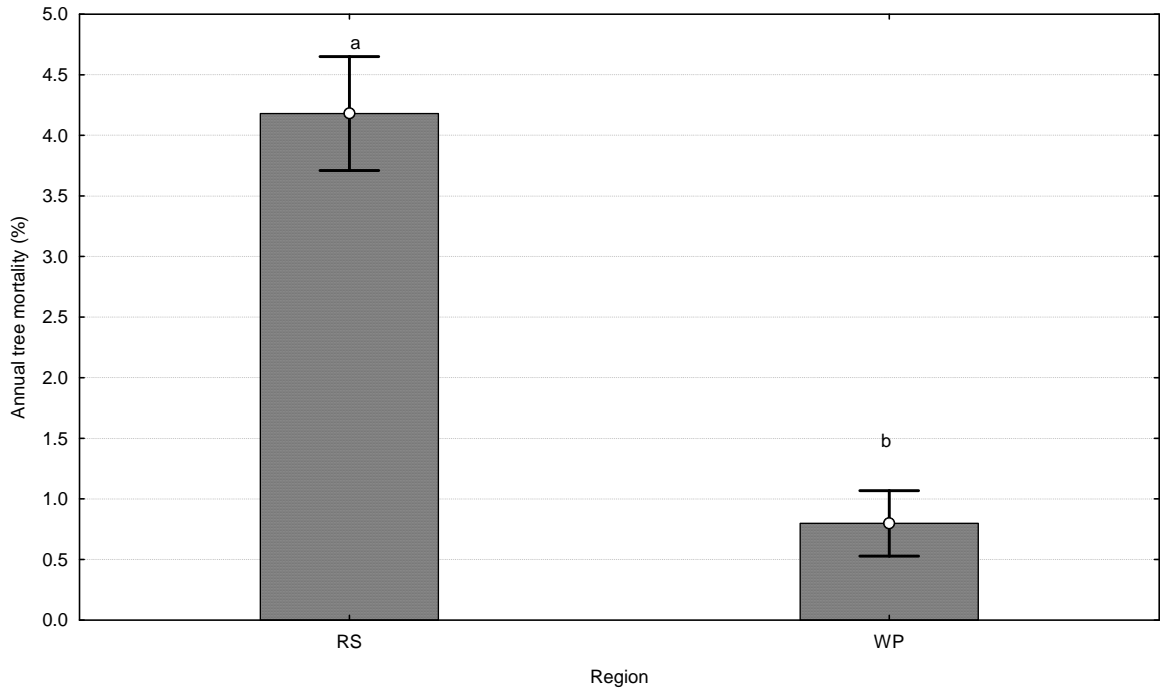


Figure 20: Mean (\pm SE) annual tree mortality (%) between 2007 and 2009 on Ridge and Slough (RS) and Wet Prairie (WP) islands. Different letters above the bars represent significant difference (One-way ANOVA; $p < 0.05$) in mortality between regions.

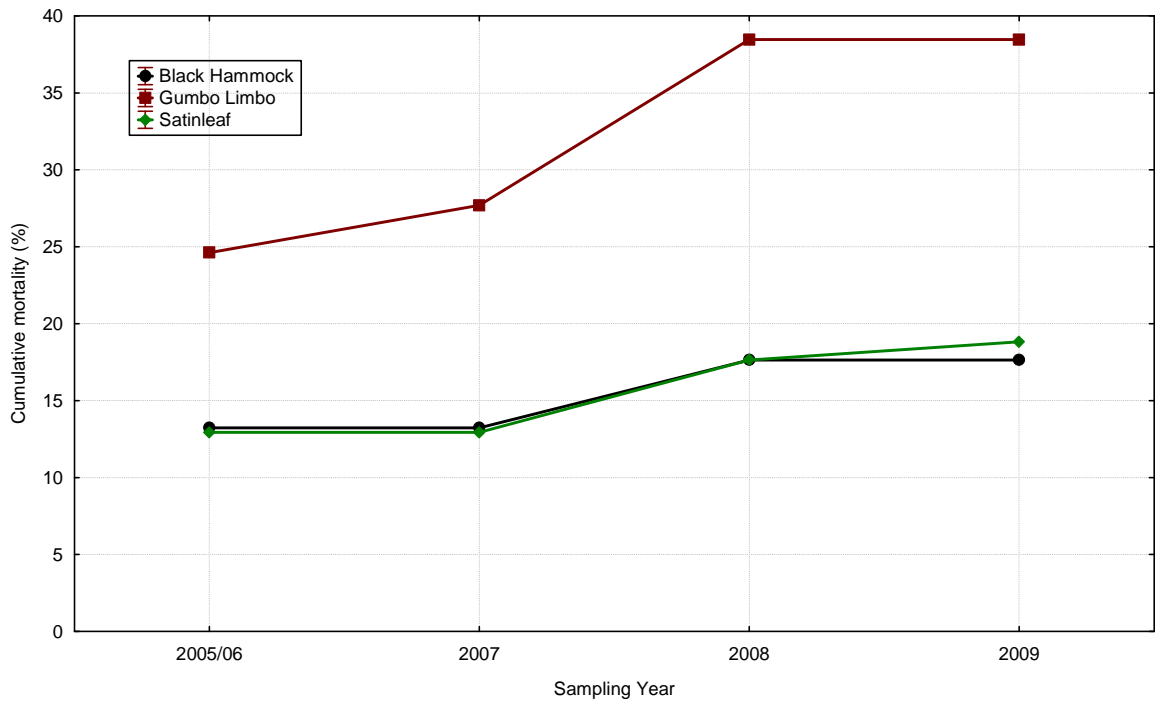


Figure 21: Cumulative mortality (%) between 2001/2002 and 2009 on three tree islands in Shark Slough regions. After 4 years, the trees on the Islands were re-surveyed in 2005 (Satinleaf) or 2006 (Black hammock and Gumbo Limbo), and thereafter annually.

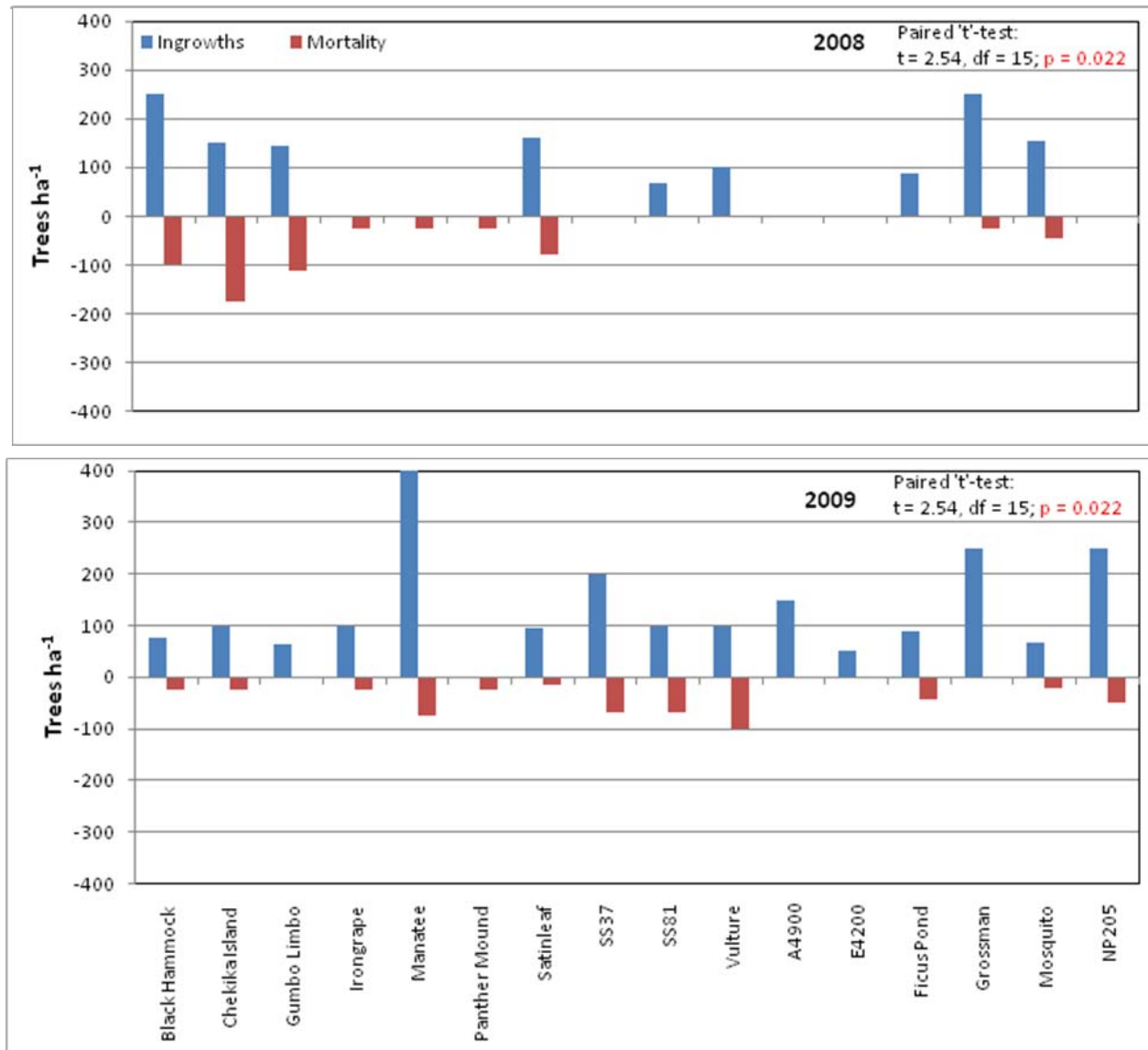


Figure 22: Tree mortality and ingrowths (trees ha⁻¹) in 16 tree island hammocks in 2008 and 2009.

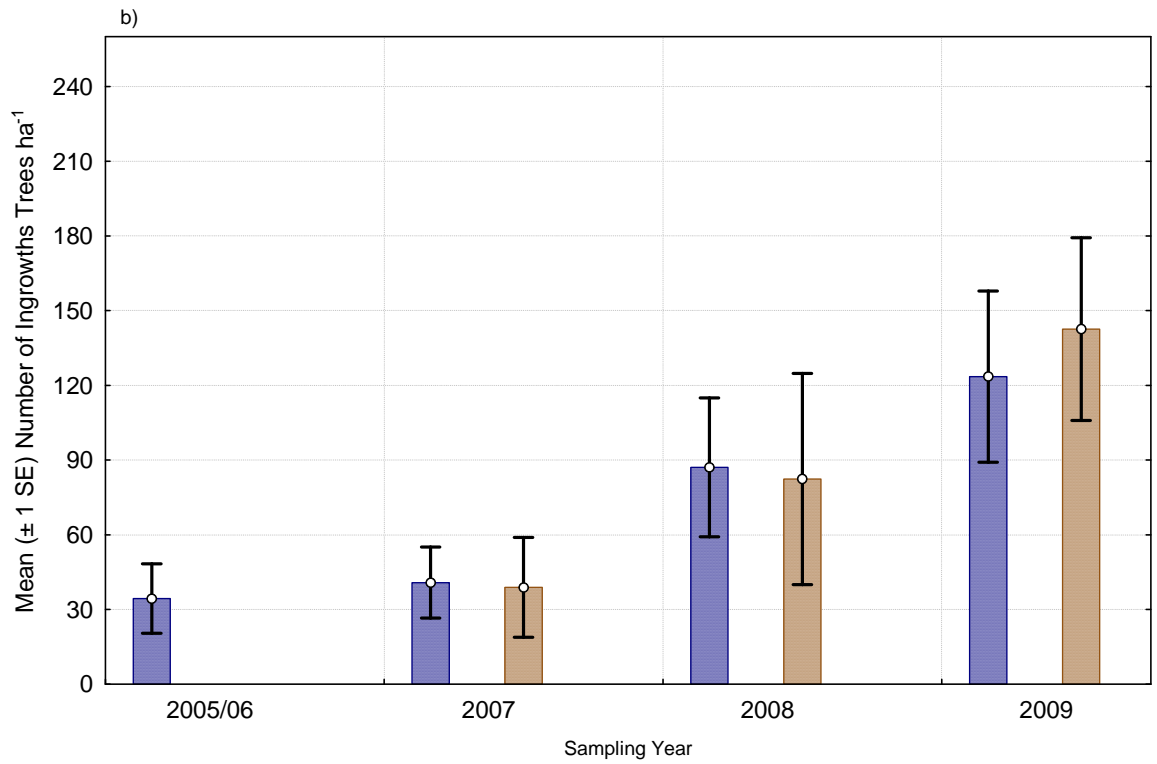
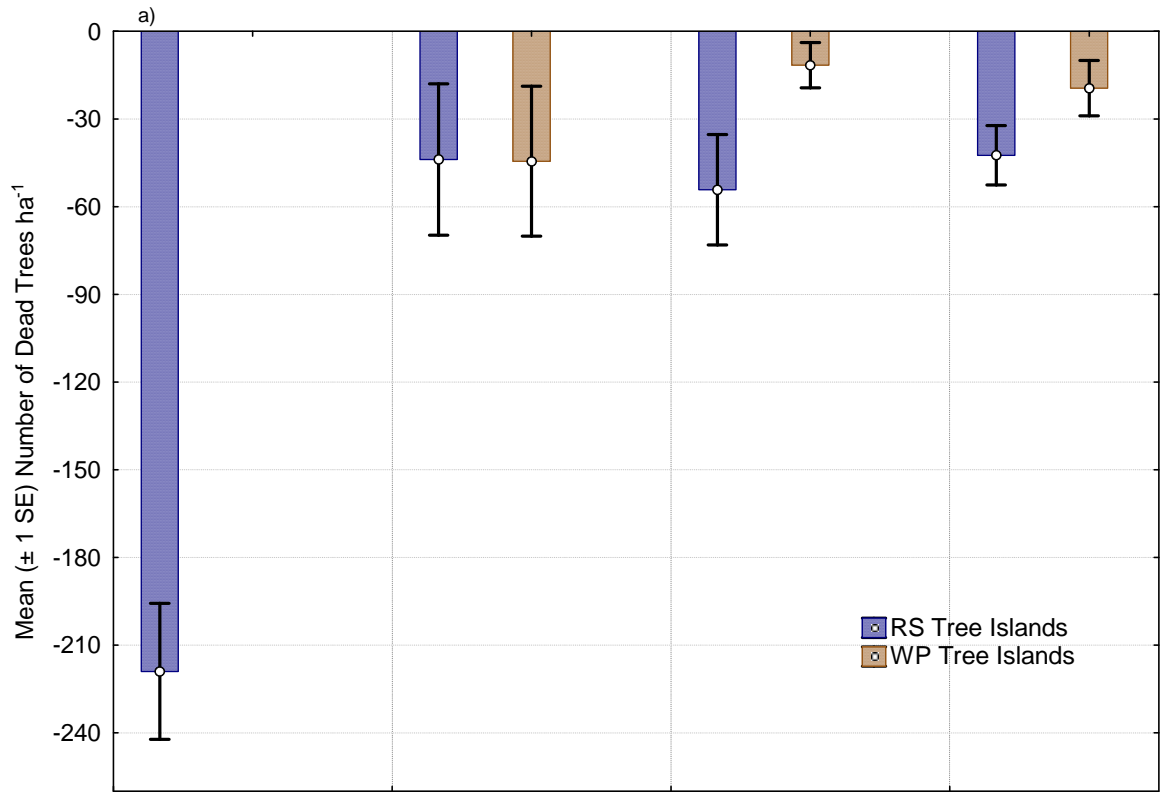


Figure 23: Regional differences in tree island tree mortality (a) and ingrowths (b).

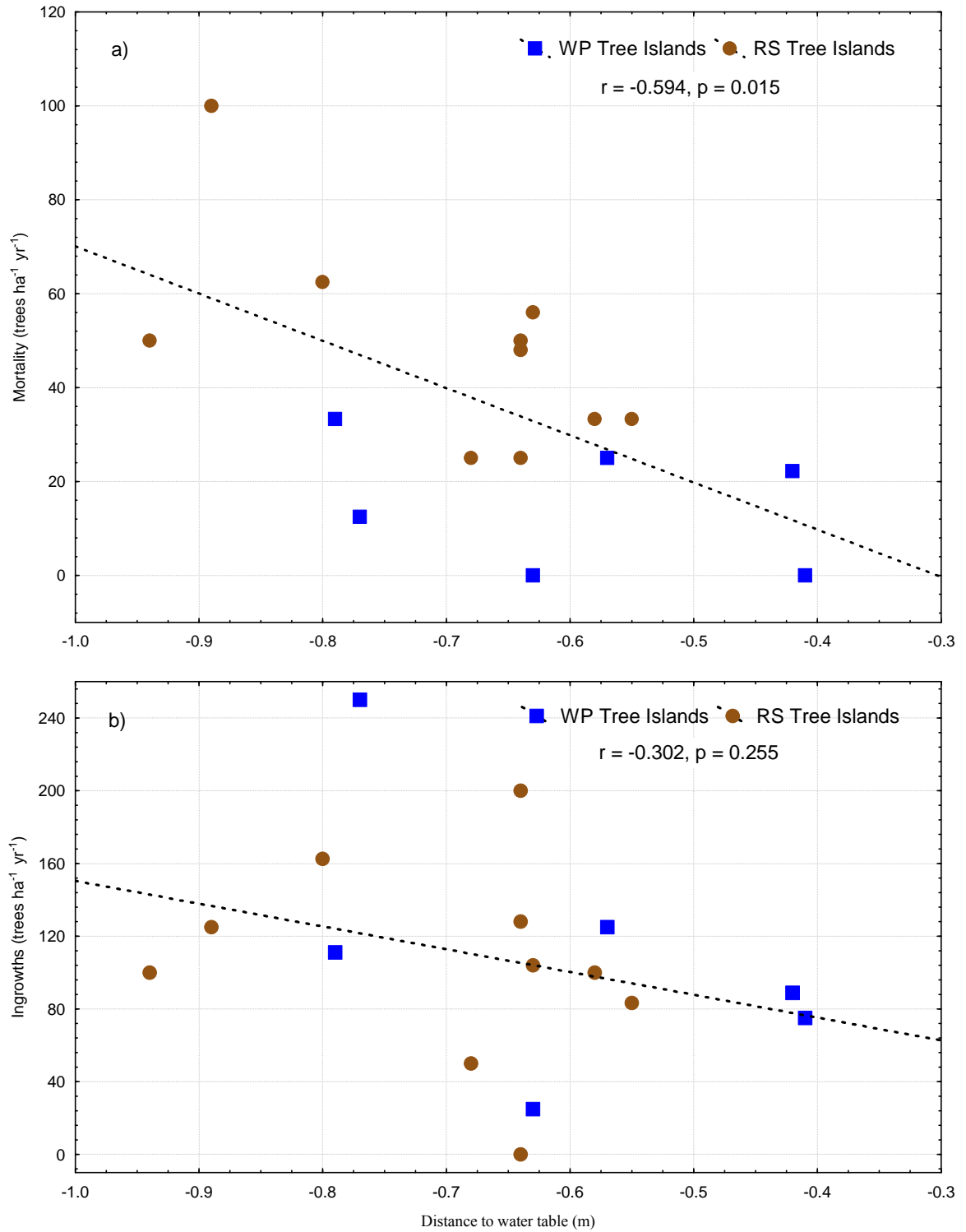


Figure 24: 2-D scatter diagram showing the relationship between mean water table depth (m) and annual mean tree mortality (a) and ingrowths (b) on 16 tree islands in RS and WP landscapes sampled between 2007 and 2009.

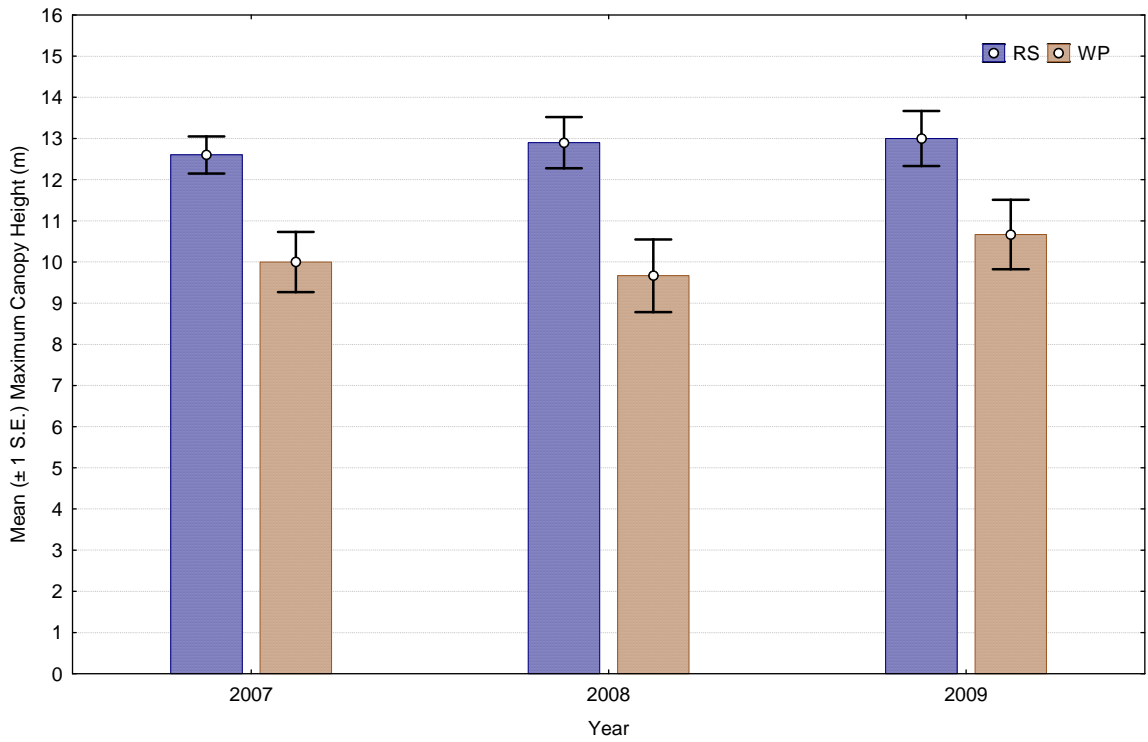


Figure 25: Regional differences in annual tree island mean maximum canopy height.

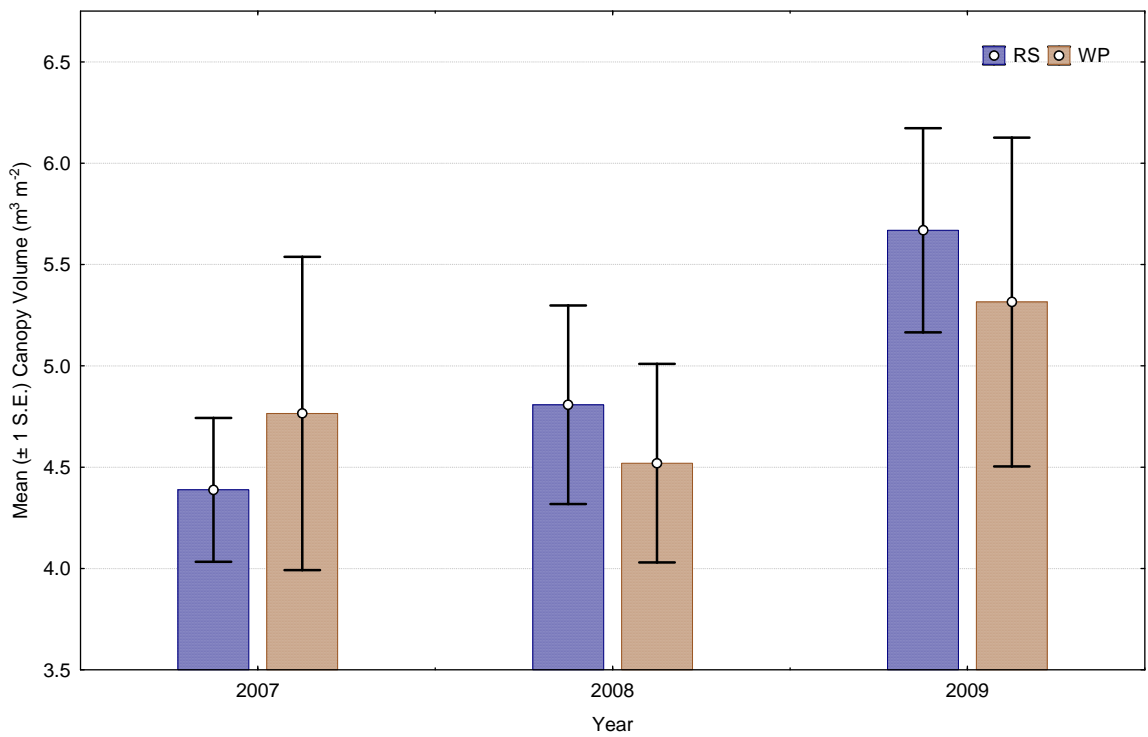


Figure 26: Regional differences in annual tree island mean mean canopy volume.

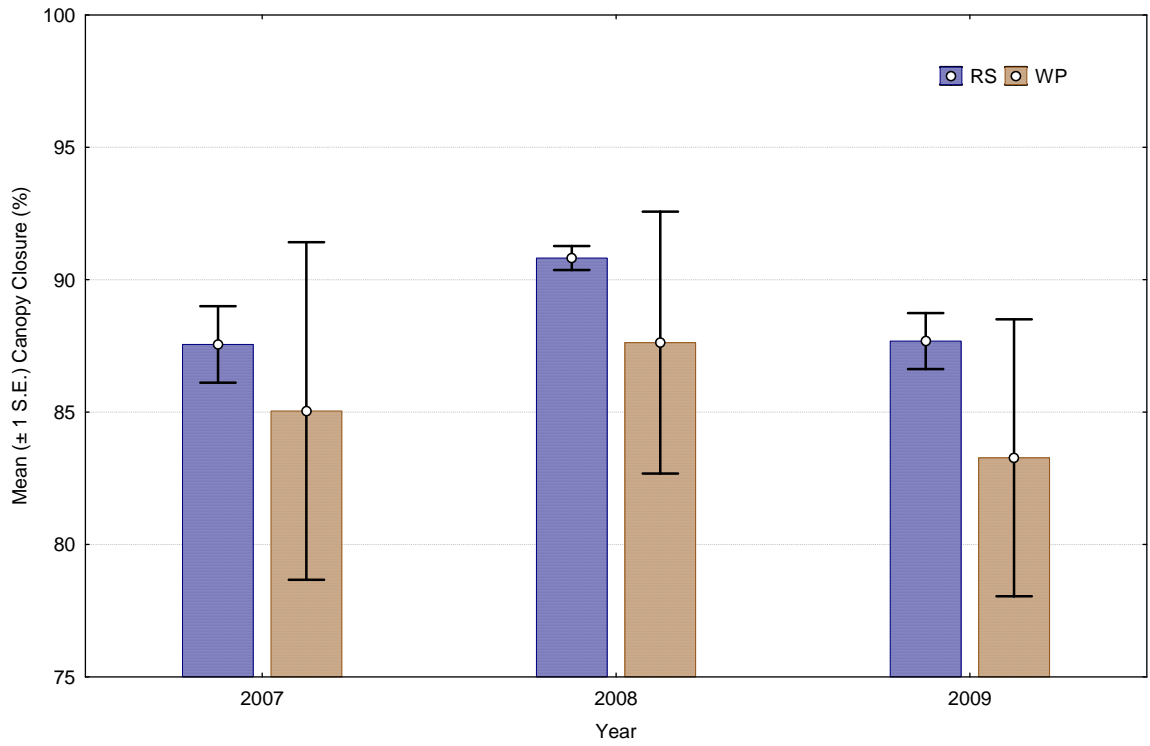


Figure 27: Regional differences in annual tree island mean canopy closure.

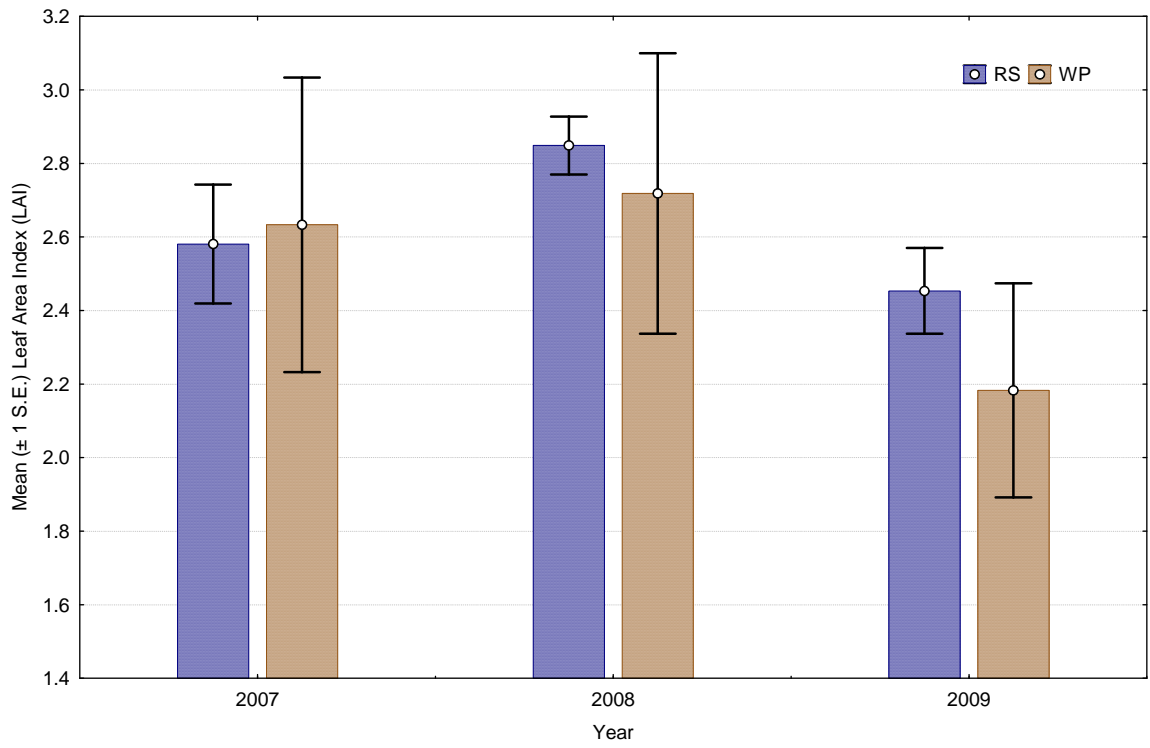


Figure 28: Regional differences in annual tree island leaf area index (LAI).

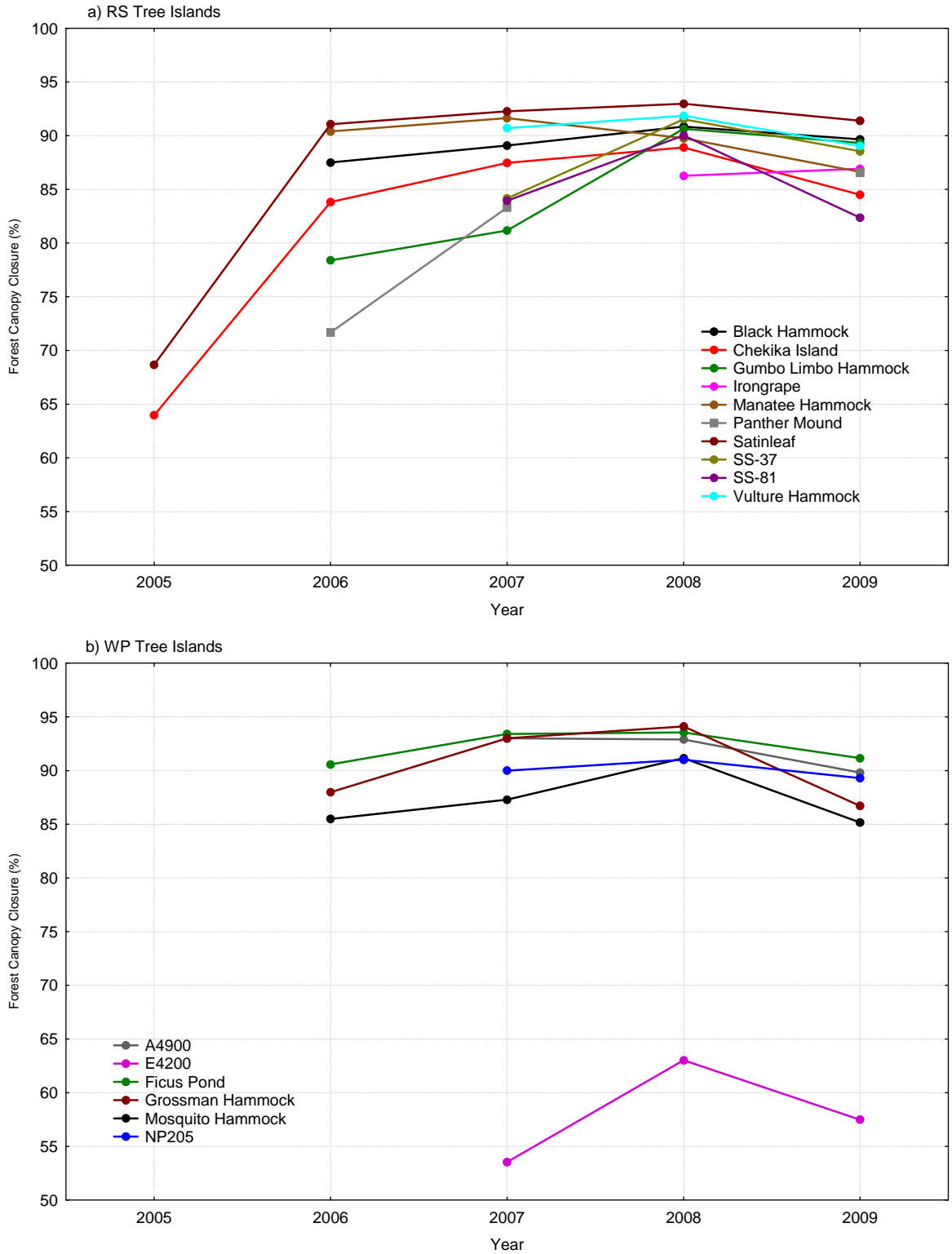


Figure 29: Annual differences in forest canopy closure for ridge and slough (RS) tree islands (a) and wet prairie tree islands (b).

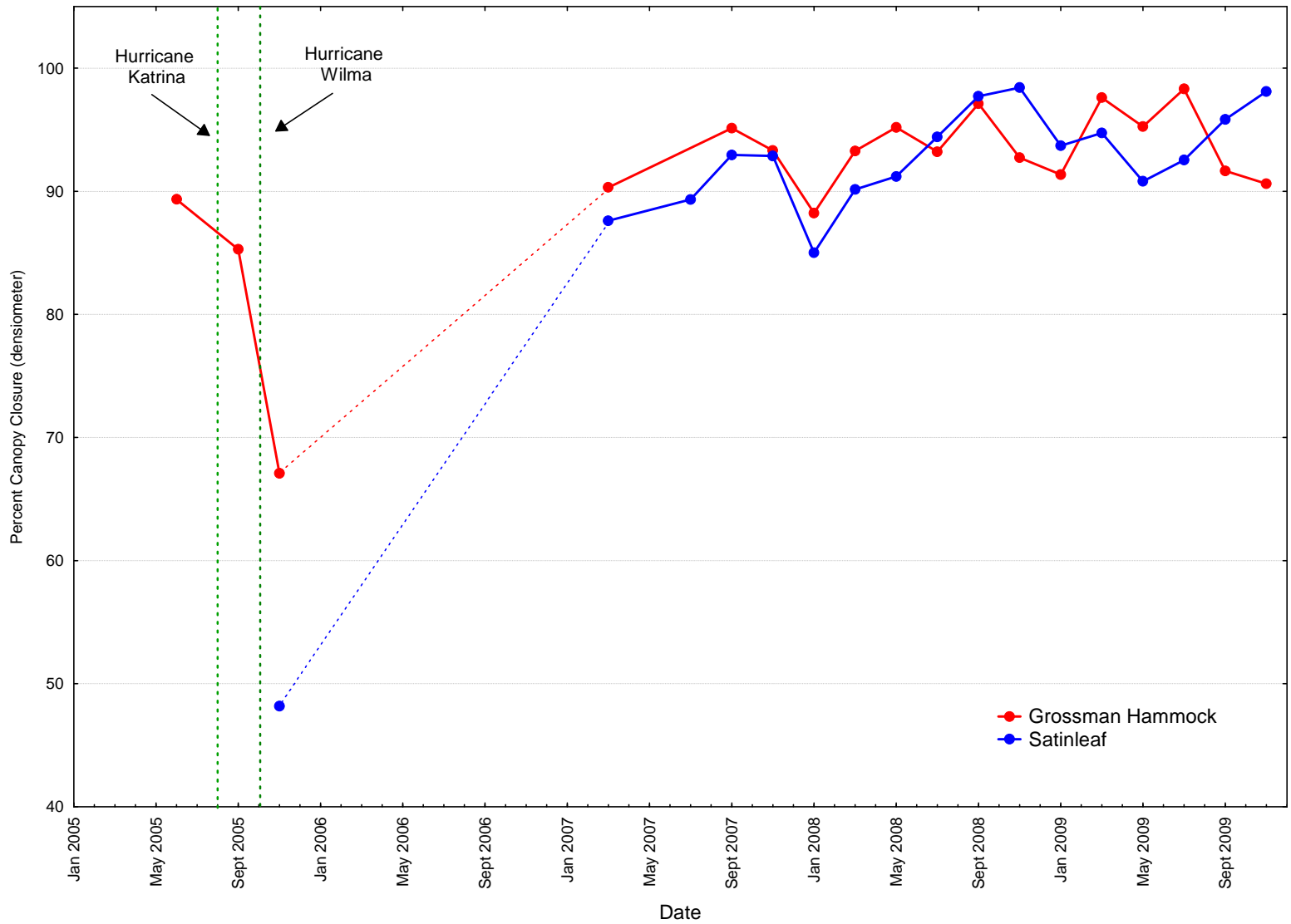


Figure 30: Seasonal variation in densiometer estimated mean canopy closure for Grossman Hammock and Satinleaf Hammock

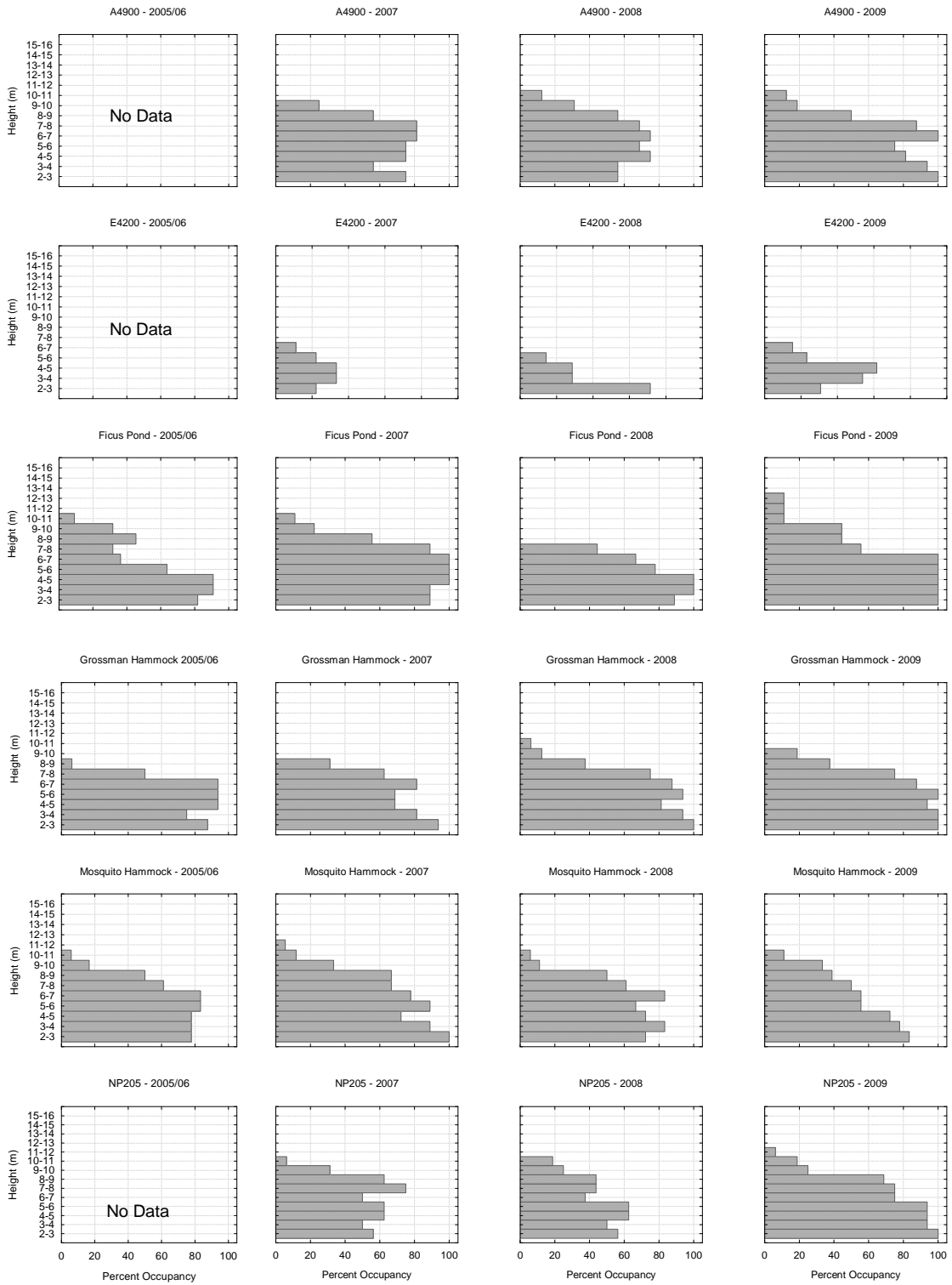


Figure 31: Annual variation in the vertical canopy profile for six wet prairie tropical hardwood hammock tree islands.

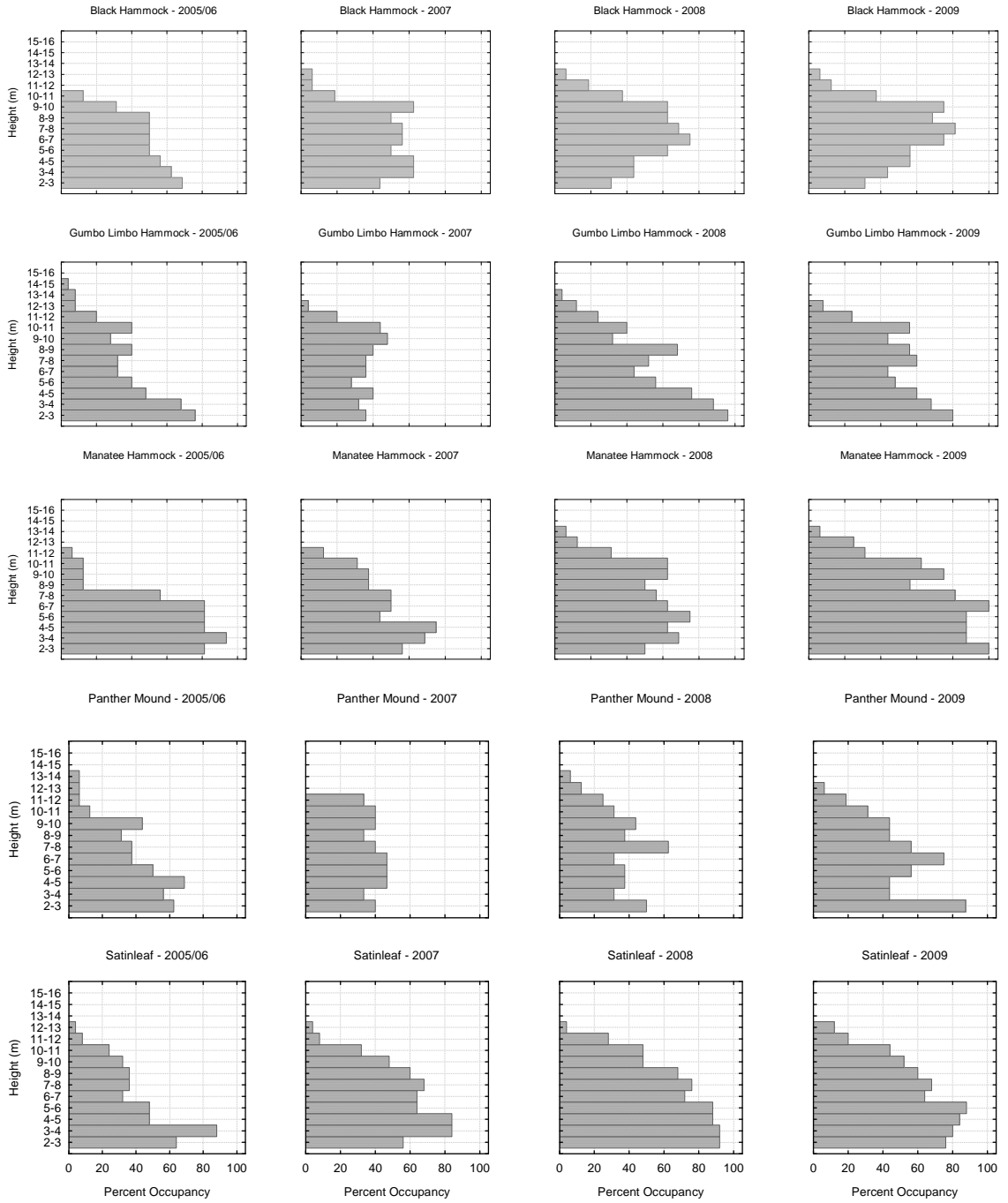


Figure 32a: Annual variation in the vertical canopy profile for five ridge and slough tropical hardwood hammock tree islands

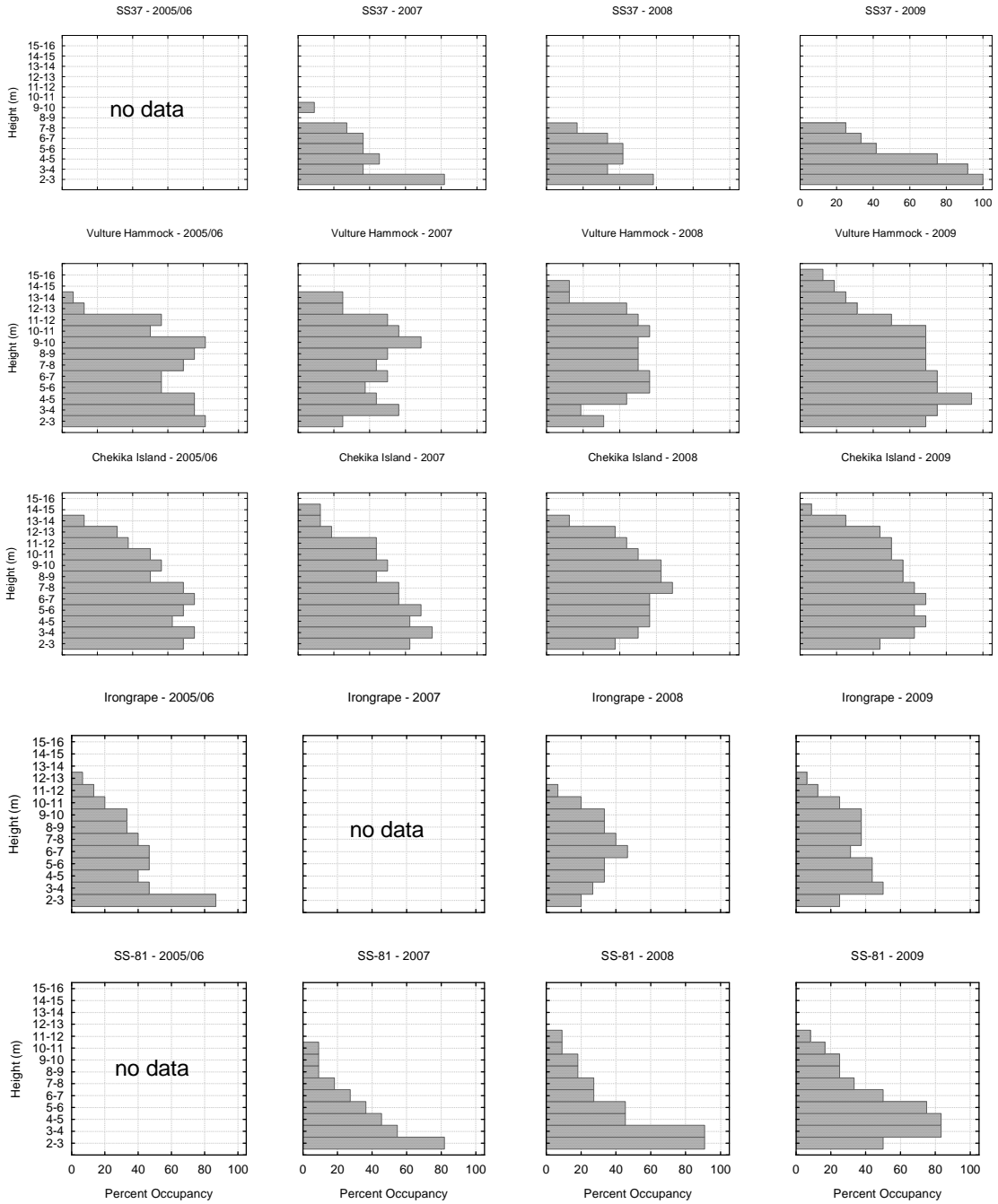


Figure 32b: Annual variation in the vertical canopy profile for five ridge and slough tropical hardwood hammock tree islands.

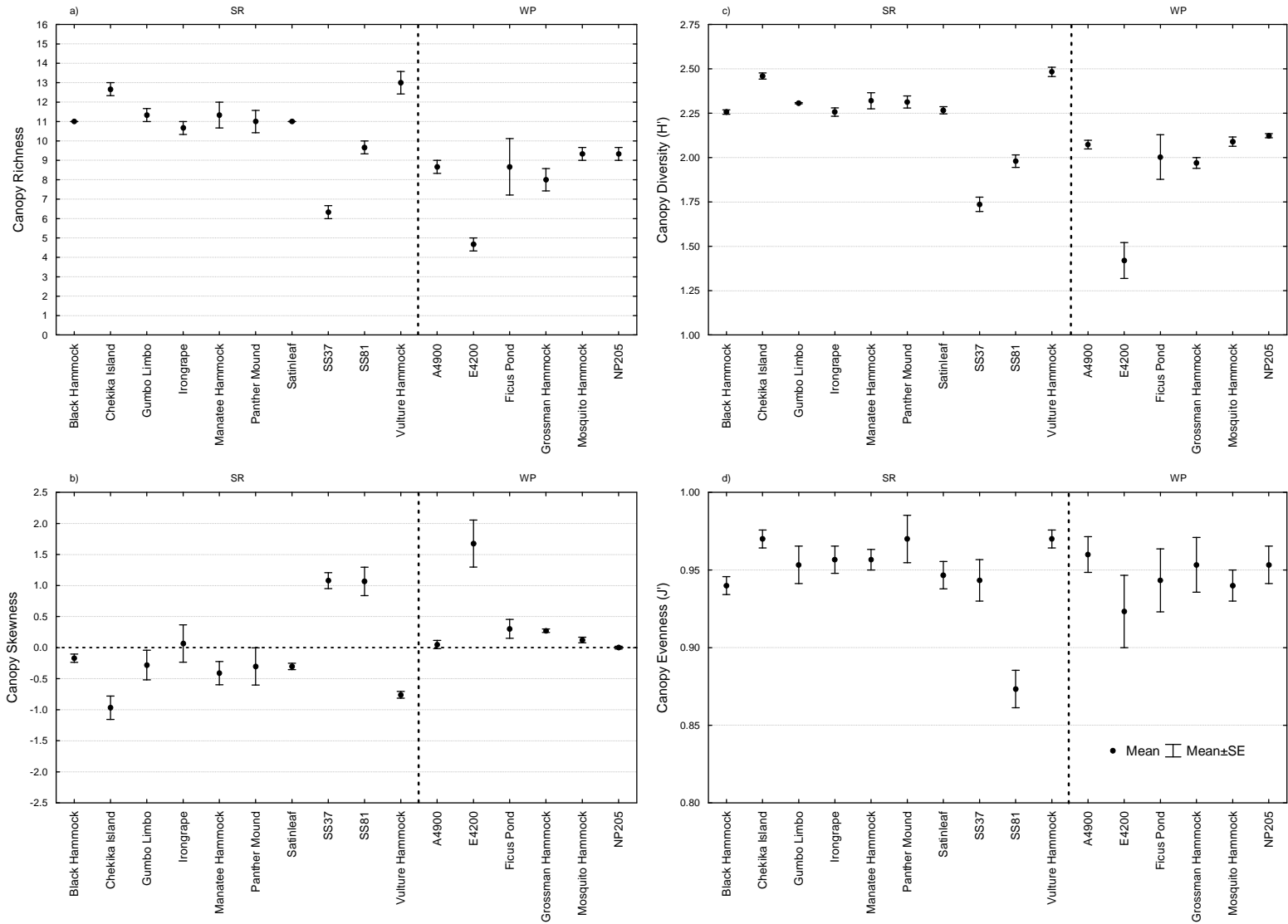


Figure 33: Tree island differences in canopy richness (a), canopy skewness (b), canopy diversity (c), & canopy evenness (d).

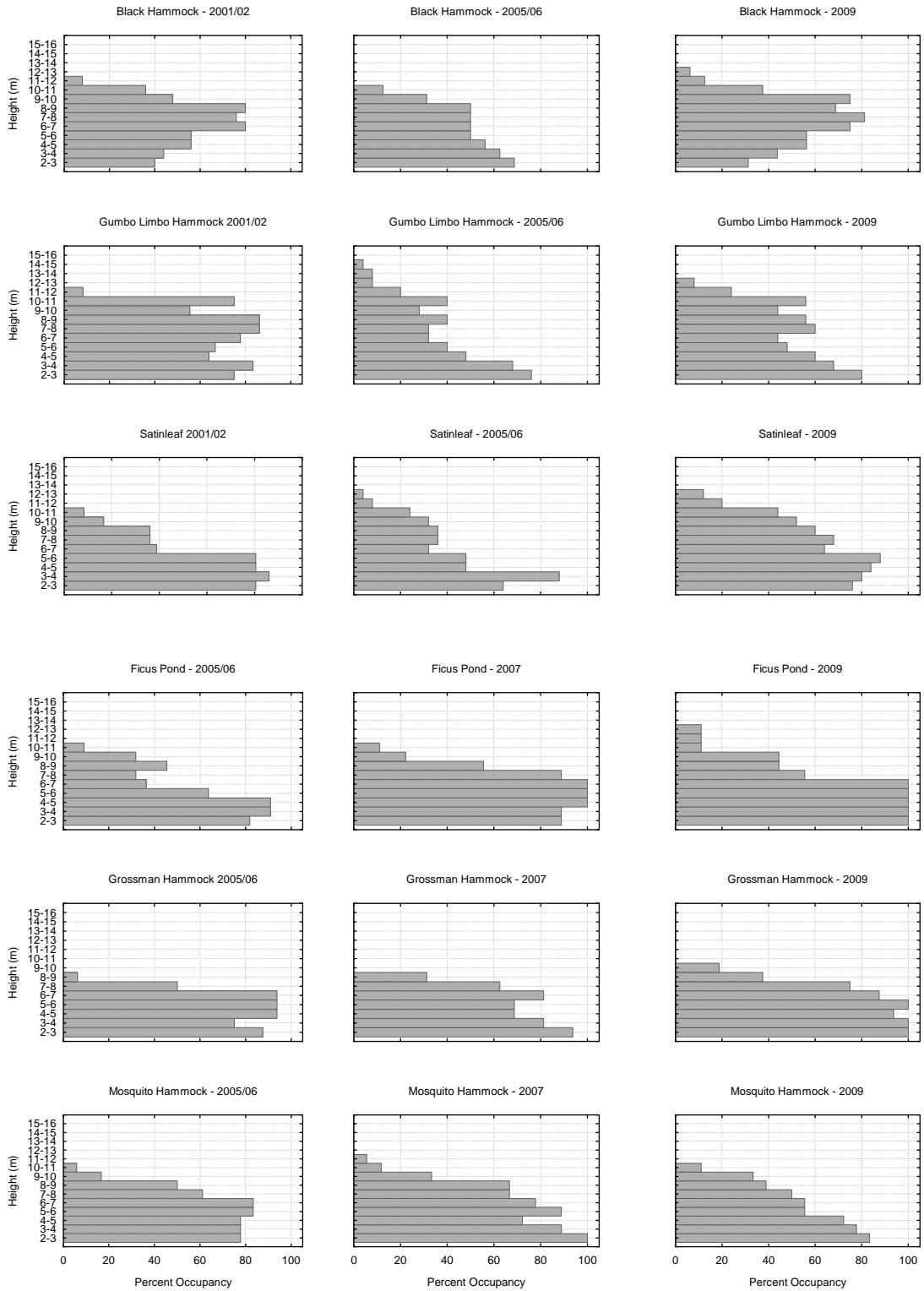


Figure 34: Pre & Post-hurricane differences in the vertical canopy profiles of three ridge and slough (RS) tree islands and three wet prairie tree islands (WP).

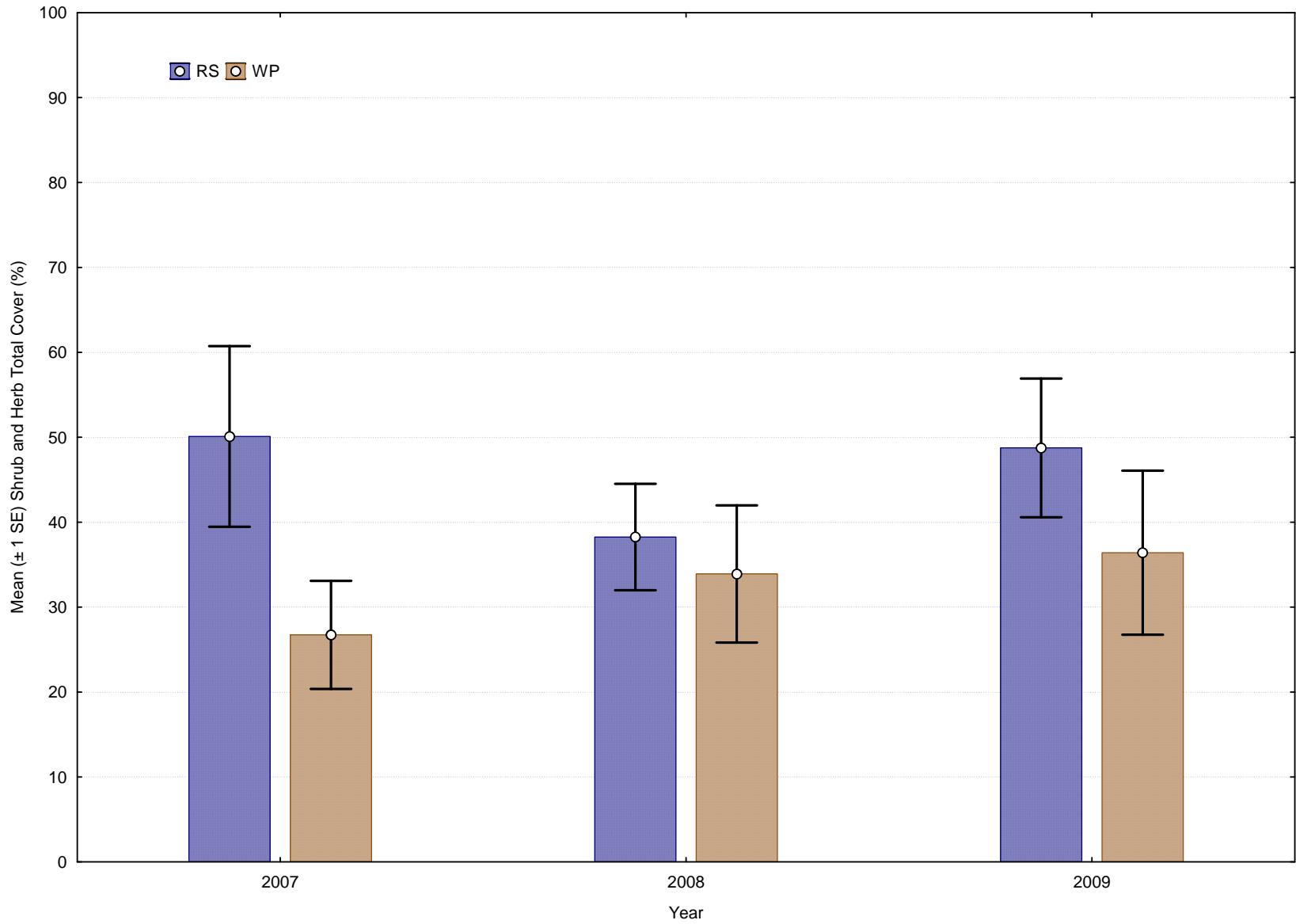


Figure 35: Regional differences in annual tree island mean shrub and herb total cover (%).

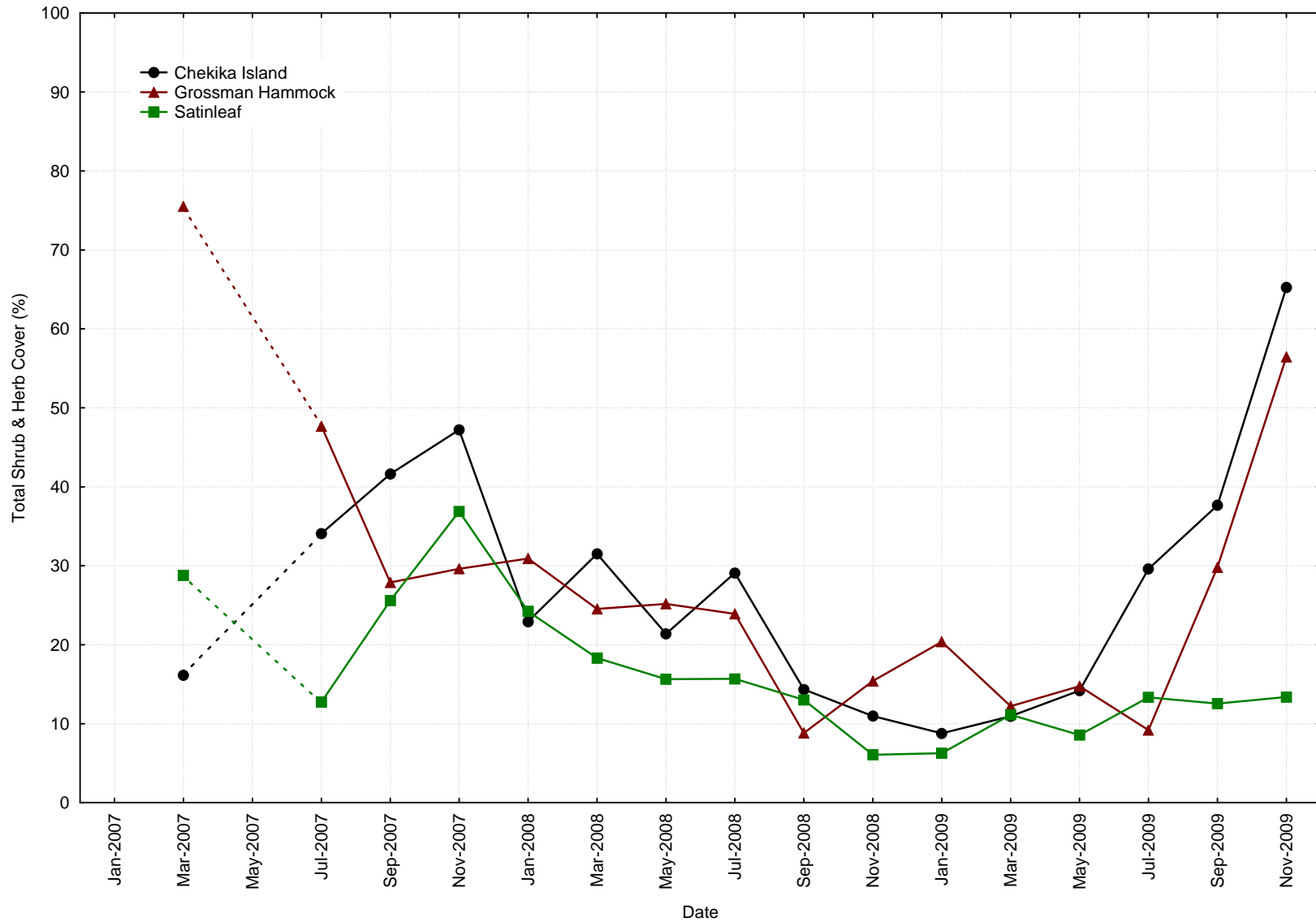


Figure 36: Bi-monthly differences in tree island shrub and herb total cover for the three high frequency sampling tree islands: Chekika Island, Grossman Hammock, & Satinleaf.

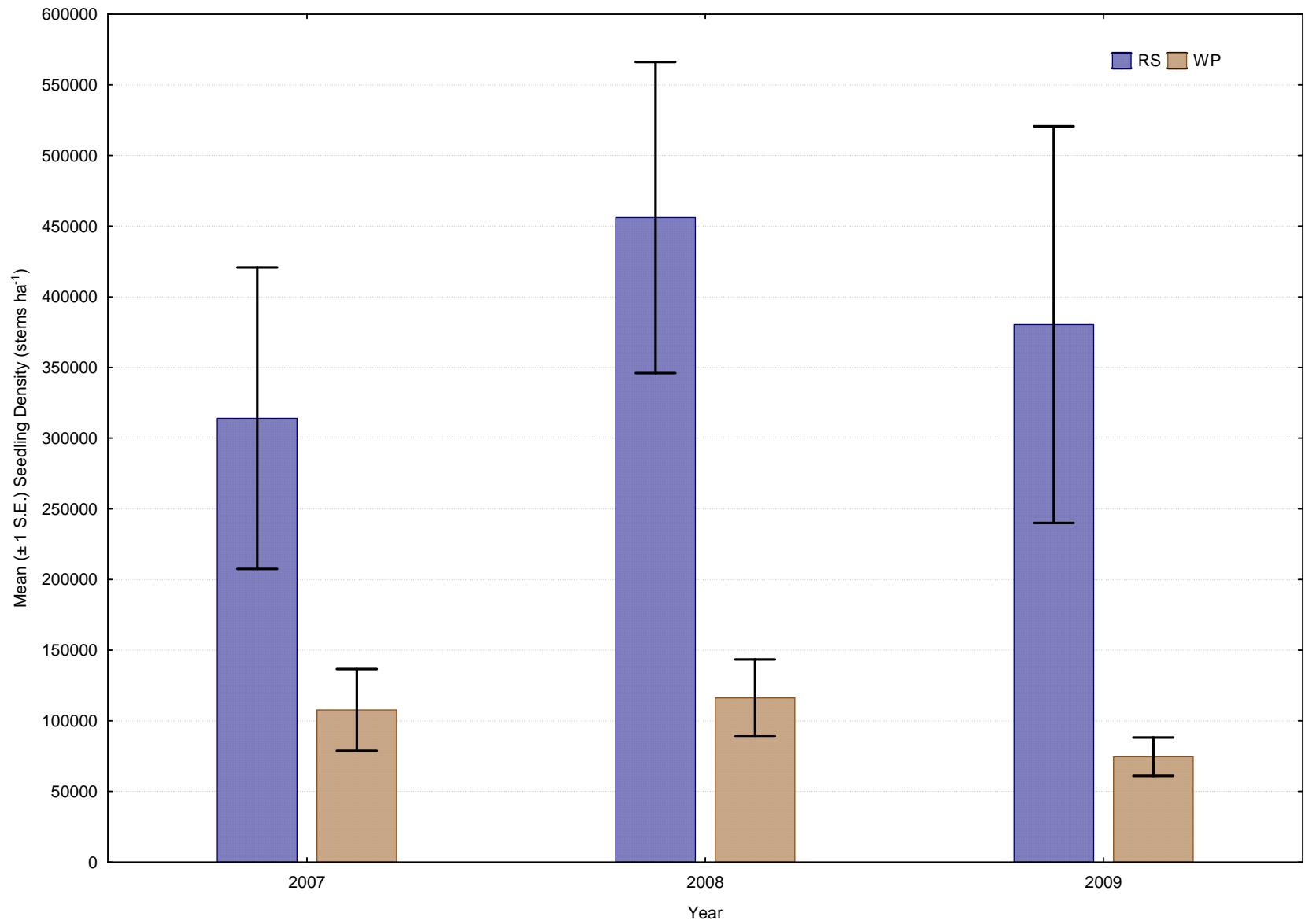


Figure 37: Regional differences in annual mean seedling density.

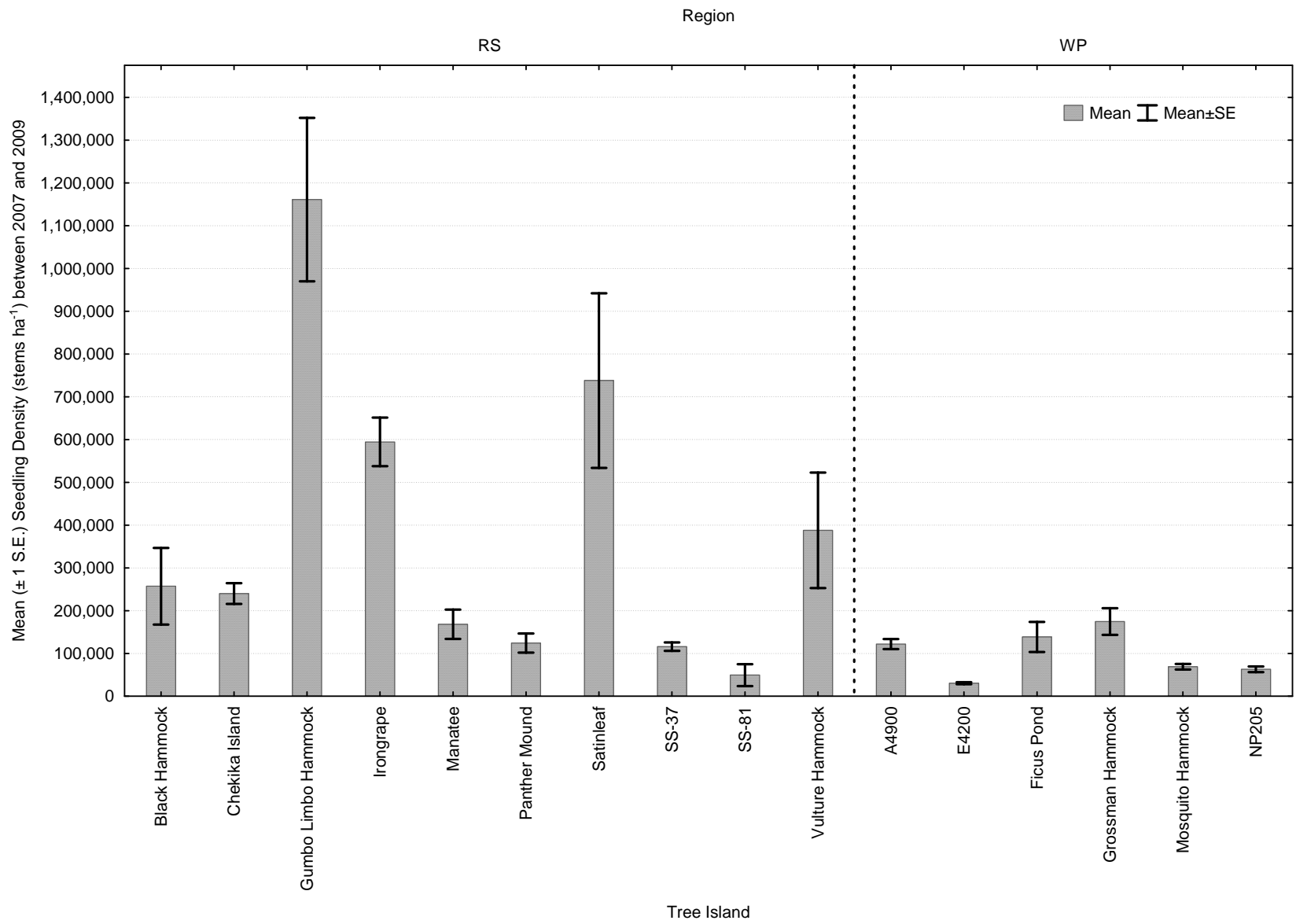


Figure 38: Differences in tree island mean seedling densities between 2007 and 2009.

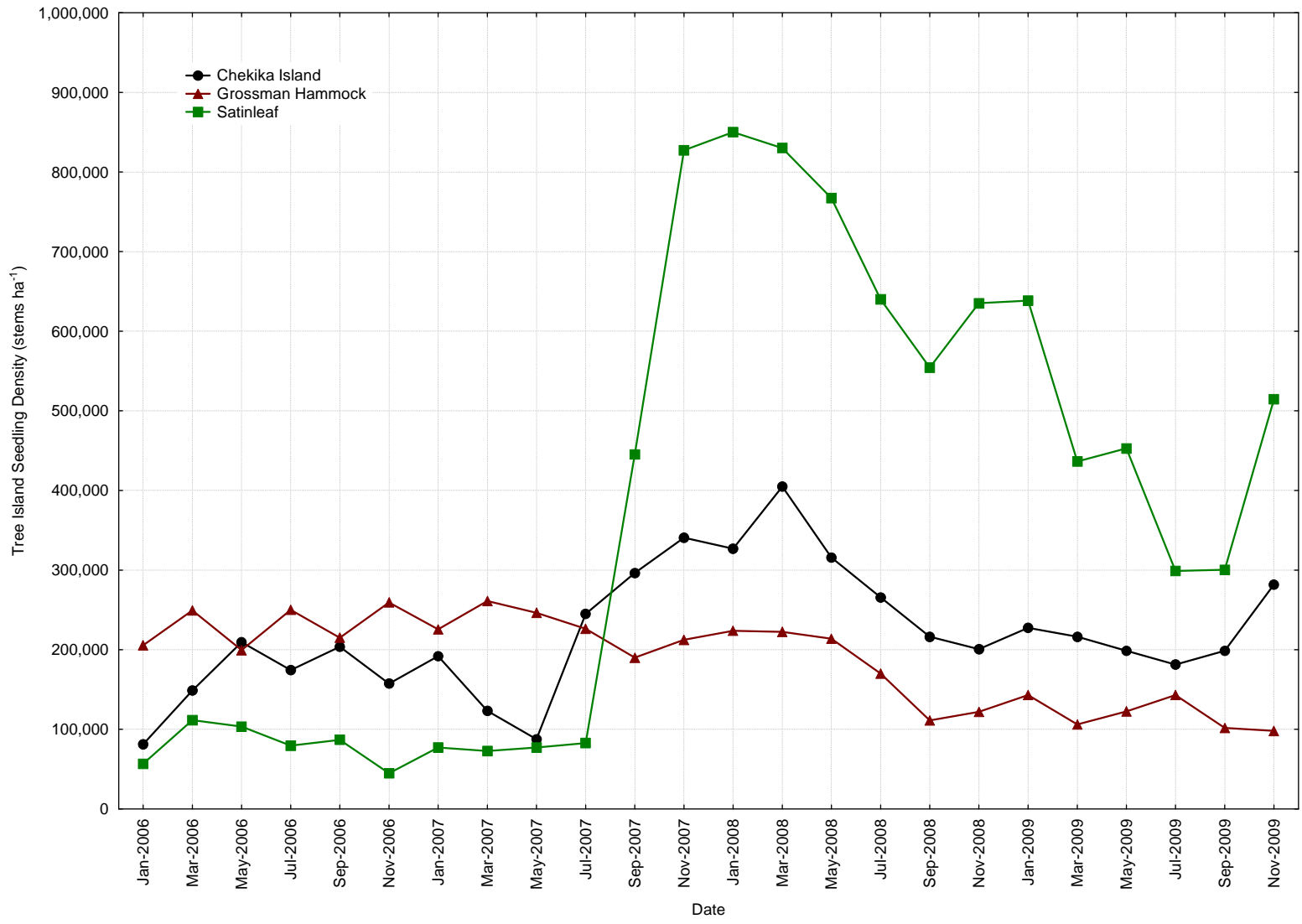


Figure 39: Bi-monthly seedling densities (stems ha⁻¹) for the three high frequency sampling tree islands: Chekika Island, Grossman Hammock, & Satinleaf.

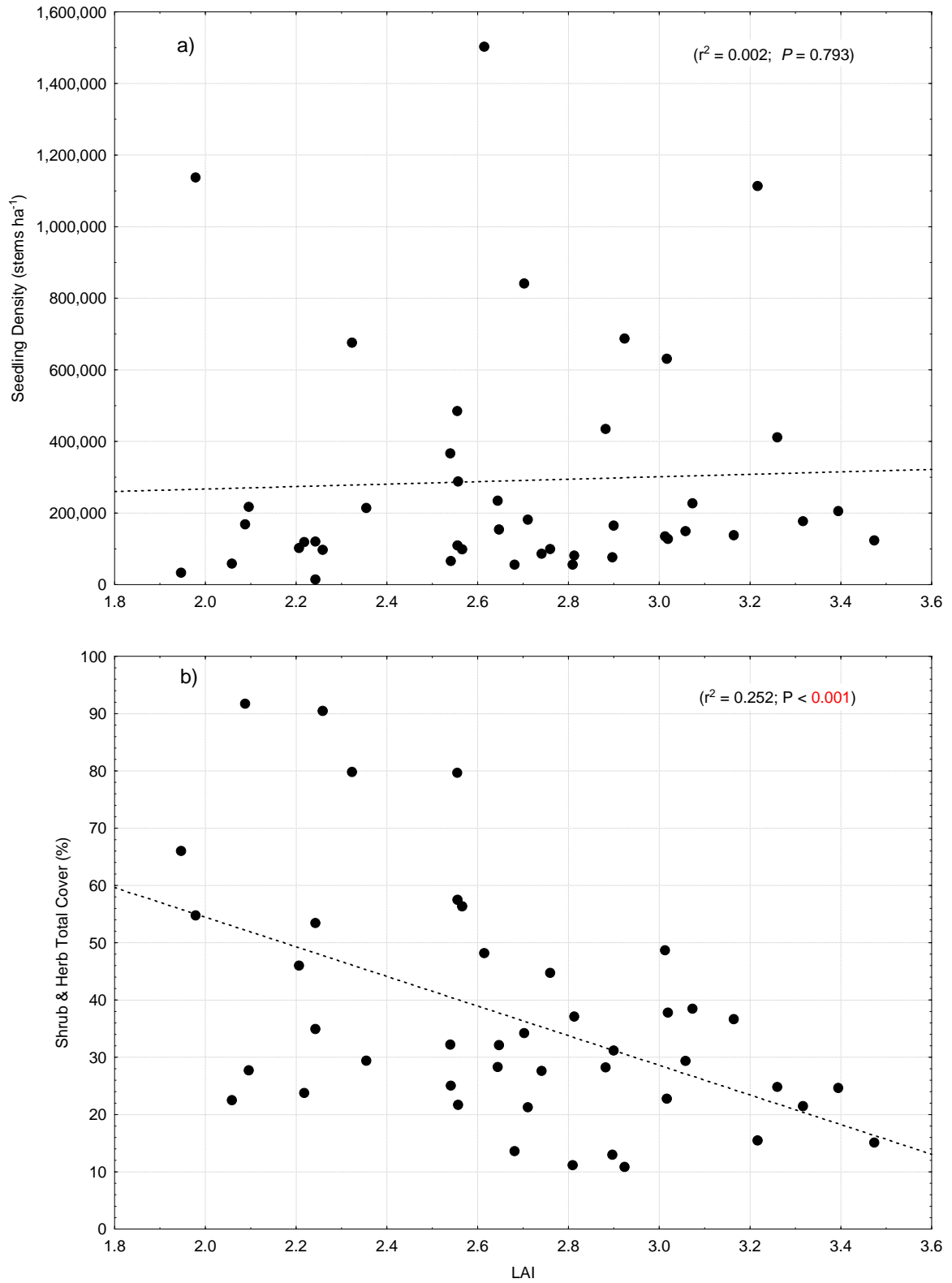


Figure 40: Correlation between LAI and seedling density (a) and shrub & herb total cover (b)

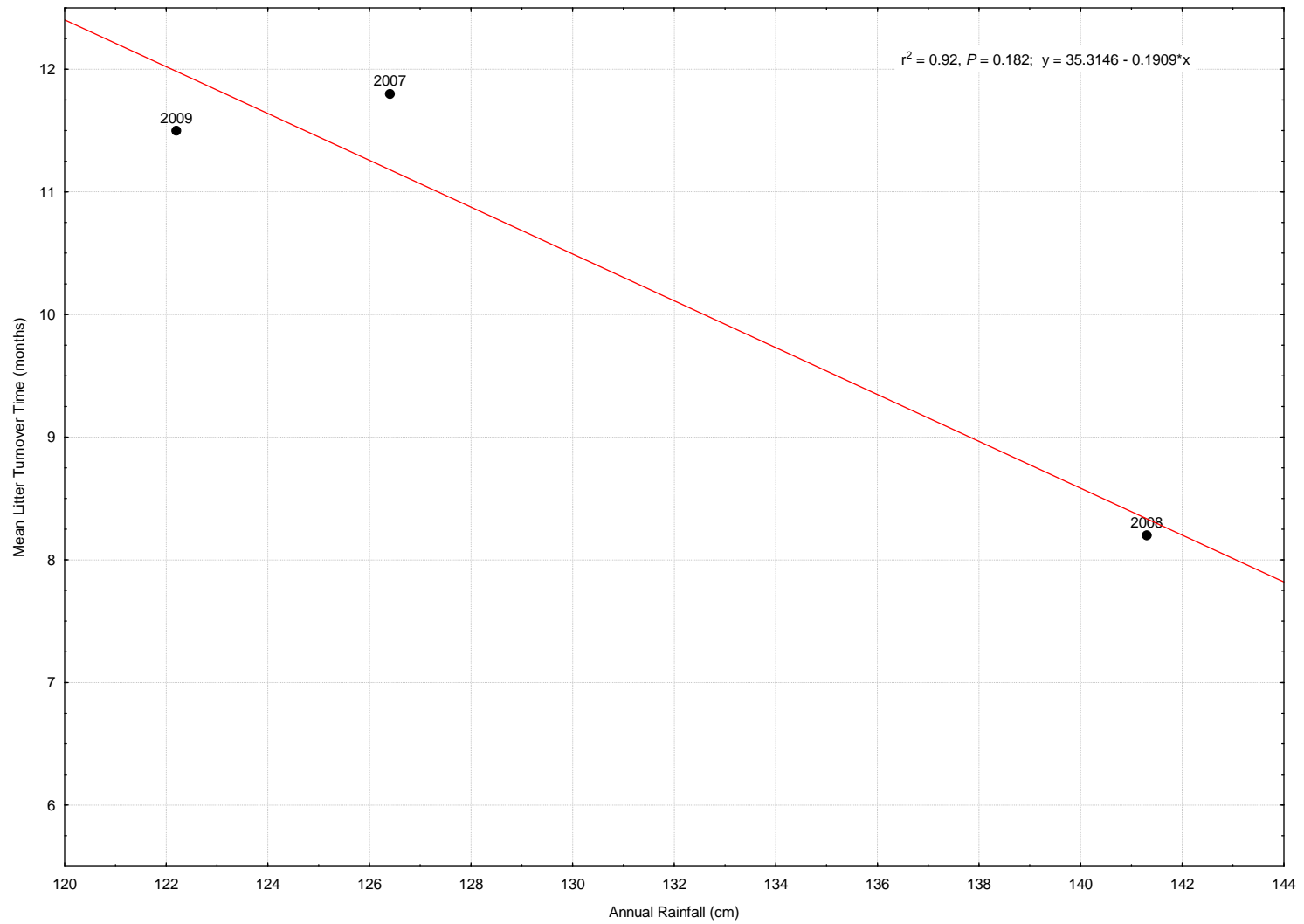


Figure 41: Correlation between mean litter turnover time (months) and precipitation (cm)

Appendix 1

(Paper accepted for publication in the peer-reviewed journal, "Ecosystems")

Forest resource islands in a sub-tropical marsh: soil:site relationships in Everglades hardwood hammocks: Shortened version: Soil:site relationships in Everglades tree islands

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Abstract

Spatial heterogeneity in soils is often characterized by the presence of resource-enriched patches ranging in size from a single shrub to wooded thickets. If the patches persist long enough, the primary constraint on production may transition from one limiting environmental factor to another. Tree islands that are scattered throughout the Florida Everglades basin comprise nutrient-enriched patches, or resource islands, in P-limited oligotrophic marshes. We used Principal Component Analysis and multiple regressions to characterize the belowground environment (soil, hydrology) of one type of tree island, hardwood hammocks, and examined its relationship with the three structural variables (basal area, biomass, and canopy height) indicative of site productivity. Hardwood hammocks in the southern Everglades grow on two distinct soil types. The first, consisting of shallow, organic, relatively low-P soils, is common in the seasonally-flooded Marl Prairie landscape. In contrast, hammocks on islands embedded in long hydroperiod marsh have deeper, alkaline, mineral soils with extremely high P concentrations. However, this edaphic variation does not translate simply into differences in forest structure and production. Relative water depth was unrelated to all measures of forest structure and so was soil P, but the non-carbonate component of the mineral soil fraction exhibited a strong positive relationship with canopy height. The development of P-enriched forest resource islands in the Everglades marsh is accompanied by the buildup of a mineral soil; however, limitations on growth in mature islands appear to differ substantively from those that dominate incipient stages in the transformation from marsh to forest.

Key words: *resource island, tree islands, limiting resource, soil phosphorus, non-carbon materials, forest production, marl prairies, sloughs, organic soil, mineral soil.*

Introduction

Coincident patterns in the spatial heterogeneity of belowground resources and vegetation may be observed at a range of scales, from fine textures associated with concentrations of roots (Kleb and Wilson 1997) or individual plants (Kershaw 1962; Jackson and Caldwell 1993) to patterns expressed at larger scales associated with landscape gradients or patches (Schimel et al. 1985; Blackmore et al. 1990). In wetlands, vegetation patterning may also be organized around slight discontinuities in surface topography (Huenneke and Sharitz 1986; Titus 1990), though these variations do not always translate into edaphic differences (Ehrenfeld 1995). Ecological theory suggests that environmental heterogeneity may also structure emergent properties of the plant community such as species diversity (Tilman 1988; Huston 1994; Rosenzweig 1995). However, interactions between environmental heterogeneity and vegetation structure are often reciprocal, involving positive and negative feedbacks that create a joint dynamic and common history (Pickett et al. 2000).

In arid and semi-arid ecosystems, numerous investigators have found spatial heterogeneity in soils to be characterized by the presence of resource-enriched patches that range in size from the crown area of a single shrub to wooded thickets (Schlesinger et al. 1990, 1996; Schlesinger and Pilmanis 1998; Titus et al. 2002). The development and persistence of such patches are often dependent on feedbacks between the biota, i.e., herbivores as well as primary producers, and the resource in question, usually nitrogen and/or water (Wilson and Agnew 1992; Schlesinger and Pilmanis 1998; Rietkerk et al. 2002; Rango et al. 2006). Through biotic responses such as canopy development, transpiration, soil accretion, or litter deposition, enhancement in a limiting resource may alter other aspects of the environmental regime, for instance microclimate, infiltration, or water retention. If the patch persists long enough, the

primary constraint on production may transition from one limiting environmental factor to another. Working in the southwestern U.S., Jackson and Caldwell (1993) called such patches “islands of fertility”, and Reynolds et al. (1999) characterized them more broadly as “resource islands”.

In wetlands as well, positive and negative feedback loops involving vegetation, nutrients and the movement of water can produce patterned landscapes in which resources are concentrated in one or more of the constituent patch types (Cohen et al. in press). In large wetland landscapes such as the Florida Everglades, geophysical variation within the basin, or management-related hydrologic alteration may result in different landscape patterning from one sub-region or management unit to another. Most of the freshwater Everglades is an oligotrophic, phosphorus-limited marsh (Noe et al. 2001), but the slightly elevated forest patches, or tree islands, that are scattered throughout the basin do not exhibit similar P-deficiency. Instead, tree island soils sometimes contain extraordinary concentrations of phosphorus. Wetzel et al. (2009) reported that volumetric concentrations of P in tree island heads supporting tropical hardwood species in Water Conservation Area 3, north of Everglades National Park, averaged about 1%, or 70 times higher than in adjacent marshes. Orem et al. (2002) also found elevated soil P concentrations (~0.3% by weight) in two tree islands in the Central Everglades. Higher values were reported by Ross et al. (2006), who found mean soil P to be nearly 5% by weight in well-drained portions of three Shark Slough (ENP) tree islands, while the phosphorus content of soils in swamp forests and marshes immediately downslope were one and two orders of magnitude lower, respectively. The P-enriched tree island heads serve not only as islands of fertility, but as full-fledged resource islands, providing food and cover for terrestrial wildlife, and a well-drained substrate and shaded microclimate for forest plants. Accordingly, the restoration of tree islands

in areas where they have been degraded, and their maintenance in areas where they remain in good number and conditions, have provided a major rationale for embarking on the Comprehensive Everglades Restoration Project (CERP).

In this paper we present a study of one type of Everglades tree island – slightly elevated, broadleaved forests known as hardwood hammocks, beneath which the water table fluctuates widely, affecting moisture availability in the unsaturated zone but rarely rising high enough to flood the surface. Our first objective was to describe the belowground environment (soil, hydrology) in hammocks occupying several regions of the Everglades. The survey was extensive enough to allow generalization about the nature of these rich soils, whose diagenesis is currently little understood. Our second objective was to examine associations between features of the belowground environment and several indices of forest production. We used regression analysis to indicate which soil factors might be limiting plant production in the hammocks, thereby focusing on the internal functioning of these resource islands, rather on their role in resource provision to the surrounding landscape.

Study area

The freshwater wetlands of the southern Everglades fall into two broad sedimentary environments: peat-forming environments associated with marshes in the center of the historical flow-way (including Shark Slough and Water Conservation Area 3), and marl-forming environments in the prairies on the eastern and western flanks of Shark Slough, in Everglades National Park and Big Cypress National Preserve. The peats (Lauderhill, Pennsuco series) are 80-150 cm thick over limestone, while the marls (Biscayne series) are thinner, usually less than 50 cm thick, interspersed with extensive areas of outcropping limestone. The critical physical

driver is the hydrologic regime that characterizes each zone. The marshes of Shark Slough and WCA-3 are inundated 9-12 months per year by a water column that may approach or exceed 1 m. Peats accumulate because the flooding regime permits relatively high vascular plant production, but creates sufficiently anaerobic conditions in the sediments that decomposition of organic materials, especially plant roots, is reduced. Immediately upslope, in what may be viewed as the floodplain of the River of Grass, the marl prairie is characterized by shallow seasonal flooding (3-8 months per year). Macrophyte production and cover are sparse in this variable environment, but conditions favor the growth of a luxuriant, benthic algal mat. The physiological activities of the algae result in precipitation of calcium carbonate from the warm, well-lit waters, contributing to the development of marl soils (Gleason 1972).

Tree islands are common inclusions in these marsh and prairie communities. As such, the islands are affected by the ecosystems that surround them, including hydrologic and sedimentologic processes in the grassy matrix. Everglades tree islands are complex forests that typically display a vegetation gradient from an open mixture of flood-tolerant trees and herbaceous plants near the marsh interface to a less hydrophytic assemblage, with a more closed canopy, at the island interior. In the most complex tree islands, the surface of the interior forest is raised well above the surrounding marsh and supports a mixture of tree species, mostly of tropical origin, that are intolerant to flooding of more than a few weeks' duration. Unlike tree islands dominated by swamp forest species, which may form above bedrock depressions or on bedrock-neutral surfaces, the hardwood hammocks occupy sites whose surface elevation is directly or indirectly attributable to the underlying bedrock; in the southern Everglades, this bedrock surface is almost always higher than the limestone that surrounds it. Some hammocks occupy outcroppings of a meter or more, but in other settings variation in the bedrock surface of

0.1 m or so is enough to initiate the development of a forest ecosystem in which the vegetation and soils differ dramatically from those of the adjacent marsh (Hanan and Ross 2010).

Tree islands with hardwood hammock vegetation are distributed widely in the Everglades, but vary regionally in number, size, orientation, and composition/structure. The density of such islands decreases from south to north, and from the peripheral marl prairies to the marshes of the central peatland. Hammocks in the center of the Everglades are usually small, but form the nuclei for large teardrop-shaped forests, comprised mostly of swamp forest species and oriented in the predominant direction of water flow. In contrast, the shape and orientation of prairie hammocks generally reflect the underlying bedrock, with less evidence of sculpting by flowing water. Hammocks in the central peatland host a limited suite of tree species, most of them among the more common in the regional flora (Armentano et al. 2002). Prairie hammocks are more species-rich, including a broader selection of tropical hardwoods common in the Florida Keys (Olmsted et al. 1980, Loope and Urban 1980).

Everglades tree islands are also the product of a history of human use that dates back at least 5000 years (Graf et al. 2008), when the wetland was first forming. Long distance travel through the Everglades by Native Americans was most rapid by canoe. Due to the deep water which surrounded them for much of the year, the scattered, sentinel islands of the central peatland may have received more intensive use than the countless islands embedded in the marl prairie, which even in the wet season was only minimally flooded. Use of tree islands by people of European origin in the 19th and 20th centuries probably followed a similar pattern, with airboats eventually supplanting canoes as the primary means of transportation. Of course, the last century also featured the establishment and operation of roads and canals that compartmentalized the Everglades marsh, reducing flow and water levels overall, while creating

hydrologic patchiness and anthropogenic gradients that induced variable responses in the tree islands. For instance, tree island density and area in Water Conservation Areas 2 and 3 declined precipitously (Hofmockel et al. 2008), though similar trends have not been observed in Everglades National Park.

The tree islands we studied were distributed among four sub-regions with distinctly different physiography and/or management history (Figure 1). Three of them --- Shark Slough (SS), Northeast Shark Slough (NESS), and Water Conservation Area 3B (WCA-3B) --- are in the central peatland, while the fourth is in the Marl Prairie (MP) landscape. SS and MP have been managed essentially as wilderness areas by the National Park Service since the creation of Everglades National Park in 1947. WCA-3B, the northernmost of the sub-regions, is an impounded marsh managed by the Florida Fish and Game Commission. It is generally open to airboat use by hunters, fishers, and other recreationists. Prior to incorporation into ENP in 1989, NESS was also open to recreational users with minimal restriction.

Methods

In this research we examined soils in 76 hardwood hammocks in central and southern Everglades tree islands (Figure 1). Based on aerial photos and helicopter overflights, we identified and sampled from all islands with significant representation of upland species in Shark Slough (41 sites), Northeast Shark Slough (19 sites), and WCA-3B (10 sites). We also collected soils from six representative islands in the marl prairie landscape on the Slough's eastern and western peripheries. Sampling method differed between two sets of islands present in these regions. The first set comprised 60 islands, on which we conducted a one-time vegetation survey in 2005–2007 (Extensive islands). The second set included 16 islands in SS, NESS, and adjacent

marl prairies, where we established permanent plots in 2005-2006 to support repeated vegetation sampling (Intensive islands). Each plot on the intensive islands was gridded into 5 x 5 m cells. In these islands, soil depth was determined at regularly spaced locations (3-5 and 9-55 points in Extensive and Intensive islands, respectively) by probing to bedrock with a metal rod. In each island, a sample was collected by auger from the surface soil (upper 10 cm) at two locations, and the samples were bulked for analysis. Measured soil parameters were total C, N, and P (TC, TN, TP); ash content, inorganic carbon (IC, based on ash %C); and pH. TC and TN were measured on a dry weight basis using a CHN analyzer (Perkin Elmer, Inc, Wellesley MA, USA), and TP was determined colorimetrically following the method of EPA-365.1 after ashing-acid digestion (Solorzano and Sharp 1980). Total inorganic carbon (IC) was determined in ash (residual after combustion at 500⁰C) and scaled as % IC to total dry weight. Soil pH was determined in 1:1 (w/v) soil:water suspension using a pH meter. Organic C (OC) was determined by difference (TC- IC). The percentage of carbonate material in the soil was estimated from IC, assuming all IC to be in the form of calcium carbonate. Soil organic matter content was estimated from OC on the basis of equations developed for carbonatic and organic soils in Florida (Kasozi et al. 2009). Non-carbon-based soil material (NCM) was calculated as the percentage of soil weight not accounted for by carbonates or organic matter. Soil samples from the 16 Intensive islands were also analyzed for bulk density (Blake and Hartge 1986). These data were used to develop a linear regression ($R^2 = 0.85$; $p < 0.001$) between total organic carbon and bulk density, and the relationship was subsequently used to predict the bulk density of surface soils on the Extensive islands. Finally, using mean soil depth and the estimated bulk density values, we estimated the total phosphorus (on a volume basis) present in the soils of the hammocks.

Values of several hydrologic and landform variables were also estimated for a subset of 69 islands. Mean water level was estimated from a topographic survey from 5-25 regularly distributed points within the hardwood hammock portion of each island to a datum represented by the nearest free water surface, whose elevation could be estimated for the day of the survey through the Everglades Depth Estimation Network (EDEN; <http://sofia.usgs.gov/eden/>) model (Palaseanu and Pearlstine 2008). The position of the water surface at each location over the previous seven water years (May 1, 2000 to April 30, 2007) was also derived from EDEN, and mean Relative Water Level over the period was calculated based on the difference between island and water table elevation. The topographic surveys were also used to calculate island height, i.e., the difference in elevation between the surface of the tree island and the surface of the surrounding marsh, as estimated by USGS surveys (Desmond 2003; Johns and Price 2007). Beyond its influence on the relative position of the water table, tree island height may reflect the mode and timing of landform development, thereby influencing soil characteristics.

Forest structure was assessed in 15 of the 16 Intensive islands, including tree islands in MP (5 sites), SS (7 sites), and NESS (3 sites); we excluded one Intensive island because much of the surface was disturbed and lacking in tree cover. Rectangular 225 - 625 m² plots were established in 2006-07, with each plot incorporating as much of the available extent of hardwood hammock as possible. Plots were gridded into 5 x 5 m cells, trees were mapped and tagged, and the DBH of each tree was measured in summer-fall of 2007 - 2009. Using individual tree diameters from 2009, we estimated basal area and biomass, on the basis of a generic equation for dry tropical forests developed by Brown et al. (1989). We also measured canopy height by extending a leveled, telescoping height pole from the center of each cell, recording the height of

the highest leaf that intercepted a 1-m diameter cylinder centered on the pole. The median of the 9-25 measurements taken in fall 2009 was used as a metric of canopy height.

We tested for sub-regional variation in relative water level, island height, and the seven soil variables (soil depth, TN, TP, pH, IC, OC and NCM). Many of the variables were not normally distributed within regions, and transformations were unsuccessful in normalizing the data. Consequently, regional differences for each variable were tested with the non-parametric Kruskal-Wallis test, followed by a multiple comparison 'Z'-test when the experiment-wide result indicated a significant effect at $\alpha = .05$. To reduce the dimensionality of the data for further examination of among-site patterns, we used principal component analysis (PCA) to identify a smaller number of orthogonal factors. PCA was applied to the site:environment matrix from the 69 sites for which mean relative water level, island height, and seven soil variables were available. Variable loadings of the factors with the highest explanatory value were interpreted, and the distribution of site scores for these factors was examined. Using the intensive islands, multiple stepwise regression was used to identify significant predictors of three metrics of stand stature, e.g., basal area, stand biomass and canopy height. Scores for the three most important PCA factors, their squares, and first-order interaction terms were used as independent variables in the forward stepwise regression.

Results

Soils, landforms, and hydrology

On average, the surfaces of hardwood hammocks in the Everglades marsh were 87 cm above the surrounding marsh, and 65 cm above the mean water table. As a group, hammock surface soils in Everglades tree islands were <0.5 m deep, and characterized by a basic reaction

(mean pH = 8.12) and very high (mean = $\sim 42,165 \mu\text{g/g}$) phosphorus concentrations (Table 1). The latter are especially notable, in that mean P not only exceeded mean N by $>2X$ in the same set of islands, it also exceeded background P concentrations in Everglades marsh soils by more than 2 orders of magnitude (Ross et al. 2006). Based on volumetric weight, the upper 10 cm of soil of the hammocks held a mean total phosphorus of $1,489 (\pm 1,030) \text{ g/m}^2$, with a range from 2.1 g/m^2 to $3,809 \text{ g/m}^2$. While the organic fraction (mean organic C = 15.82%) was abundant in tree island surface soils, carbonate compounds, represented in Table 1 by a mean inorganic carbon concentration of 3.1%, were important in many soils. Still, organic and carbonate fractions together accounted for only about half of soil weight, with the remainder (49.7%) being NCM.

Figure 2 illustrates the strong sub-regional patterns that underlie the regional means described above. The most consistent distinction was between MP hammocks and tree islands in the three sub-regions of the central peatland. Among the soil variables, MP forests were lowest in soil P, pH, inorganic carbon, and non-carbon materials, and highest in organic C and nitrogen content. With their high soil organic content, low bulk density and shallow soil depth, MP forest soils held a mean of only 41 g/m^2 phosphorus in the surface 10 cm, compared to $1,598 \text{ g/m}^2$ in slough hammock soils.

MP hammocks also had the lowest island heights, but median water table depth overlapped broadly with that found in hammocks in other sub-regions. Variation in hammock soil or physiography among peatland sub-regions was less pervasive. Significant differences were observed for four variables: island height (NESS > SS, NESS > WCA-3B), relative water level (NESS < SS, NESS < WCA-3B), soil depth (WCA-3B > SS, WCA-3B > NESS), and pH (SS > WCA-3B).

The Spearman rank correlation analyses showed that several physiographic and edaphic variables were significantly inter-correlated. Several of the P associations are of special interest. For instance, island height above the marsh surface was positively correlated with soil P (Spearman $R = 0.407$) (Table 2). Soil P was also positively correlated with pH and NCM (Spearman $R=0.351$ and 0.766 , respectively), negatively correlated with OC (Spearman $R=0.588$), and uncorrelated with IC. The first three axes of the Principal Component Analysis explained more than 85% of the variation in the eight soil, landform, and hydrology variables (Table 3). Factor 1 (eigenvalue = 3.78) distinguished alkaline, high P soils on the one hand from organic- and N-rich soils on the other. Factor 2 (eigenvalue = 2.39) represented a gradient from high-NCM soils to carbonate-rich sediments, and Factor 3 (eigenvalue = 1.49) represented an axis from high, well-drained sites to lower, less distinctive landforms with shallow water tables. Figure 3 portrays the distribution of sites in PCA factor space. MP sites are restricted to the negative (organic-rich) side of Factor 1, while sites from the three peatland sub-regions are grouped together toward the positive, P-rich side. Analysis of variance confirmed a significant effect of sub-region on Factor 1 scores ($F_{(3,65)}=27.05$, $p<.001$), with HSD post-hoc comparison indicating that Factor 1 scores for MP were less than each of the other sub-regions (which did not differ among themselves). Unlike Factor 1, sites from the four sub-regions appear to be inter-mixed on Factors 2 and 3 (Figure 3), and ANOVA identified no sub-regional effects.

Forest structure and growth relationships

Median basal area, biomass, and canopy height in the 15 tropical hardwood forests sampled were modest, at $25.96 \text{ m}^2 \text{ ha}^{-1}$, $130.13 \text{ Mg ha}^{-1}$, and 8.4 m, respectively (Table 4). Medians for all three variables were lowest in MP, but no effect of sub-region was indicated by

Kruskal-Wallis tests, due to substantial within-region variation and minimal replication (Table 4).

Regressions predicting forest structure from PCA factor scores gave different results depending on the metric used. Stepwise regression analysis identified Factor 2 as an independent predictor of canopy height, suggesting that soil composition weighted toward non-carbon materials was beneficial to growth (Figure 4). However, neither basal area nor biomass exhibited a significant relationship to any single factor or combination.

Discussion

Hardwood hammocks in the southern Everglades grow on two very distinct soil types. The first, consisting of shallow organic soils developed directly on limestone bedrock outcroppings, is common in tree islands in the seasonally-flooded Marl Prairie landscape. In contrast, hammock soils on islands embedded in long hydroperiod marshes in the central Everglades peatland are deeper, with much higher mineral content, alkaline pH, and extremely high P concentrations. However, our data suggest that this edaphic variation does not result in clear differences in forest structure and production between Marl Prairie and Slough hammocks.

Soil development

The arrangement of tree island surface soils along a gradient from circumneutral organic soils on the one hand, to highly alkaline, mineral soils on the other is a common theme in south Florida wetlands, but has not been previously described for these forested inclusions in the Everglades marsh. In the palustrine portions of the Everglades, flooding depth and duration are critical drivers of soil formation, through their effects on the primary producers and the rate of organic matter decomposition (Mitsch and Gosselink 2000). In semi-permanently flooded (8-12

months yr^{-1}) marshes, emergent graminoid or floating-leaved aquatic macrophytes are the dominant primary producers, and their detrital remains decompose slowly. In seasonally flooded (3-8 months yr^{-1}) prairies, macrophyte productivity is lower, and periphytic and benthic algal communities predominate (Davis et al. 2005; Ewe et al. 2006). The photosynthetic consumption of CO_2 within the water column by these algae leads to the precipitation of calcium carbonate and the formation of mineral soils (marls) (Gleason and Spackman 1972). However, while the peatland and marl prairie environments may influence soil development in the hammocks, there is little evidence that hammock soils developed under flooded conditions, or that palustrine developmental models apply.

Surface soils in MP hammocks are characterized by relatively high OC and total N, low IC and total P, and neutral to slightly basic pH (Figure 2). On the Miami-Dade County soil survey (USDA 1996), these soils are mapped as Dania or Matecumbe mucks, and Craighead (1971) described them as Gandy Peats. In both physical and chemical characteristics, they resemble the Folists (Lithic Troposaprists) that support hardwood hammock vegetation in the upper Florida Keys (Ross et al. 2003). Fibric organic soils that develop in upland settings, Folists are especially common on limestone or young volcanic surfaces (Collins and Kuehl 2001). Maintenance and development of an organic soil in a well-drained, subtropical environment requires high aboveground production, because decomposition is likely to be rapid. In the most productive Key Largo hammocks, decomposition rates are initially rapid, approaching 60% in the first twenty-four months after leaf drop, but leaving recalcitrant materials behind that form the bulk of the soils (Ross et al. 2003). The same is likely in Marl Prairie tree islands, where litter turnover rates (net annual litterfall/average detrital biomass) > 1 have been observed (Ross unpublished data). As in the Keys, soil development in the Marl

Prairie tree islands in the present study consists primarily of a reprocessing of dead roots and remains of aboveground organic materials.

The high mineral content observed in almost all sites in our extensive survey of central peatland hammock surface soils is consistent with two full soil profiles recently described by Coultas et al. (2008) at Crandon and Heartleaf Hammocks in NESS. Profiles in both hammocks exceeded 1.5 m in depth, and included abundant bones, shells and artifacts throughout. Organic matter was 10-15% at the surface, but decreased downward in the profile, such that the soils were classified morphologically as Mollisols (Fluventic Calcudoll and Cumulic Hapludoll, respectively). Most notably, a petrocalcic layer of ~ 20 cm thickness was present mid-profile, beginning ~60 cm below the surface. The mechanism of development of the petrocalcic layer was uncertain, but was hypothesized by the authors to involve the precipitation of calcite from calcium-rich capillary waters originating in the shallow water table. McCarthy et al. (1993) documented a similar subsurface precipitation of calcium, magnesium, silica and sodium minerals in tree islands developing in anastomosing channel systems in the Okavango Delta of Botswana. Water movement into the islands was driven by the transpiration of large trees, and mineral precipitation was responsible for soil accretion and landform aggradation. Both physicochemical and biological mechanisms (i.e., exclusion of cations at the root surface) were responsible for the precipitation of minerals from solution. Since the process depended on the proximity of tree roots to the groundwater table, soil accretion would proceed only when the islands were surrounded by permanent surface water, and ceased when the channel system shifted away from the islands.

In the Everglades context, McCarthy et al.'s model may apply well to incipient tree islands embedded in the continuously flooded conditions of the central peatland. Wetzel et al.

(in press) reported high Na and Cl ionic concentrations in groundwater beneath an elevated tree island in Water Conservation Area 3, particularly during the dry season. These observations suggest the focused transport and deposition documented in the Botswanan islands, with salts being drawn toward the island in the transpiration stream, but then excluded at the root interface. Besides a groundwater source, the high mineral content of hammock sediments in interior Everglades tree islands could be derived from other allochthonous sources (dust, bones and human artifacts) or from residuum remaining after partial dissolution of the underlying limestone bedrock. While the origin of these soils remains an open question, future development of models to explain the dynamics of patterned Everglades peatlands (Cohen et al. in press; Larsen and Harvey 2010) should endeavor to incorporate the minerogenic nature of these embedded elements.

Phosphorus and other soil properties

The mechanism(s) by which extremely high concentrations of soil P have developed in some Everglades tree islands is controversial. Most thinking has revolved around the means by which P arrives at the island (Wetzel et al. 2005; Ross et al. 2006). Alternatives include (1) faunal deposition by animals feeding elsewhere, (2) entrapment of aerosol-P by tree crowns, (3) disposal of P-rich bones in kitchen middens by native Americans, who used the islands as temporary or more permanent campsites, or (4) the drawing-in of dilute-P marsh water to the tree island in response to the rapid transpiration stream of trees in mesic sediments and favorable growing conditions. Less attention has been paid to the means and efficiency with which P is sequestered in tree island soils once it arrives, though Jayachandran et al. (2004) and Ross et al. (2006) hypothesized that P may be especially prone to fixation in insoluble forms in Ca-rich tree island soils. In fact, despite the recent interest in the origin of these P hot spots, our study is the

first to describe the associations between P concentrations and other soil and hydrologic parameters in hardwood hammocks across a broad spatial landscape.

One important finding of our analysis was the strong positive association of soil P content and soil alkalinity (Table 2), with enormous concentrations found in soils of pH>8. This suggests that much of the phosphorus sequestered in Everglades tree islands may be in forms unavailable to plants, as P availability generally declines sharply at pH values outside the range 5.5-7.5 (Black 1968; Wright et al. 2009). While the predominant forms of phosphorus in hammock soils are not well known at present, our findings do provide some direction in this regard. Soil P was negatively associated with the organic fraction (Table 2), in direct contrast to the pattern exhibited over a wide range of Everglades marl and peat marshes (Scheidt and Kalla 2007), including P-enriched marshes (Noe et al. 2001; Craft and Richardson 2008). Given the relationship with pH discussed above, the absence of correlation between soil P and IC was surprising. Instead, P exhibited a strong positive association with non-carbon materials, which represented, on average, about half of soil weight in the sampled islands. Working with soils from the agricultural areas immediately east of the Everglades, Zhao and Li (2001) also found phosphorus-sorption to be strongly correlated with non-carbonate clays at low P-concentrations, though carbonates became important in binding P at high concentrations. Several studies have shown that amorphous and crystalline calcium phosphate compounds can form secondarily in association with calcite surfaces (Freeman and Rowell 1981; von Wandruszka 2006). However, if P-sorption in the hammocks was primarily through reaction with calcite, a positive association between P and IC likely would have resulted. Another possibility is that much of the P was deposited in bound form, as hydroxylapatite ($\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$) in the bones that suffused the profiles described by Coultas et al. (2008). In any case, the large volumes of bones present in

these soil profiles are indicative of amplified human activity, which is likely to have been more concentrated on the taller islands than others, resulting in high soil phosphorus in those islands. The nature of P-sorption in hammock soils remains very much an open question.

Resource islands and forest production

The data presented above clearly mark Everglades tree islands as islands of fertility in a nutrient-limited wetland landscape. However, they are also distinguished from the rest of the landscape by attributes of the belowground environment other than their nutrient contents. Soils have built up to present a surface raised well above the water table, and their mineral component prominently includes a non-carbonate fraction whose presence has not been reported elsewhere in the southern Everglades. Most importantly, these soils are occupied and influenced by trees, which are known to alter soils by their impacts on microclimate, and on the cycling and redistribution of water, nutrients and materials (Binkley and Giardina 1998). Like the ecosystems that form around desert shrubs, tree island ecosystems play an essential role in the life cycles of many organisms and in the biogeochemistry of the landscape (Givnish et al. 2007, Wetzel et al. 2009), and are resource islands in the broadest sense. Our study focused on mature tree islands well beyond the individual tree stage, in which processes of resource island formation may be inferred. We therefore examined our data for associations that might suggest which belowground resources or stresses might limit the productivity of tree islands, once formed.

We tested for relationships of site variables representing soil constituency, soil depth, and water table position with three structural indicators of relative site productivity. The relationships that emerged should be interpreted with caution, because the structural response variables we employed are likely to be imperfect indicators of production in subtropical

hardwood forests of the Everglades. Stand structure in these forests is mixed-species and uneven-aged, reflecting not only site potential but also the forests' long history of human use. Furthermore, fragment size is irregular, variable and small (< 0.1 ha to several ha), creating edge effects such as increased exposure to natural disturbances, especially tropical storms and hurricanes, with influences on forest structure that may be independent of site. Among the structural variables examined, basal area and biomass are not only sensitive to these disturbances, but are also slow to recover in their aftermath, as replacement of killed gap-forming trees by ingrowth of seedlings and advance regeneration requires many years, even in the absence of further disturbance (Weaver 1986). Gap-filling by new individuals may be an especially prolonged process in forests used intensively prior to the creation of Everglades National Park, and many such stands show evidence of severe understocking (Ross et al. 2010). While canopy height also can be substantially reduced by windstorms, it may serve as a better indicator of site potential than basal area or biomass, because canopy recovery after disturbances that leave significant live structural legacy requires only the relatively rapid reiteration and expansion of the crowns of residual trees, a relatively speedy process. In our earlier work in the Florida Keys, we found that canopy height correlated well with direct measures of forest production (tree biomass increment and litter production), and adequately reflected a climatically-controlled productivity gradient from islands near the south Florida mainland to more distal locations (Ross et al. 1992; Ross et al. 2003). Presuming, then, that canopy height represents a good structural indicator of stand productivity, how then are we to interpret the relationships that were revealed by the regression analyses --- both soil nutrients and the relative position of the water table without apparent effects, but a positive association between productivity and the proportion of non-carbon materials in the mineral soil component?

The finding that production does not vary along the gradient in soil N:P ratio (Factor 1) seems at first rather remarkable, given more than a hundred-fold difference in total P in the sample data, and the extensive P-limitation of growth reported for Everglades marshes. However, several authors have suggested that tree islands with very high soil P in the Everglades interior may become nitrogen-limited, based on leaf N:P ratio (Ross et al. 2006) or leaf $\delta^{15}\text{N}$, which becomes enriched when high P availability increases plant demand for nitrogen (Inglett et al. 2007, Wang et al. 2010). With phosphorus potentially limiting growth at one end of the Factor 1 gradient, and nitrogen limiting growth at the other, it is not surprising to find no relationship across the data set.

The absence of an association between productivity and water table depth (Factor 3) is likewise unexpected, until one considers the relatively narrow range of hydrologic conditions represented among the sample locations from which canopy height data were available. Tear-drop shaped tree islands in the interior Everglades exhibit a consistent decrease in canopy height and litter production from elevated, rarely flooded heads to the seasonally flooded swamp forests in the islands' tails (Armentano et al. 2002, Sah 2004). However, the 15 hardwood hammocks in our data set included only well-drained sites, with mean water table position recessed 25-92 cm from the surface. Our analysis suggests that within this narrow range, seasonal fluctuations in the water table do not in themselves create soil drought or saturation severe enough to limit forest growth.

Complete interpretation of the strong increase in canopy height from high-carbonate soils to soils high in non-carbon materials (Figure 4) await further study, including a full elaboration of the composition of the mineral fraction in the sample tree islands. Nevertheless, some informed speculation is possible based on the published literature. Sodek et al. (1990) described

minerals in the clay size class from several south Florida soils, including the marl prairies that surround some of the islands, as well as sites that support slightly elevated pine rockland forests. Calcite predominated in the prairie soils, but silicate materials, particularly hydroxyl-interlayered vermiculite, were proportionally abundant within the relatively small clay fraction in the rockland soils. If vermiculite clays are similarly well-represented in the much larger mineral component of tree island soils, then positive effects on growth may ensue. Vermiculite clays have high cation exchange capacity, enhance water retention, and thus may improve moisture and nutrient availability to plants. The capacity of south Florida tropical hardwood forests to make rapid growth on shallow, organic-rich soils frequently beset by mid-summer rainless periods has previously been noted (Ross et al. 2003), and the role of clay minerals in the process deserves more study.

Conclusion

In this study, we examined soils of well-drained tree islands embedded in Everglades marshes, finding them to be distinct in character from those in the surrounding landscape, and also exhibiting considerable regional variation. Tree island soils in the short-hydroperiod prairies most closely resembled the shallow organic soils reported from hammocks in the Florida Keys (Ross et al. 2003). In contrast, the P-rich mineral soils we found in central peatland tree islands had no local analogue, differing from the sandy profiles described for hammocks in the Big Cypress National Preserve, for instance (Craighead 1971; Duever 1986). Viewed from either below- or above-ground perspectives, both of these distinctive Everglades ecosystems serve as excellent examples of resource islands. From below, the well-aerated soils include sharply elevated concentrations of phosphorus, not present in abundance in adjacent, anaerobic marsh

sediments. From above, the forests provide shade, cover, and feeding opportunities for a broad faunal assemblage of permanent residents or seasonal opportunists drawn there from elsewhere in the ecosystem. Moreover, data presented here and by others suggest that the resources provided by soil and forest are interdependent, developing in tandem over many years. At early stages in their development, the establishment of communities dominated by woody plants may have depended on the availability of phosphorus, but in the mature forest ecosystems we examined there was no evidence of P-limitation to growth. Just as multiple resources may alternate in limiting individual or community production over periods of days to years (Chapin et al. 1987), the resource fundamentally limiting tree island function may have changed drastically over the millennia of their development.

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Figure 1: Study area and locations of sample tree islands.

Figure 2: The distribution of nine physiographic and edaphic variables within the four sub-regions. Box plots represent boxes with 1st quartile, median, and 3rd quartile, whiskers with non-outlier range of data (the maximum or minimum value within 1.5 times the quartile), outliers (o), and extreme (*) values. P-values represent the Kruskal-Wallis test of the effect of sub-region on median values of each variable. Sub-regions followed by the same letter did not differ at $\alpha=.05$.

Figure 3: Projection of tree islands, grouped by sub-region, in the factor space formed by PCA Axes 1, 2, and 3.

Figure 4: Regression model for prediction of canopy height of Everglades tropical hardwood forest structure from PCA factor-2.

Figure 1.

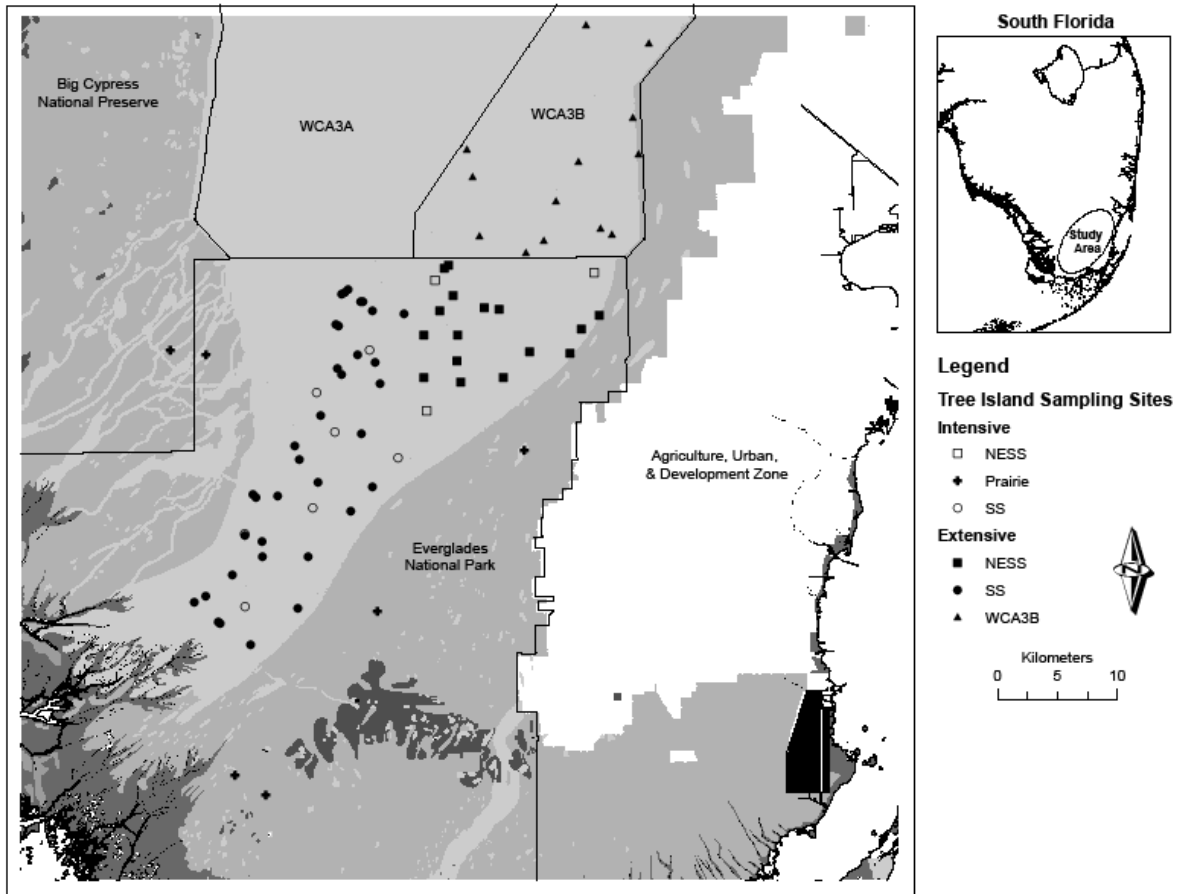


Figure 3.

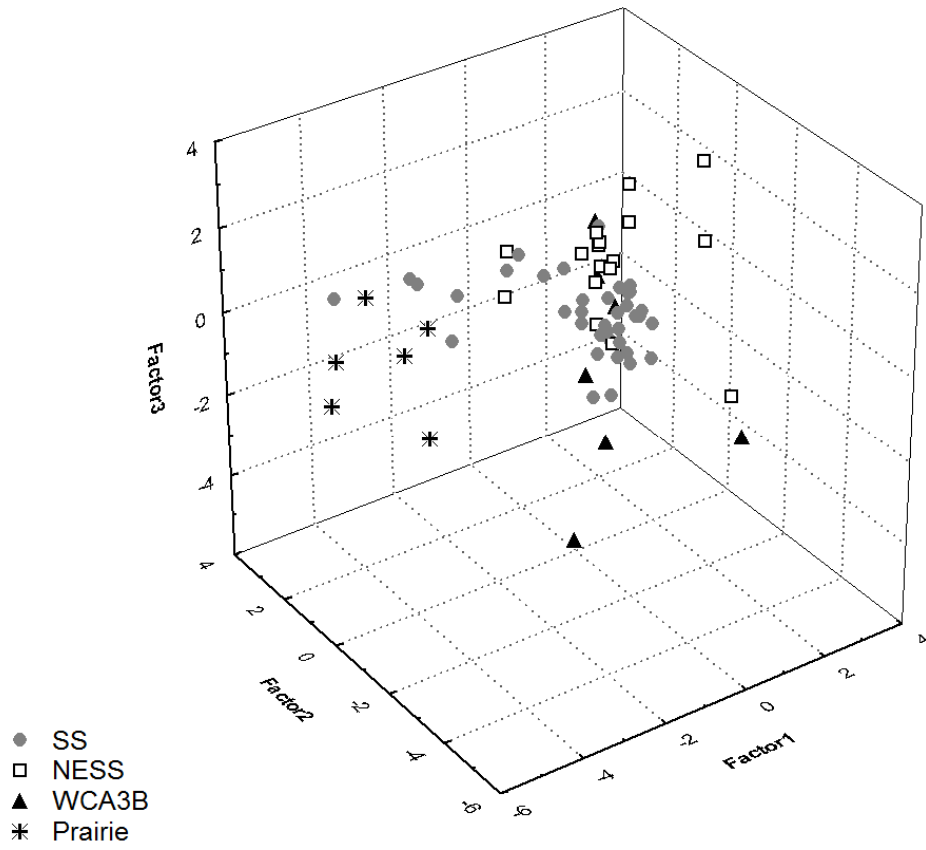


Figure 4.

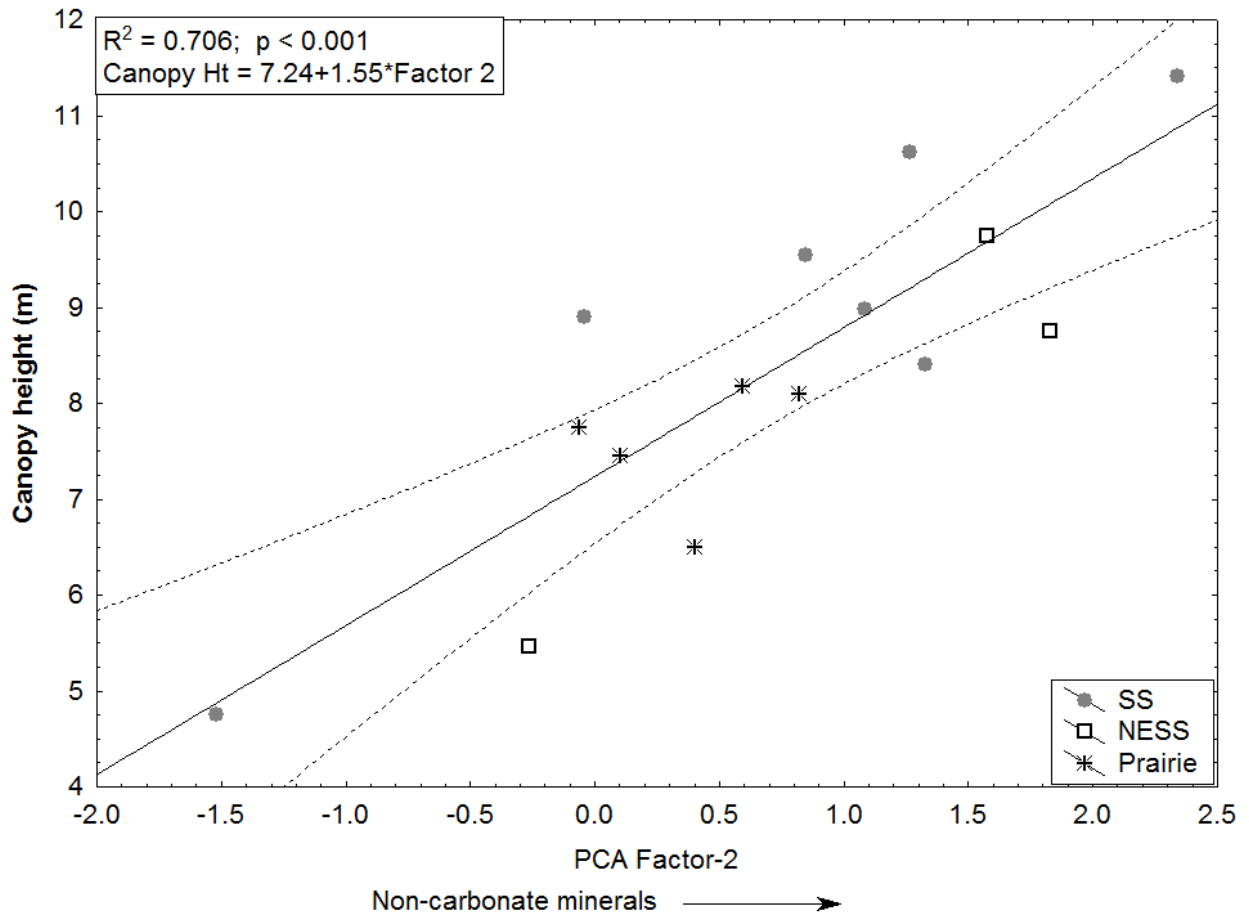


Table 1: Environmental characteristics of hardwood hammocks in the Everglades

landscape. Estimates based on samples from 76 islands, except for soil bulk density (n = 15).

Environmental characteristics (unit)	Mean	Median	Min	Max
Island height (cm)	87.5	87.2	16.3	174.5
Relative water level (cm)	-64.6	-65.1	-136.0	10.0
Soil depth (cm)	46.5	34.5	8.4	150.0
pH	8.12	8.18	6.36	8.76
TP ($\mu\text{g/gdw}$)	42,165	47,311	239	103,660
TN (%)	1.21	1.00	0.40	2.49
IC (%)	3.13	2.89	0.60	9.12
OC (%)	15.82	12.62	5.96	40.60
NCM (%)	49.70	51.41	13.36	81.46
Soil bulk density (g/cc)*	0.262	0.287	0.060	0.451

Table 2: Spearman rank correlation matrix of environmental characteristics of hardwood hammocks (n=69) in the Everglades

Environmental characteristics (unit)	Island height (cm)	Relative water level (cm)	Soil depth (cm)	pH	TP (µg/gdw)	TN (%)	IC (%)	OC (%)
Relative water level (cm)	-0.829							
Soil depth (cm)	0.134	-0.096						
pH	0.034	0.043	0.260					
TP (µg/gdw)	0.407	-0.346	0.224	0.351				
TN (%)	-0.315	0.196	-0.391	-0.476	-0.543			
IC (%)	-0.073	0.109	0.421	0.497	-0.173	-0.414		
OC (%)	-0.310	0.216	-0.353	-0.484	-0.588	0.920	-0.356	
NCM (%)	0.372	-0.296	-0.007	0.087	0.766	-0.215	-0.627	-0.307

Correlations significant at $p < 0.05$ are in bold.

Table 3: Factor loadings of first three factors of Principal Component Analysis, applied to two physiographic and seven edaphic variables measured at 69 Everglades hardwood hammocks. Most important variables on each factor are printed in bold face.

	Factor 1 “Alkaline, high P”	Factor 2 “Non-carbon materials”	Factor 3 “Well-drained”
Eigenvalue	3.78	2.39	1.49
% of total variation	42.0	26.6	16.6
Variable			
Island height	0.61	0.27	0.70
Relative water level	-0.46	-0.38	-0.76
Soil depth	0.18	-0.63	-0.14
pH	0.79	-0.22	-0.23
Total P	0.73	0.48	-0.32
Total N	-0.91	0.27	0.08
IC	0.33	-0.89	0.23
OC	-0.94	0.20	0.17
NCM	0.42	0.78	-0.40

Table 4: Median values for three structural variables in tropical hardwood forests in tree islands in three southern Everglades sub-regions. Minimum and maximum values for each category are in parentheses.

Region	n	Basal area (m ² ·ha ⁻¹)	Biomass (Mg·ha ⁻¹)	Canopy height (m)
SS	7	29.37 (16.26, 72.64)	149.70 (80.92, 365.14)	8.98 (4.76, 11.41)
NESS	3	23.45 (17.96, 33.19)	130.13 (88.82, 153.98)	8.75 (5.47, 9.75)
Prairie	5	23.17 (20.98, 33.49)	91.94 (75.52, 158.74)	7.75 (6.50, 8.18)
All	15	25.96 (16.26, 72.64)	130.13 (75.52, 365.14)	8.40 (4.76, 11.41)

Appendix 2

Species Codes & Growth Form

Appendix 2: Species names and codes used to identify trees, saplings, shrubs and seedlings.

Species	Code	Tree	Sapling	Shrub	Seedling
<i>Annona glabra</i>	ANGLA	x	x	x	x
<i>Ardisia escallonioides</i>	ARDESC	x	x	x	x
<i>Bursera simaruba</i>	BURSIM	x	x	x	
<i>Caesalpinia bonduc</i>	CAEBON		x	x	x
<i>Calyptanthes pallens</i>	CALPAL	x	x	x	x
<i>Carica papaya</i>	CARPAP	x	x	x	x
<i>Celtis laevigata</i>	CELLAE	x	x	x	x
<i>Chiococca alba</i>	CHIALB			x	
<i>Chrysobalanus icaco</i>	CHRICA	x	x	x	x
<i>Chrysophyllum oliviforme</i>	CHROLI	x	x	x	x
<i>Citrus aurantium</i>	CITAUT	x	x	x	
<i>Coccoloba diversifolia</i>	COCDIV	x	x	x	x
<i>Diospyros virginiana</i>	DIOVIR	x	x	x	x
<i>Erythrina herbacea</i>	ERYHER		x		
<i>Eugenia axillaris</i>	EUGAXI	x	x	x	x
<i>Exothea paniculata</i>	EXOPAN	x	x		x
<i>Ficus aurea</i>	FICAUR	x	x	x	x
<i>Ficus citrifolia</i>	FICCIT	x	x		
<i>Hamelia patens</i>	HAMPAT				x
<i>Ilex cassine</i>	ILECAS				x
<i>Ilex krugiana</i>	ILEKRU		x	x	
<i>Lysiloma latisiliquum</i>	LYSLAT	x			x
<i>Magnolia virginiana</i>	MAGVIR	x	x		x
<i>Metopium toxiferum</i>	METTOX	x	x	x	x
<i>Myrica cerifera</i>	MYRCER	x	x	x	x
<i>Myrsine floridana</i>	MYRFLO	x	x	x	x
<i>Myrcianthes fragrans</i>	MYRFRA	x	x	x	x
<i>Nectandra coriacea</i>	NECCOR	x	x	x	x
<i>Persea borbonia</i>	PERBOR	x	x	x	x
<i>Prunus myrtifolia</i>	PRUMYR		x		
<i>Psidium guajava</i>	PSIGUA		x		
<i>Quercus virginiana</i>	QUEVIR	x	x	x	x
<i>Sabal palmetto</i>	SABPAL	x		x	x
<i>Salix caroliniana</i>	SALCAR	x	x		
<i>Sambucus canadensis</i>	SAMCAN	x	x	x	x
<i>Sapindus saponaria</i>	SAPSAP		x		x
<i>Schefflera acinophylla</i>	SCHACT				x
<i>Schoepfia chrysophylloides</i>	SCHCHR	x	x		x
<i>Schinus terebinthifolia</i>	SCHTER	x	x	x	x
<i>Sideroxylon foetidissimum</i>	SIDFOE	x	x	x	x
<i>Sideroxylon salicifolium</i>	SIDSAL	x	x	x	x
<i>Simarouba glauca</i>	SIMGLA	x	x	x	x
<i>Solanum erianthum</i>	SOLERI	x	x	x	x
<i>Thrinax radiata</i>	THRRAD		x		
<i>Trema micrantha</i>	TREMIC	x	x		x
<i>Zanthoxylum fagara</i>	ZANFAG	x	x		x

Appendix 3

Tree Island Tree and Sapling Density and Species Composition

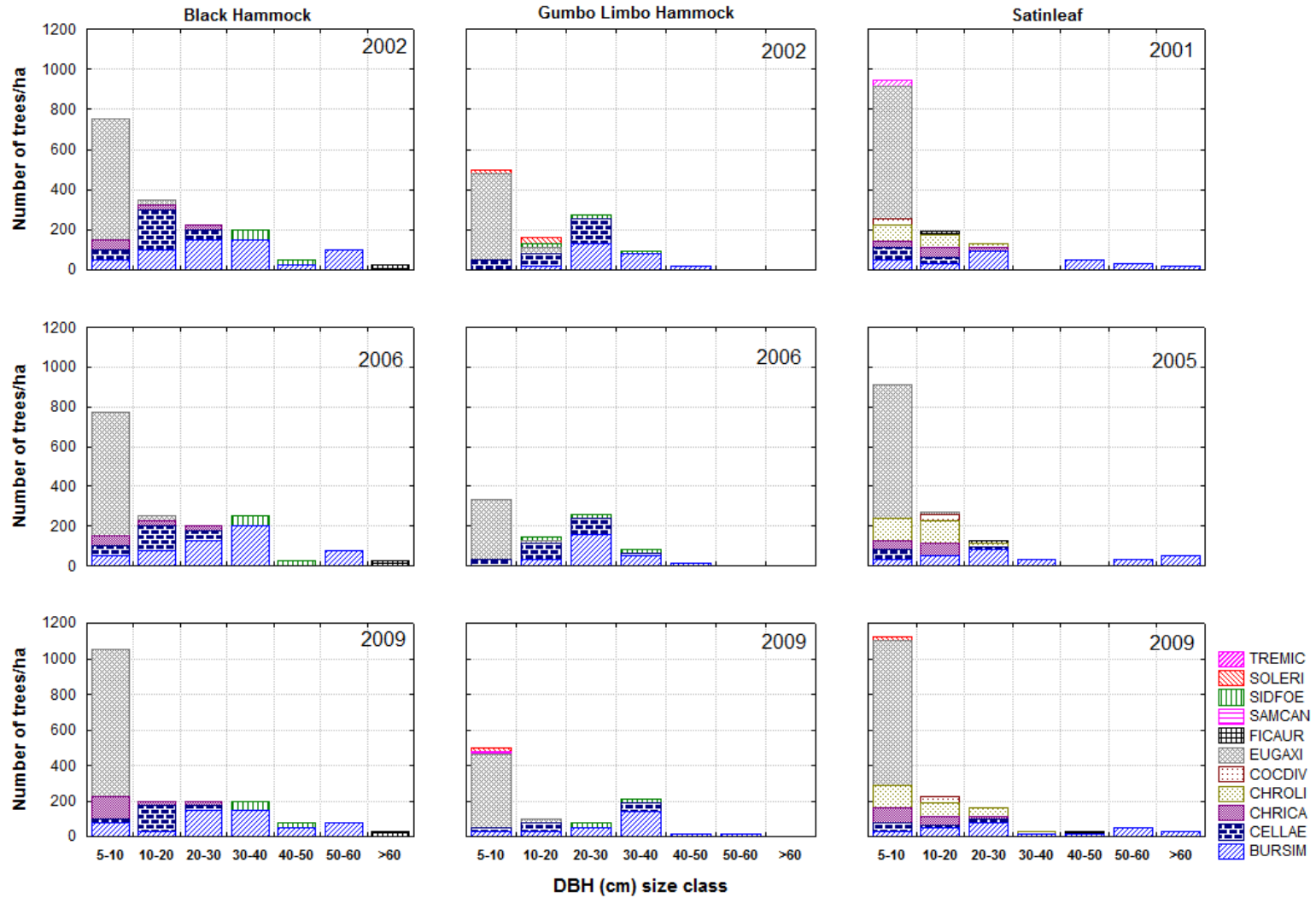


Figure A3-1: Density (individuals/ha) of different tree species in different diameter classes in hardwood hammocks of three Shark Slough tree islands (Black Hammock, Gumbo Limbo and Satinleaf) sampled between 2001 and 2009.

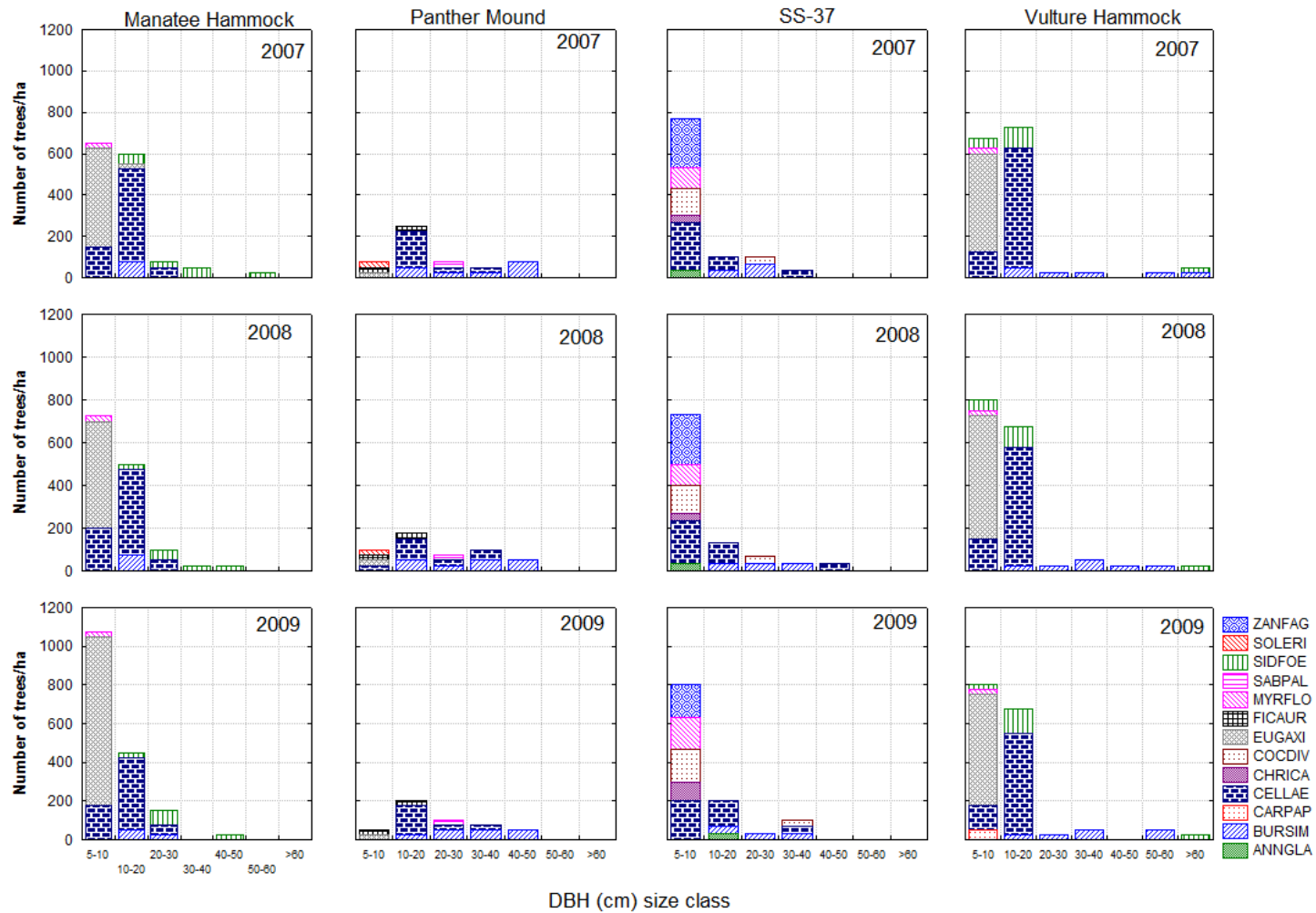


Figure A3-2: Density (individuals/ha) of different tree species in different diameter classes in hardwood hammocks of four Shark Slough tree islands (Manatee Hammock, Panther Mound, SS-37 and Vulture Hammock) sampled annually during 2007-2009.

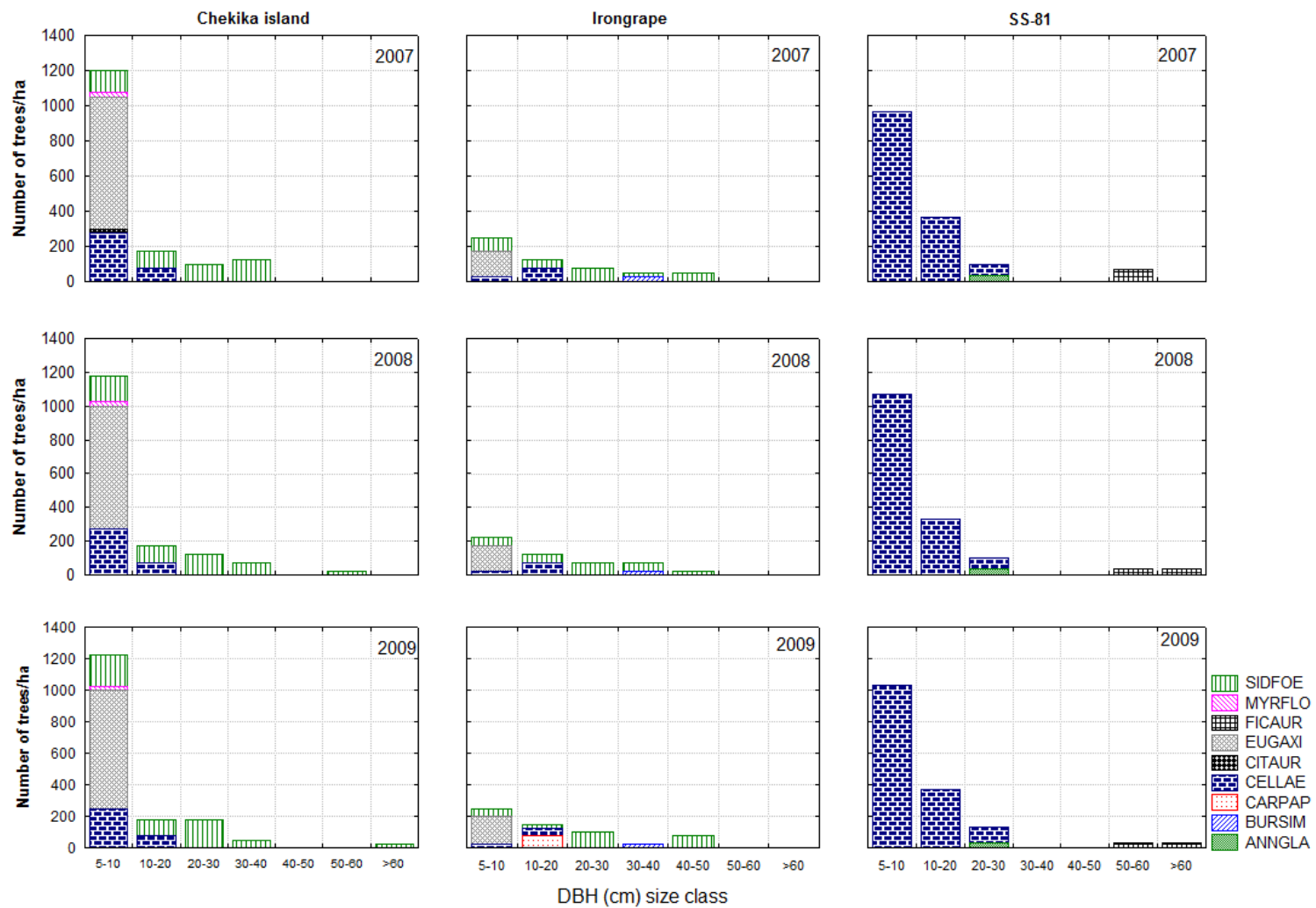


Figure A3-3: Density (individuals/ha) of different tree species in different diameter classes in hardwood hammocks of three Northeast Shark Slough tree islands (Chekika Island, Irongrape, and SS-81) sampled annually during 2007-2009.



Figure A3-4: Density (individuals/ha) of different tree species in different diameter classes in hardwood hammocks of three Prairie tree islands (Grossman Hammock, Ficus Pond, Mosquito) sampled between 2005 and 2009.

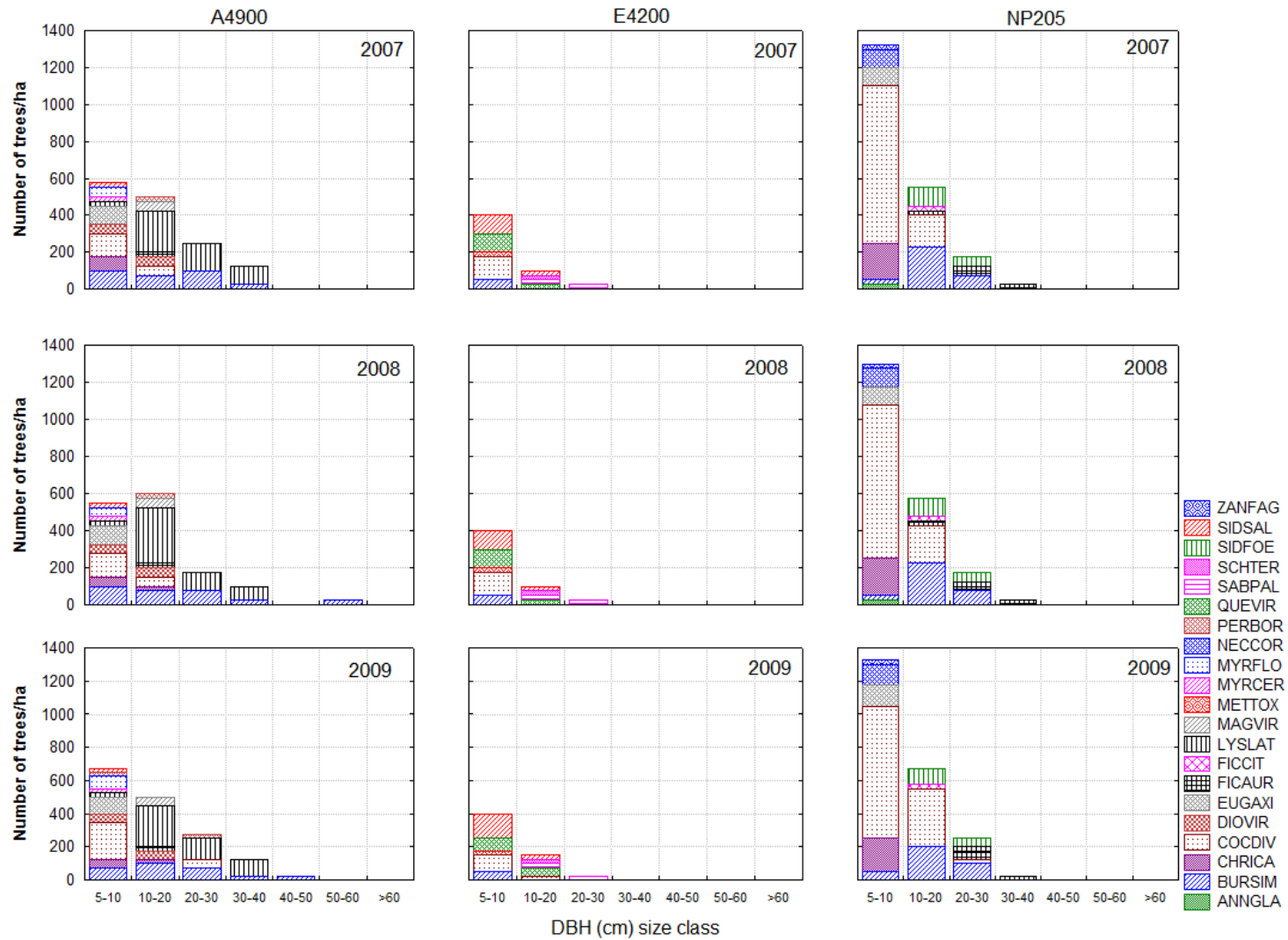


Figure A3-5: Density (individuals/ha) of different tree species in different diameter classes in hardwood hammocks of three Prairie tree islands (A4900, E4200, and NP-205) sampled annually during 2007-2009.

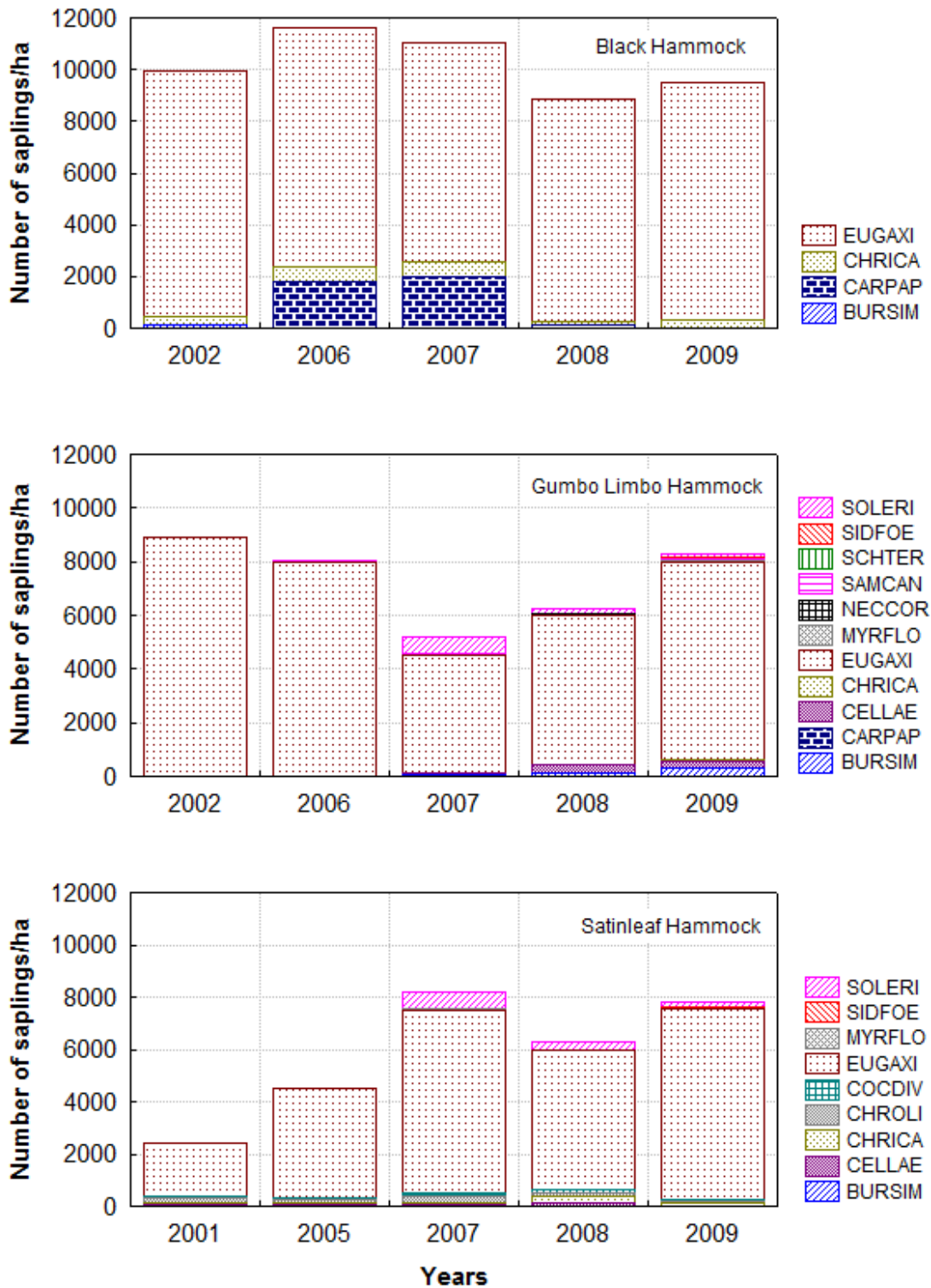


Figure A3-6: Sapling (<5 cm dbh) density (individuals/ha) of different species in hardwood hammocks of three Shark Slough tree islands (Black Hammock, Gumbo Limbo and Satinleaf) sampled between 2001 and 2009.

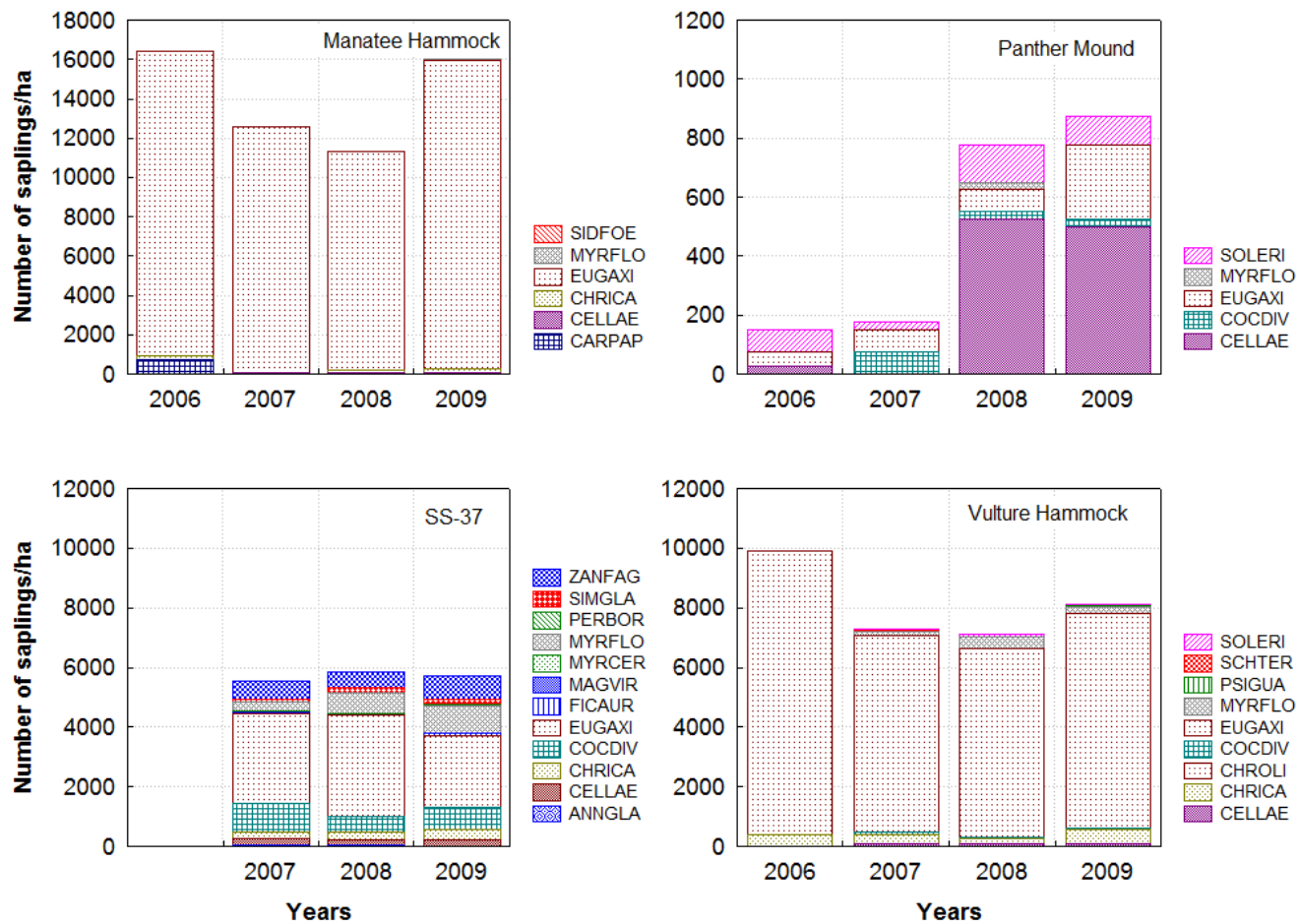


Figure A3-7: Sapling (<5 cm dbh) density (individuals/ha) of different species in hardwood hammocks of four Shark Slough tree islands (Manatee Hammock, Panther Mound, SS-37 and Vulture Hammock) sampled annually during 2007-2009.

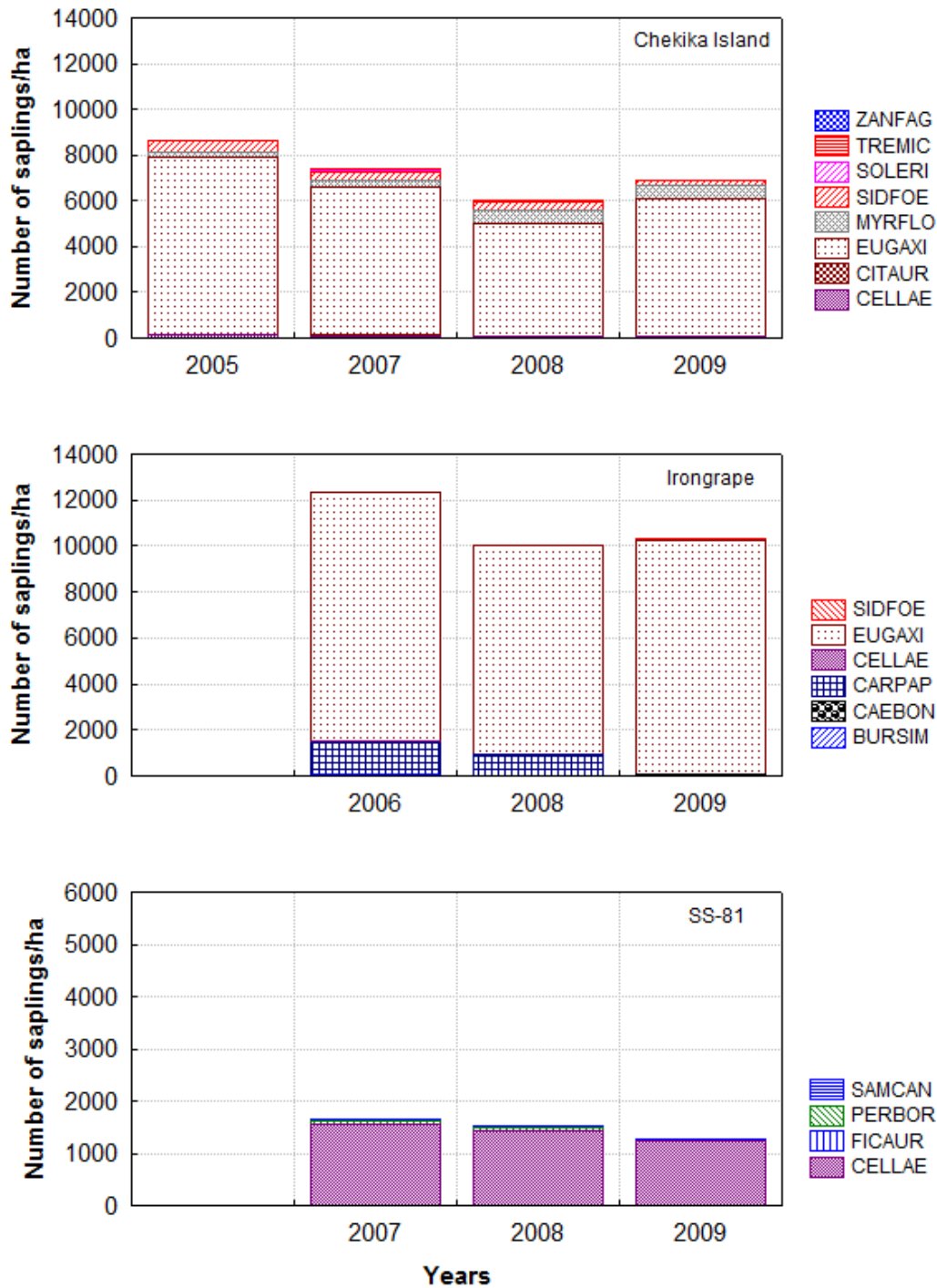


Figure A3-8: Sapling (<5 cm dbh) density (individuals/ha) of different species in hardwood hammocks of three Northeast Shark Slough tree islands (Chekika Island, Irongrape, and SS-81) sampled annually during 2007-2009.



Figure A3-9: Sapling (<5 cm dbh) density (individuals/ha) of different species in hardwood hammocks of three Prairie tree islands (Grossman Hammock, Ficus Pond, Mosquito) sampled between 2005 and 2009.

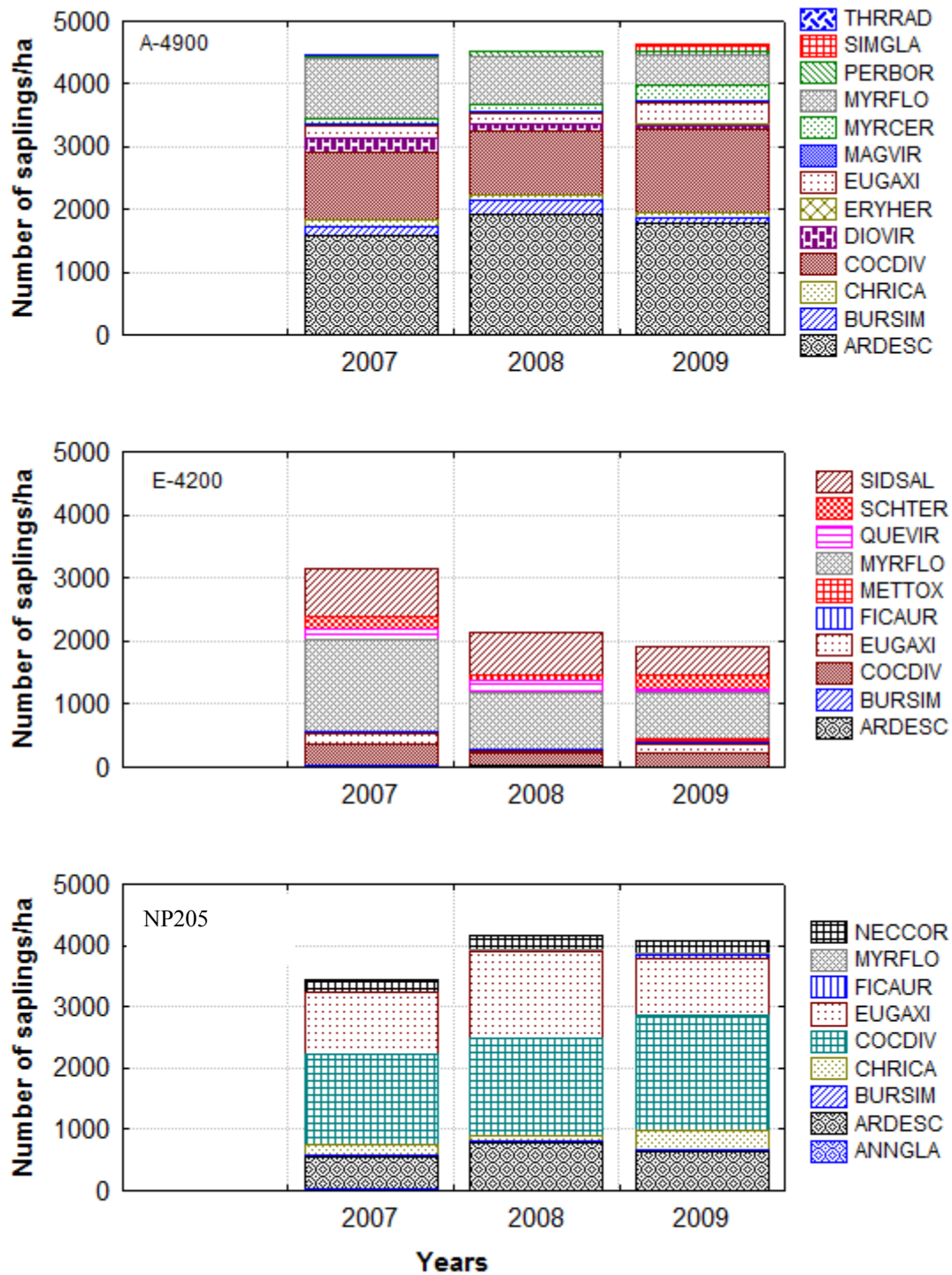


Figure A3-10: Sapling (<5 cm dbh) density (individuals/ha) of different species in hardwood hammocks of three Prairie tree islands (A4900, E4200, and NP-205) sampled annually during 2007-2009.