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Monitoring of Tree Island Condition in the Southern Everglades: Hydrologic Driven Decadal Changes in Tree Island Woody Vegetation Structure and Composition: 2012 Annual Report

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Southeast Environmental Research Center
FLORIDA INTERNATIONAL UNIVERSITY

**Monitoring of Tree Island Condition in the Southern Everglades:
Hydrologic Driven Decadal Changes in Tree Island Woody
Vegetation Structure and Composition**



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2012 Annual Report Submitted to

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Cover photograph: Image of tree island Bayhead Forest vegetation associated with the Bayhead Forest plot at Gumbo Limbo Hammock, Everglades National Park, FL, USA.

Photographed by Pablo L Ruiz (27 April 2012)

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Executive Summary

This report examines the interaction between hydrology and vegetation over a 10-year period, between 2001/02 and 2012 within six permanent tree island plots located on three tree islands, two plots each per tree island, established in 2001/02, along a hydrologic and productivity gradient. We hypothesize that: (H1) hydrologic differences within plots between census dates will result in marked differences in a) tree and sapling densities, b) tree basal area, and c) forest structure, i.e., canopy volume and height, and (H2) tree island growth, development, and succession is dependent on hydrologic fluxes, particularly during periods of prolonged droughts or below average hydroperiods.

The results reported herein reinforce the concept that tree islands are dynamic successional communities that expand and contract over time in response to variation in hydroperiod. Temporal differences observed in species importance values (IV) reinforce this concept. In general, flood tolerant species like *Annona glabra* and *Salix caroliniana* saw their IV decline while moderately tolerant species like *Chrysobalanus icaco*, *Ilex cassine*, and *Ficus aurea* increased in importance. At the same time, increases in tree density, basal area and species richness as well as significant canopy development, e.g., increases in canopy height and volume, were observed within our study plots in response to below average water levels and shortened hydroperiods within Shark River Slough during the study period.

Documentation of the strong correlation between tree island vegetation structure and hydrology is highly suggestive that hydrologic modifications brought about through the Comprehensive Everglades Restoration Plan (CERP) will affect tree island dynamics throughout the Everglades. Depending on the magnitude of hydrologic alterations achieved by the CERP, the balance between flood-tolerant and flood-intolerant woody and herbaceous vegetation within tree islands is likely to change. Ideally, the CERP should strive to achieve system wide hydrologic conditions that result in a spatially balanced mosaic of tree islands with different successional states, with no specific bias towards tree islands of one type or another or of a single successional state.

Introduction:

Paleoecological data indicates that tree island nucleation, formation, and development in the Everglades began between 500 and 4,000 years before present in response to global and regional multidecadal fluxes in the periodicity and duration of flooding and drought events, which permitted the establishment and proliferation of weedy and woody vegetation on sawgrass marshes or ridges during periods of sustained drought (Willard *et al.* 2002, Willard *et al.* 2006, Bernhardt 2011). Over time, soil accretion resulting from higher productivity rates within these incipient tree islands led to higher surface elevations and shortened hydroperiods, which in turn promoted the establishment of shrubs and trees. Soil core data from multiple tree islands within the Everglades suggest that the woody plant successional sequence leading to the formation and development of tree islands followed a somewhat linear pathway, by which *Cephalanthus*, a small to medium size hydrophilic shrub commonly found at the marsh-tree island interface of tree islands, gave way to *Salix* which preceded the presence of *Morella* and ultimately the establishment *Chrysobalanus* (Stone and Chmura 2004). The establishment of woody vegetation on these incipient tree islands increased transpiration, leading to the translocation and accumulation of nutrients from the adjacent marsh into the incipient tree island environment (Wetzel *et al.* 2005, Wetzel *et al.* 2008). This plant-initiated change enhanced productivity within the developing tree islands and led to increased accretion rates and soil development. The result was a shortening of local hydroperiod, and continued recruitment, expansion, and maturation of the woody vegetation (Wetzel *et al.* 2008). As these incipient tree islands developed into tree patches over hundreds of years, they became faunal focal points, attracting not only mammals and birds seeking food and shelter but pollinators as well (Willard *et al.* 2006). Inadvertently, these faunal vectors would contribute to the further development of these tree patches by enhancing the recruitment of woody plants through pollination and seed transport between neighboring tree patches or nearby forest and by the deposition of nutrients, mainly phosphorus, in the form of bones and fecal matter (Wetzel *et al.* 2005). Consequently, as the tree islands developed they were transformed from nutrient limited communities to nutrient sinks (Orem *et al.* 2002); phosphorus concentration on modern tree islands may be several orders of magnitude greater than in the adjacent marsh (Willard *et al.* 2002, Gann *et al.* 2005, Ross *et al.* 2006, Hanan and Ross 2009).

As recently as 300 AD, many Everglades tree islands had yet to fully form and exhibited many of the characteristics of a transitional community consisting of sawgrass marshes and weedy annuals with a minor woody component (Willard *et al.* 2002, Stone and Chmura 2004). However, by around 1400 AD, following several extensive and prolonged local and regional drought episodes, the modern vegetation structure and hierarchy on most large fix-tree islands within the Everglades was forming (Willard *et al.* 2002, Bernhardt 2011).

Today, tree islands are a prominent feature in the ridge and slough landscape of the Everglades, where they provide a network of refuges for forest-dwelling plants and animals and perform important biodiversity and nutrient cycling functions (Gaines *et al.* 2002, Meshaka *et al.* 2002, Jayachandran *et al.* 2004, Hanan and Ross 2009). As such, tree islands have evolved over several millennia to serve as biological hot spots and may be thought as keystone habitats indicative of the overall health of the Everglades (Gawlik *et al.* 2002). Thus, any systemic loss in tree island abundance and/or coverage, whether in the long-hydroperiod ridge, slough, and tree island

mosaic or in the short-hydroperiod marl prairies (Figure 1), could be interpreted as a sign of broad-scale environmental change and degradation within the Greater Everglades.

During the latter part of the 19th century and continuing through the 20th century, anthropogenic alterations to the Greater Everglades resulted in the continued rapid development and succession of tree islands into well developed forested communities, in some regions (Johnson 1958, Kolipinski and Higer 1969, Willard *et al.* 2006), as well as in their degradation and loss from the landscape in other regions (Patterson and Finck 1999, Sklar and van der Valk 2002). Natural and management-related hydrologic fluxes in mean water depth and hydroperiods, due to the compartmentalization of the Everglades, have been linked to quantitative and qualitative changes in the structure, composition, and geochemistry of tree islands and in their recession and/or complete loss (Patterson and Finck 1999, Avineon 2002, Sklar and van der Valk 2002, Sklar *et al.* 2004, Hofmockel *et al.* 2008). 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 that have culminated in the total loss of tree island habitat (Schortemeyer 1980, Patterson and Finck 1999, Sklar and van der Valk 2002, Wetzel 2002, Wetzel *et al.* 2005). At the same time, however, within Shark River Slough in the southern Everglades, tree island development and expansion proceeded rapidly during the mid-20th century in response to a decrease in sheetflow and reduced hydroperiods resulting from upstream public works projects, which restrict the timing and volume of water reaching the area (Kolipinski and Higer 1969, Willard *et al.* 2006).

Much of what is known about the distribution or function of tree species in Everglades tree islands, or of tree island loss in the Everglades, has been viewed in relation to hydrologic fluxes resulting in prolonged high water conditions. However, tree islands are also susceptible to the direct and indirect effects of fire, particularly, during drought conditions, which not only kill trees but consume the rich organic soils, in the process altering water regime by lowering the surface elevation (Zaffke 1983). Under these circumstances, immediate post-fire flooding can be detrimental to tree island recovery, and may lead to their recession or complete loss (Ruiz *et al.* 2013). Furthermore, even under high water conditions, fire may encroach into tree islands, completely top-killing many of the trees present if fuel loading in the vicinity is such that it will carry a fire (author's personal observation¹).

Tree islands are also likely to be sensitive to the restoration efforts currently under way as part of the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) of 2000. Within the CERP, changes in water management associated with restoration will result in changes in the internal water economy of tree islands. Depending on the extent of hydrologic alterations achieved, the balance between flood-tolerant and flood-intolerant woody and herbaceous species within tree islands is expected to change, resulting in a shift in species assemblages and tree island function. Such change might culminate in a regime shift, i.e., large, abrupt, and deleterious long-term changes to the structure, composition, and function of a system or community, which may be permanent (Biggs *et al.* 2009), and the further degradation and loss of tree islands from the Greater Everglades.

¹ Observations made during two late season fires where water levels in the marsh were seasonally high and tree island soils were well saturated and inundated in many locations, conditions typically not associated with high fire risks to tree islands. However, sawgrass biomass and other fuel loads in and around the tree island were high and easily carried the fire into the tree island resulting in severe fire damage and high tree mortality.

However, CERP activities are just as likely to lead to the formation of new tree islands in areas where they recently disappeared or, at minimum, prevent any further degradation or loss of tree islands from the Everglades.

Because of the uncertainties associated with the restoration of the Everglades, it is imperative that managers formulate meaningful hydro-vegetative tree island Performance Measures and monitor how restoration activities brought about by the CERP affects them. To strengthen our ability to assess the “performance” of tree island ecosystems and predict how hydrologic restoration will translate into ecosystem response, an improved understanding of tree island reference conditions is needed.

With this as a backdrop, the work outlined below describes results from the monitoring of vegetation structure and associated biological processes within three tree islands, Black Hammock (BH), Gumbo Limbo Hammock (GL), and Satinleaf Hammock (SL), in Shark River Slough, Everglades National Park that were part of an earlier study dating back to 2001/02 (Sah *et al.* 2004; Figure 1). This report examines the interaction between hydrology and vegetation over a 10-year period, between 2001/02 and 2012 within six seasonally flooded tree island plots, two plots each per tree island, established in 2001/02, along a hydrologic and productivity gradient (Sah *et al.* 2004). We hypothesize that: (H1) hydrologic differences within plots between census dates will result in marked differences in a) tree and sapling densities, b) tree basal area, and c) forest structure, i.e., canopy volume, height, and richness and (H2) tree island growth, development, and succession is dependent on hydrologic fluxes, particularly during periods of prolonged droughts or below average hydroperiods.

Methods:

Study Area:

This study was conducted in the Bayhead Forest and Bayhead Swamp portions of three large teardrop-shaped tree islands, BH, GL, and SL, located in Shark River Slough, Everglades National Park (ENP; Figure 1). These three tree islands are characterized by a Tropical Hardwood Hammock 'head' associated with a topographic high or limestone outcrop that rises well above the marsh surface (Olmsted and Armentano 1997, Stone and Chmura 2004, Armentano *et al.* 2002, Ruiz *et al.* 2011) and a well defined extended 'tail' (~1-3 km long) aligned with the prevailing surface water flow direction (Loveless 1959, Snyder *et al.* 1990). The 'head' of these tree islands have inherently high productivity rates and a well developed mixed-species canopy of flood-intolerant hardwood trees (e.g., *Bursera simaruba*, *Celtis laevigata*, *Chrysophyllum oliviforme*, *Coccoloba diversifolia*, *Eugenia axillaris*, *Nectandra coriacea*, *Sideroxylon foetidissimum*, *Simaruba glauca*, among others) of both temperate and tropical origins (Armentano *et al.* 2002, Ruiz *et al.* 2011). In contrast, the 'tail' portion of these landscape features are generally less productive than the 'head' and are dominated by a mixed-species assemblage of flood-tolerant trees (e.g., *Annona glabra*, *Chrysobalanus icaco*, *Ilex cassine*, *Magnolia virginiana*, *Morella cerifera*, *Persea borbonia*, and *Salix caroliniana*), and ferns (e.g., *Acrostichum danaeifolium*, *Blechnum serrulatum*, *Osmunda regalis*, *Thelypteris interrupta*, and *Thelypteris palustris* var. *pubescens*), vines, forbs and graminoids that are distributed along a very gradual, downward sloping topographic gradient originating at the

bedrock outcrop or 'head' of the tree island and extending through the tail (Olmsted and Armentano 1997). The subtle decrease in elevation usually leads to decreasing productivity, lower canopy heights, increased hydroperiod and nutrient limitation along its length. Consequently, this topographic vector typically leads to the zonation or discrimination of three distinct vegetation units or assemblages; Bayhead Forest, Bayhead Swamp, and Sawgrass Tail, that grade into each other (Figure 2). These three tail units maybe thought of as chrono-successional communities where the Sawgrass Tail represent the earliest successional tree island community, analogous to the primordial marsh prior to tree island formation, followed by the Bayhead Swamp zone that represents a transitional phase between the primordial marsh and a Bayhead Forest climax community typifying tree island maturation in the absence of a Tropical Hardwood Hammock head.

Within the 'tail' environment, the Bayhead Forest has the highest canopy height (*ca.* 4 to 8 m tall) and tree cover (> 50 %) as well as productivity. Understory vegetation is mostly limited to shrubs and ferns with little or no graminoid cover. The Bayhead Swamp, which follows, has considerably reduced canopy heights (2 to 3.5 m tall) and tree cover (*ca.* 10 % to 75 %) and is generally less productive than the Bayhead Forest. However, forb and graminoid species diversity is generally higher than that of both the Bayhead Forest and Sawgrass Tail. The Sawgrass Tail, which may extend by more than 2x to 3x the combined length of the Bayhead and Bayhead Swamp portions of the tree island, particularly in Shark River Slough, ENP (Figure 2), is typified by mono-dominant stands of densely growing two to three meter tall sawgrass (*Cladium jamaicense*) with little or no tree or shrub cover (< 10 %). Ferns, forbs, and other graminoids species are common but are generally not abundant. Species diversity within the sawgrass tail is relatively low. In general, however, the Sawgrass Tail tends to be the most dynamic and least stable of the three tree island 'tail' vegetation assemblages associated with many of the larger tree islands found within the Everglades. Sawgrass Tails tend to be: 1) highly sensitive to hydrologic fluxes, which can lead to long-term shifts in species composition and/or woody plant encroachment; 2) highly pyrogenic and susceptible to fires, which may consume all standing biomass within this zone and, depending on post-fire hydrologic conditions, can take years to recover (Wade et al 1980); and 3) prone to, for reasons not yet understood, episodes of decadence or die-off that lead to the complete collapse, mortality, and loss of sawgrass within this zone for several years (Wade *et al.* 1980, Alexander and Crook 1984).

The paleoecological record from BH, GL, and SL as well as other tree islands in Shark River Slough depict a mostly linear but not necessarily unidirectional successional pathway leading to the formation, development, and expansion of tree islands within the Everglades (Kremer and Spackman 1981, Stone and Chmura 2004). Pollen records from these islands clearly show distinct species assemblages or communities appearing, disappearing, and, sometimes, reappearing again in response to hydrologic fluxes and disturbance, particularly fire, as tree islands develop and mature over time (Stone and Chmura 2004). However, the overall trend has been for the drying out of tree islands and an increase in woody vegetation (Willard *et al.* 2002, Stone and Chmura 2004, Willard *et al.* 2006, Bernhardt 2011).

The pollen chronology of woody species in these tree islands appears to follow a general but consistent successional trend. *Cephalanthus* appears first in the pollen record and is then

followed by *Salix*, *Morella*, and ultimately *Chrysobalanus* (Stone and Chmura 2004; Figure 3). Ferns spores reveal an interesting successional trend, as well, with the importance of *Osmunda* peaking at an intermediate stage in the late developmental phase of tree island formation but declining in importance with tree island drying conditions and maturation, i.e, the formation of a Bayhead Forest climax community (Stone and Chmura 2004, Willard *et al.* 2006; Figure 3). In contrast, Polypodiaceae spores, which include *Blechnum* and *Thelypteris* species, appear early on in the tree island formation phase and increase in importance over time (Stone and Chmura 2004; Figure 3). However, because of species specific differences in hydrologic tolerances and light requirements between these two species, it is likely that the single distribution recorded for *Blechnum* and *Thelypteris* actually reflects two distinct distributions where *Blechnum* is an early successional species, tolerant of extended hydroperiods and a high light environment, and *Thelypteris* a late successional species whose importance increases in response to decreased light availability and lower hydroperiods, environmental conditions typifying the late developmental phase of tree island formation and maturation typified by a Bayhead Forest.

Vegetation Sampling:

Between 2001 and 2002, permanent plots of 20 x 20 m (400 m²) and 15 x 15 m (225 m²) were established in the Bayhead Forest and Bayhead Swamp, respectively, on each of the three study tree islands (Figure 1). Each plot was gridded into 5 x 5 m 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 plot and cells were set up using a compass, measuring tape, sighting pole(s), and right-angle prism. These plots were revisited, reestablished, and censused in 2012.

Changes in 1) tree and sapling dynamics and 2) forest canopy structure and volume, between 2001/02 and 2012 in the Bayhead Forest and Bayhead Swamp plots on BH, GL, and SL were assessed as followed:

Tree and Sapling Dynamics:

During the 2001/02 plot census trees (≥ 5 cm) were identified to species, tagged using numbered aluminum tags, and their diameter (cm) at breast height (DBH) measured and recorded. The location of each tagged tree was recorded to the nearest 0.1 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 and recorded as well. The density and species of all tree saplings (stems ≥ 1 and < 5.0 cm in DBH) within each 5 x 5 m cell was recorded, and assigned to one of two DBH size classes: 1 to 2.9 cm or 3 to 4.9 cm. Saplings with multiple stems between 1 and 4.9 cm DBH originating from the base of a sapling were treated as individuals but assigned or grouped to the largest sampling stem category, e.g., 1 to 2.9 cm or 3 to 4.9 cm, for that grouping.

During the 2012 census, all Bayhead Forest and Bayhead Swamp plots were re-censused to access changes in tree and sapling densities as well as tree ingrowth and mortality. Ingrowth of new individuals or sprouts from existing trees were tagged and added to the plot's tree database at this time as well.

For each plot, the total tree density was estimated by summing the total number of 'parent' trees per plot and then dividing by the total area sample per plot, 400 m² or 225 m² for Bayhead Forest and Bayhead Swamp plots, respectively. Total stand basal area was calculated by adding the total basal area of all stems ≥ 5 cm DBH in each plot. Sapling densities and basal area were similarly calculated but all shoots were treated as individuals, for density purposes, even if they were members of a multi-stem clonal group.

Changes in tree and sapling species' importance value (IV), for each Bayhead and Bayhead Swamp plot, was calculated by summing the relativized density (R_d) and basal area (R_{ba}) of each species, within each plot, as a proportion of the total plot using the following equation:

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

Canopy Vertical Structure and Volume:

During both census periods, 2001/02 and 2012, the canopy's vertical structure or profile, including maximum canopy height, volume (m³ · m⁻²), mean canopy height, and skewness was determined using a vertical line intercept sampling technique (Ross *et al.* 1998, Sah 2004). Starting at 1.5 m above the ground, we recorded the species and 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 at the corners of each 5 x 5 m 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 occupied 1-m interval in the plot. Canopy volume (m³ · m⁻²) was calculated as the mean number of occupied 1-m strata above each sampling point. Mean canopy height represents the weighted mean height of all 1-m canopy cells present in the plot, where weighting is based on the percent canopy occupancy for each stratum across all sampling locations. Canopy skewness is a measure of asymmetry in the cumulative canopy occupancy profile among all 1-m height strata.

Hydrology:

The hydrologic regime of each Bayhead Forest and Bayhead Swamp plot, for the 21-year period between 1991-2011 and the seven-year period² preceding each census date (1994-2000 and 2004-2010), was estimated using topographic data from existing elevation surveys conducted in 2001/02 for each vegetation plot (Reed and Ross 2004, Sah 2004) and long-term water level records from the nearest stage recorder to each tree island, i.e., P33, NP203, and

²Within Shark River Slough, tree island vegetation composition had the highest correlation with the preceding mean seven-year hydroperiod (Sah 2004).

G620 (Figure 1). The mean annual hydroperiod, i.e., the mean annual number of days per year that the ground surface of the plot was inundated, was estimated for each plot by assuming a flat water surface and averaging the number of days that the water table elevation at the corresponding gage station (P33, NP203, and G620) was above the ground surface of the plot during each year. Daily averages were derived using elevations from all plot corners; 25 and 16 corners each for Bayhead Forest and Bayhead Swamp plots, respectively. Differences in hydroperiod between plots and census years were analyzed using either paired *t*-test or one-way ANOVA. All statistics were performed using Statistica v7.1 (StatSoft, Inc. 2006).

Results:

Vegetation:

Tree and Sapling Dynamics - Density:

Average tree densities across all three Bayhead Forest plots increased by 41% between 2001/02 and 2012 (Figure 4a). The SL Bayhead Forest plot had the highest overall density of trees during both sampling periods with 1,700 stems ha⁻¹ in 2001/02 vs. 2,475 stems ha⁻¹ in 2012. However, the greatest increase in stem density occurred in the BH Bayhead Forest plot where the tree density increased by 55 %, from 950 stems ha⁻¹ to 1,475 stems ha⁻¹ (Figure 4a). Stem densities in GL Bayhead Forest increased by 18 % from 950 stems ha⁻¹ to 1,125 stems ha⁻¹ (Figure 4a).

Increases in tree density between the two census dates were also observed for two of the Bayhead Swamp Plots (Figure 4b). Tree stem densities increased by more than 100 % in both the BH and SL Bayhead Swamp plots where stems densities increased from 267 stems ha⁻¹ to 622 stems ha⁻¹ and from 0 stems ha⁻¹ to 89 stems ha⁻¹, respectively (Figure 4b). At the GL Bayhead Swamp plot tree density remained unchanged at 0 stems ha⁻¹ (Figure 4b).

In the case of sapling densities, a different pattern emerged. For the three Bayhead Forest plots, sampling densities decreased by an average of 64 % between 2001/02 and 2012 (Figure 5a). The greatest decrease occurred in the BH Bayhead Forest plot where sapling densities decreased by 84 % from 7,125 stem ha⁻¹ to 1,175 stems ha⁻¹ (Figure 5a). In contrast, sapling densities at the GL and SL Bayhead Forest plots decreased by only 8 % and 36 %, respectively.

Increases in sapling densities between the two census dates were observed in two of the Bayhead Swamp Plots (Figure 5b). Sapling densities were 7 % and 18 % higher in 2012 than in 2001/02 for the BH and GL Bayhead Swamp plots but 52 % lower at the SL Bayhead Swamp plot (Figure 5b).

Tree and Sapling Dynamics - Basal Area:

Between 2001/02 and 2012, tree basal area increased by 32 % from 35.3 to 46.7 m² • ha⁻¹ and 105 % from 12.5 to 24.6 m² • ha⁻¹ in the GL and SL Bayhead Forest plots, respectively. However, at the BH plot, basal area decreased by 14 % from 19.7 to 16.9 m² • ha⁻¹ (Figure 6a).

Tree basal area in the Bayhead Swamp plots at BH and SL increased from 1.1 to 2.1 m² • ha⁻¹ and from 0.0 to 0.2 m² • ha⁻¹, respectively (Figure 6b). However, because of the lack of trees present in the GL Bayhead Swamp plot during both sampling periods, tree basal remained unchanged at 0.0 m² • ha⁻¹ (Figure 6b).

Sapling basal area at all three Bayhead Forest plots decreased between 2001/2 and 2012 by an average of 58 % (Figure 7a). The Bayhead Forest plot at BH saw the sharpest decline in basal area with a 79 % decline (Figure 7a). At the two other Bayhead Forest plots, GL and SL, basal area declined by 39 % from 0.33 to 0.20 and 29 % from 2.51 to 1.79, respectively between 2001/02 and 2012 (Figure 7a). In contrast, sapling basal areas increased across all Bayhead Swamp plots between 2001/02 and 2012 by an average of 31 % (Figure 7b). The greatest increase occurred at the GL plot where sapling basal area increased by almost 100 % from 2.5 to 4.9 (Figure 7b). The BH and SL plots had modest gains of 19 % from 7.8 to 9.2 and 2 % from 2.6 to 2.7, respectively (Figure 7b).

Tree and Sapling Dynamics - Species Richness:

Nine different tree and sapling species were identified and recorded during both census periods across all Bayhead Forest and Bayhead Swamp plots located within the three study islands (see Table 2 for species list). During both census periods, mean tree and sapling species richness were higher in the Bayhead Forest plots than the Bayhead Swamp plots (Table 1). With one exception, the BH Bayhead Forest plot, tree species richness, in both the Bayhead Forest and Bayhead Swamp plots, were greater in the 2012 census than the 2001/02 census (Table 1). Mean tree species richness in the Bayhead Forest plots in 2001/02 averaged 5.7 while the same plots in 2012 averaged 6.3. A similar pattern was observed in the Bayhead Swamp plots where mean tree species richness was lower in the 2001/02 census than in the 2012 census, 1.0 vs. 2.0, respectively. This trend, however, did not hold true for saplings in the Bayhead Forest plots where species richness was slightly lower in 2012, but mostly unchanged, between both census dates, 5.3 vs 5.7, respectively (Table 1). Only the GL Bayhead Forest plot saw an increase in the species richness of sapling species between 2001/02 and 2012, 5.0 vs. 8.0 respectively (Table 1). In the Bayhead Swamp plots, average sapling species richness remained unchanged at 3.7 between 2001/02 and 2012, respectively (Table 1).

Tree and Sapling Dynamics - Importance Value (IV):

Spatio-temporal differences in Bayhead Forest and Bayhead Swamp tree and sapling species importance values (IV) are shown in Figures 8 - 11. In general, tree and sapling IV varied by tree island and plot location (e.g., Bayhead Forest vs. Bayhead Swamp plots) with many species showing a general, but not significant, decrease in IV between census dates, particularly within the Bayhead Forest plots. The lone exception being *Persea borbonia* and *Salix caroliniana*, which were not recorded during the 2012 census, in the Bayhead Forest and Bayhead Swamp plots, respectively (Table 2). However, some species not present in the original 2001/02 census gained importance in several plots (Tables 2 and 3).

Across all Bayhead Forest plots, the average IV of most tree species declined between 2001/02 and 2012 (Table 2). However, the IV of three tree species *Ilex cassine*, *S. caroliniana*, and, most notably, *Chrysobalanus icaco* increased during this period (Table 2). Increases in the IV

of *S. caroliniana* were observed in the BH and GL Bayhead Forest plots while for *I. cassine* an increase in IV was recorded in the GL and SL Bayhead Forest plots and BH Bayhead Swamp plot (Figures 8 and 9). *C. icaco*, however, was the only tree species whose IV increased across all Bayhead Forest plots and in one of the Bayhead Swamp plots between 2001/02 and 2012 (BH; Figure 8 and 9). As a sapling, within individual plots, the IV of *C. icaco* remained mostly unchanged with only one of the three Bayhead Forest plots, SL, showing an increase in its IV between 2001/02 and 2012 (Figure 10).

Table 1: Tree and sapling species richness in the three Bayhead Forest and Bayhead Swamp plots between 2001/02 and 2012.

Plot	Tree Island	Tree Species Richness		Sapling Species Richness	
		2001/02	2012	2001/02	2012
Bayhead Forest	Black Hammock	5	4	5	3
	Gumbo Limbo Hammock	6	8	5	8
	Satinleaf Hammock	6	7	7	5
Mean		5.7	6.3	5.7	5.3
Bayhead Swamp	Black Hammock	3	5	5	4
	Gumbo Limbo Hammock	0	0	2	3
	Satinleaf Hammock	0	1	4	4
Mean		1.0	2.0	3.7	3.7

Table 2: Mean (± 1 S.E.) tree importance value (IV) for the three Bayhead Forest and Bayhead Swamp plots between 2001/02 and 2012.

Species	Bayhead Forest IV (%)		Bayhead Swamp IV (%)	
	2001/02	2012	2001/02	2012
<i>Annona glabra</i>	44.0 \pm 13.4	34.3 \pm 4.0	13.8 \pm 13.8	50.1 \pm 28.7
<i>Chrysobalanus icaco</i>	4.4 \pm 4.4	18.9 \pm 9.8	0.0 \pm 0.0	2.0 \pm 2.0
<i>Ficus aurea</i>	11.7 \pm 11.7	9.5 \pm 9.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Ilex cassine</i>	2.8 \pm 1.8	3.5 \pm 2.2	0.0 \pm 0.0	4.2 \pm 4.2
<i>Magnolia virginiana</i>	14.9 \pm 9.5	10.6 \pm 5.7	0.0 \pm 0.0	6.7 \pm 6.7
<i>Morella cerifera</i>	3.1 \pm 1.8	2.5 \pm 0.7	4.1 \pm 4.1	4.3 \pm 4.3
<i>Persea borbonia</i>	0.7 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Salix caroliniana</i>	17.0 \pm 3.6	20.2 \pm 0.2	15.5 \pm 15.5	0.0 \pm 0.0
<i>Sambucus nigra</i> ssp. <i>canadensis</i>	1.5 \pm 0.8	0.4 \pm 0.4	0.0 \pm 0.0	0.0 \pm 0.0

With one exception, the GL Bayhead Forest plot where *Ficus aurea* was the dominant tree species, *Annona glabra* was the dominant or co-dominant tree species during both censuses in all Bayhead Forest and Bayhead Swamp plots (Figures 8 and 9). As a sapling, the importance of *A. glabra* decreased in most Bayhead Forest plots between the two censuses but remained relatively unchanged in the three Bayhead Swamp plots (Figures 10 and 11). Likewise, *A.*

glabra had the highest IV of all sapling species in all Bayhead Swamp plots except for GL, where *S. caroliniana* was the most important species during both census dates (Figure 11).

Table 3: Mean (± 1 S.E.) sapling importance value (IV) for the three Bayhead Forest and Bayhead Swamp plots between 2001/02 and 2012.

Species	BH Sapling IV (%)		BHS Sapling IV (%)	
	2001/02	2012	2001/02	2012
<i>Annona glabra</i>	23.6 \pm 10.8	10.7 \pm 2.9	49.6 \pm 18.8	51.7 \pm 18.0
<i>Chrysobalanus icaco</i>	37.2 \pm 26.2	50.7 \pm 23.7	0.2 \pm 0.2	0.8 \pm 0.8
<i>Ficus aurea</i>	0.2 \pm 0.2	14.4 \pm 14.4	0.1 \pm 0.1	0.1 \pm 0.1
<i>Ilex cassine</i>	3.3 \pm 2.8	2.6 \pm 2.0	0.0 \pm 0.0	0.5 \pm 0.5
<i>Magnolia virginiana</i>	8.0 \pm 8.0	9.4 \pm 6.4	14.9 \pm 13.8	11.7 \pm 10.5
<i>Morella cerifera</i>	21.3 \pm 12.6	3.1 \pm 1.9	6.1 \pm 4.2	7.8 \pm 5.0
<i>Persea borbonia</i>	0.0 \pm 0.0	4.1 \pm 4.1	0.2 \pm 0.2	0.4 \pm 0.3
<i>Salix caroliniana</i>	6.2 \pm 1.8	0.0 \pm 0.0	28.8 \pm 27.8	27.1 \pm 27.1
<i>Sambucus nigra ssp. canadensis</i>	0.2 \pm 0.2	5.1 \pm 3.7	0.0 \pm 0.0	0.0 \pm 0.0

The IV of sapling species showed much greater variability between plots and census dates than did those of the tree species (Figure 10 and 11). For example, in the Bayhead Forest plots, less dominant sapling species like *P. borbonia*, *Sambucus nigra ssp. canadensis*, and *Ficus aurea* increased in IV between 2001/02 and 2012 while more important sapling species like *A. glabra* and *Morella cerifera* decreased (Table 3). *S. caroliniana*, however, was lost between 2001/02 and 2012 (Table 3). This pattern, however, was not observed in the Bayhead Swamp plots (Table 3). The average IV of the three dominant sapling species within the three Bayhead Swamp plots, *A. glabra*, *Magnolia virginiana*, and *S. caroliniana*, remained unchanged between census dates, as did most of the other sapling species (Table 3).

Canopy Vertical Structure and Volume:

The vertical canopy profiles of the three Bayhead Forest and Bayhead Swamp plots revealed distinct changes in the canopy structure of these plots between 2001/02 and 2012 (Figures 12 and 13). On average, mean canopy volume and maximum and mean canopy height increased across all plots between 2001/02 and 2012 (Table 4). Canopy skewness, which is a measure of canopy asymmetry and development, shifted towards a more positively skewed distribution in all three Bayhead Forest plots between 2001/02 and 2012 (Table 4). This shift in skewness is indicative of upper canopy development and the loss of the understory canopy as a result of resource redistribution from the lower to the upper canopy of emergent trees in response to decreasing light availability in the lower canopy. In the Bayhead Swamp plots, however, a measure of canopy skewness was not possible because of the paucity of trees present and the limited number of canopy strata occupied within these plots (Figure 13).

Table 4: Tree island canopy structure (maximum and mean canopy height and canopy volume and skewness) for the three Bayhead Forest and Bayhead Swamp plots between 2001/02 and 2012.

Plot	Tree Island	Canopy Volume (m ³ /m ²)		Maximum Canopy Height (m)		Mean Canopy Height (m)		Canopy Skewness	
		2001/02	2012	2001/02	2012	2001/02	2012	2001/02	2012
Bayhead Forest	Black Hammock	2.36	3.28	7	8	3.9	4.8	-1.012	0.353
	Gumbo Limbo	2.6	3.6	8	10	4.6	5.8	-1.377	0.056
	Satinleaf	3.24	3.24	8	8	4.2	4.7	-0.811	-0.693
Mean		2.73	3.37	8	9	4.2	5.1		
Bayhead Swamp	Black Hammock	0.44	0.69	4	4	2.6	2.9	NA	NA
	Gumbo Limbo	0	0.19	0	4	0	2.8	NA	NA
	Satinleaf	0.31	0.38	3	4	2.5	2.8	NA	NA
Mean		0.25	0.42	2	4	1.7	2.8		

Hydrology:

For the 21-year period between 1991 and 2011, daily mean marsh water elevations at the three stage recorders (P-33, NP203, & G620) used in this study closely paralleled each other within and across years, with very little variation among stage recorders (Figure 14). Differences in the daily mean marsh water elevations between stage recorders averaged 7.6 cm with a maximum difference of 10.2 cm between G620 and NP203. This range in values is a result of slight differences in regional ground surface elevations and not generally indicative of deeper water conditions at one stage recorder vs. another. On average, G620 exhibited the greatest intraannual variation, 0.817 ± 0.067 (SE) m. P33 and NP203, which were very similar to each other, averaged 0.522 ± 0.038 (SE) m and 0.625 ± 0.040 (SE) m, respectively. Annual mean water levels at the three stage recorders during both census periods, 2001/02 and 2012, were at or below the 21-year average (Figure 15). However, during the seven-year period that preceded the 2001/02 census, 1994 - 2000, yearly mean marsh water levels, at the three stage recorders, were near or above the 21-year average (Figure 15). In contrast, for the seven-year period that preceded the 2012 census, 2004-2010, annual mean water levels were generally at or below the 21-year average (Figure 15). This difference in the long-term, e.g., seven-year, annual mean water levels between censuses resulted in significantly decreased hydroperiods across all plots (Table 5). On average, hydroperiods in the Bayhead Forest and Bayhead Swamp plots decreased by 98 and 72 days, respectively, between the two census dates (Table 5). This difference in Bayhead Forest and Bayhead Swamp plot hydroperiods between census dates were significant ($P \leq 0.05$).

Mean annual hydroperiods at the three Bayhead Forests plots during the seven-year period preceding each census, 2001/02 and 2012, were not significantly (ANOVA $F_{2,18} = 0.145$, $P = 0.866$ and $F_{2,18} = 1.337$, $P = 0.288$, respectively; Figure 16a). This was also the case for the three Bayhead Swamp plots during the 2001/02 census (ANOVA $F_{2,18} = 2.438$, $P = 0.116$, Figure 16b). However, the mean hydroperiods at the three Bayhead Swamp plots during the 2012 census were significantly different from each other (ANOVA $F_{2,18} = 9.306$, $P = 0.002$,

Figure 16b). The mean hydroperiod at the GL Bayhead Swamp plot (282 days) was significantly higher than that of the BH (172 days; Paired t -test₍₆₎ = 5.957, P = 0.001) and SL (Bayhead Swamp) plots (207 days; Paired t -test₍₆₎ = 5.907, P = 0.01; Figure 16b). However, the mean hydroperiod at the GL Bayhead Swamp in 2012 was not significantly different than that of the BH and SL Bayhead Swamp plots during the 2001/02 census (ANOVA $F_{2,18}$ = 0.149, P = 0.862; Figure 16b).

Table 5: Mean seven-year hydroperiods (days) between 1991-2000 and 2004-2010 for the three Bayhead Forest and Bayhead Swamp tree plots.

Plot	Tree Island	Mean seven-year Hydroperiod (days)		Change in Hydroperiod (days)	t	df	P
		1994 - 2000	2004 - 2010				
Bayhead Forest	Black Hammock	196	82	- 114	4.961	6	0.003
	Gumbo Limbo Hammock	212	116	- 96	4.186	6	0.006
	Satinleaf Hammock	217	132	- 85	4.050	6	0.007
	Mean	208	110	- 98	7.851	20	< 0.001
Bayhead Swamp	Black Hammock	266	172	- 94	4.422	6	0.004
	Gumbo Limbo Hammock	332	283	- 49	2.777	6	0.032
	Satinleaf Hammock	282	207	- 75	3.379	6	0.015
	Mean	293	221	- 72	6.092	20	< 0.001

Vegetation:Hydrology Relationship:

Multiple regression analysis revealed a significant relationship between plot hydrology and the density ($r = -0.730$, $p = 0.007$) and basal area ($r = -0.637$, $p = 0.026$) of trees within all plots (Figure 17a and 17b). In both cases, tree density and basal area increased as a function of decreasing plot hydroperiods (Figure 17a and 17b). Surprisingly, across all plots, sapling density ($r = 0.012$, $p = 0.723$) and basal area ($r = 0.092$, $p = 0.776$) were not significantly correlated to plot hydroperiod (Figure 17c and 17d). However, a strong relationship between hydroperiod and sapling density ($r = -0.952$, $p = 0.003$) and basal area ($r = -0.834$, $p = 0.039$) was observed for the Bayhead Swamp plots (Figure 17e and 17f). In both cases, sapling density and basal area increased as a function of decreasing Bayhead Swamp plot hydroperiods (Figure 17e and 17f).

Synopsis:

1. All plots (Bayhead Forest and Bayhead Swamp), except the GL Bayhead Swamp plot, saw an increase in tree density between 2001/02 and 2012.

2. Sapling densities decreased in all three Bayhead Forest plots and in the SL Bayhead Swamp plot but increased in the BH and GL Bayhead Swamp plots between 2001/02 and 2012.
3. Except for the BH Bayhead Forest plot, tree basal area increased or remained the same in all plots between 2001/02 and 2012.
4. Sapling basal area within the three Bayhead Forest plots decreased between 2001/02 and 2012 but saw increases in the three Bayhead Swamp plots between census dates.
5. During both census, tree and sapling species richness were higher in the Bayhead Forest plots than the Bayhead Swamp plots.
6. Tree species richness was generally higher in the 2012 census than in the 2001/02.
7. Most tree and sapling species saw a general decline in importance value (IV) between 2001/02 and 2012. *A. glabra* was the dominant or co-dominant tree species during both census dates in all Bayhead Forest and Bayhead Swamp plots. *I. cassine*, *S. caroliniana*, and *C. icaco* trees saw their IV increase between census dates. Within the Bayhead Forest plots, the IV of *P. borbonia*, *S. nigra* ssp. *canadensis* and *F. aurea* saplings increased between 2001/02 and 2012 while those of *A. glabra* and *M. cerifera* decreased.
8. Mean canopy volume and maximum and median height increased in all Bayhead Forest and Bayhead Swamp plots between 2001/02 and 2012 while canopy skewness shifted towards a more positively skewed distributions in all three Bayhead Forest plots between census dates, indicating canopy development and maturation.
9. Differences in the seven-year mean hydroperiod between the three Bayhead Forest plots between 1994-2000 and 2004-2010 were significantly different (208 vs. 110 days, respectively). The same was true for the three Bayhead Swamp plots (293 vs. 221 days, respectively).
10. Across all plots, Bayhead Forest and Bayhead Swamp combined, tree density and basal area were negatively correlated to hydroperiod, i.e., tree density and basal area increased as a function of decreasing plot hydroperiods.
11. Within the Bayhead Swamp plots, sapling density and basal area increased as a function of decreasing hydroperiods.

Discussion:

In the Everglades, hydrology is a determinant factor that influences not only the spatial and temporal distribution of species but the structure and composition of plant assemblages as well. Tree islands in this vast wetland are no exception (Armentano *et al.* 2002, Wetzel 2002, Ross and Jones 2004, Espinar *et al.* 2011). Our results and analysis clearly demonstrate that long-term hydrologic fluxes within tree islands can lead to contrasting and significant differences in: 1) tree density and basal area, 2) species richness and importance, and 3) forest canopy volume and maximum and mean canopy heights. More importantly, our data and analysis demonstrate that

long-term fluxes in the hydrologic regime within these wooded communities, resulting in below average water levels and shorter hydroperiods, promote the establishment and growth of woody plants across the entire tree island 'tail' gradient, i.e., Bayhead Forest, Bayhead Swamp, and presumably the Sawgrass Tail as well, and drive successional processes that culminate in the expansion, growth, and maturation of tree islands.

The results reported here reinforce the concept that tree islands are dynamic successional communities that expand and contract over time in response to hydrologic fluxes. Between 2001/02 and 2012, Bayhead Forest and Bayhead Swamp plots saw increases in tree density, basal area and species richness as well as significant canopy development, e.g., increases in canopy volume and height, as a result of below average water levels and shorter hydroperiods within Shark River Slough. At the same time, while sapling densities decreased in the Bayhead Forest plots in response to intra- and interspecific competition for nutrients and light availability resulting from canopy closure and forest maturation, the Bayhead Swamp plots saw both an increase in the number of trees, of which most were saplings a decade ago, and a new cohort of saplings indicating a slow but steady progression in the succession of the Bayhead Swamp plots into a Bayhead Forest. Temporal changes in species importance values (IV), further reinforce the concept of a successional model of tree island development and expansion overtime, though a precise interpretation of changes in IV between 2001/02 and 2012 is difficult because of species-specific differences in their hydrologic tolerances as they germinate, develop, and mature over time. Once established, mature trees may persist at the extremes of their hydrologic range with no apparent deleterious effects. In general, however, flood tolerant species like *A. glabra* and *S. caroliniana* saw their IV decline while moderately flood tolerant species like *C. icaco*, *I. cassine*, and *F. aurea* increased. In parallel to our findings, Sah *et al.* (2011) documented a decrease in the tree cover of *A. glabra* as well as an increase in the tree cover of *C. icaco* between 2001/02 and 2011 along transects perpendicular to the main tree island axis of our study tree islands and intersecting our plots. Furthermore, transects crossing our Bayhead Swamp plots saw a marked increase in shrub cover, particularly in *Cephalanthus*, between 2001/02 and 2011 (Sah *et al.* 2011). Of these changes, the most important one appears to be the documented increase in the cover and IV of *C. icaco* in both transects and plots, which based on the paleoecological record is indicative of the latter phase of tree island development and maturation to Bayhead Forest.

The strong correlation between tree island vegetation structure and hydrology discussed above is highly suggestive of how hydrologic modifications brought about through the CERP will affect tree islands dynamic throughout the Everglades. Depending on the magnitude of hydrologic alterations achieved by the CERP, the balance between flood-tolerant and flood-intolerant woody and herbaceous vegetation within tree islands is likely to change. Biogeochemical and biogeomorphological processes, i.e., nutrient cycling and soil accretion and development, will be impacted as well. The magnitude and direction of such changes is likely to be spatially explicit in response to regional differences in tree island reference conditions and the extent of hydrologic modification achieved by the CERP. Thus, it is not unrealistic to think that long-term hydrologic changes brought about by the CERP could lead to the degradation and loss of tree islands from the system if the hydrologic changes implemented significantly alters the hydrologic regime within tree islands so that the hydroperiod exceeds the tolerance of the *in situ* vegetation. At the same time, however, tree islands currently under hydrologic stress or in a highly degradative state, e.g., ghost islands (Ewe *et al.* 2009), could see a recovery if hydrologic conditions

conducive to woody plants establishment and growth is achieved and sustained long-term. Ideally, the CERP should strive to achieve system wide hydrologic conditions that result in a spatially balanced mosaic of tree islands in different successional states with no specific preference to tree island type or successional state. System wide homogeneity in tree islands structure, composition, and type should be discouraged, since it is likely to lead to both the floral and faunal extirpation of rare species, which will likely result in a reduction in the overall species diversity of tree islands. At the same time, system wide homogeneity in tree islands significantly increases the chances of a system wide or regional perturbation event having catastrophic consequences.

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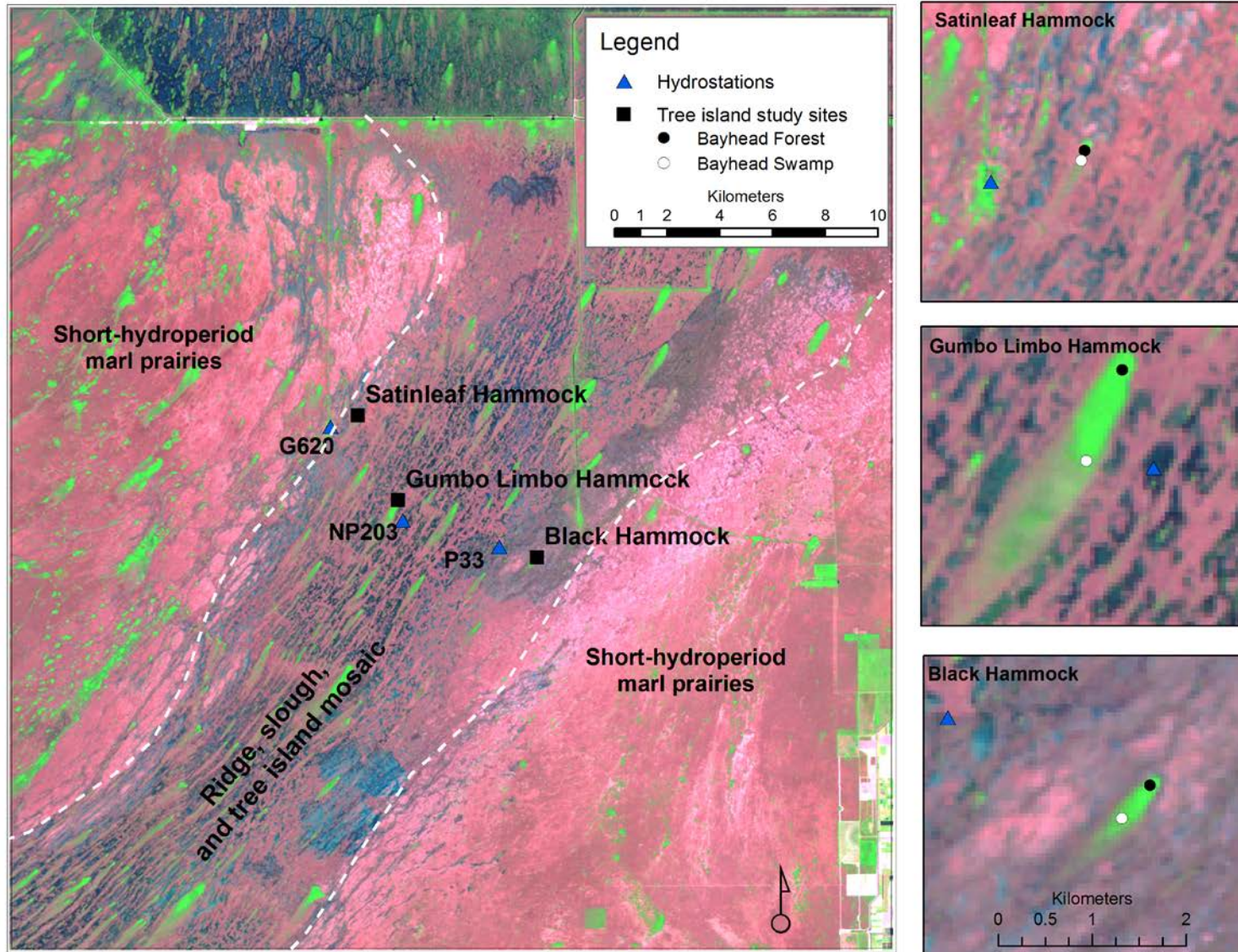


Figure 1: Location of tree islands and sampling plots within Shark River Slough, Everglades National Park, FL, USA.



Figure 2: Tree island vegetation zonation at Gumbo Limbo Hammock, Shark River Slough, Everglades National Park, FL, USA..

Gumbo Limbo 1
Analyst G.L. Chmura

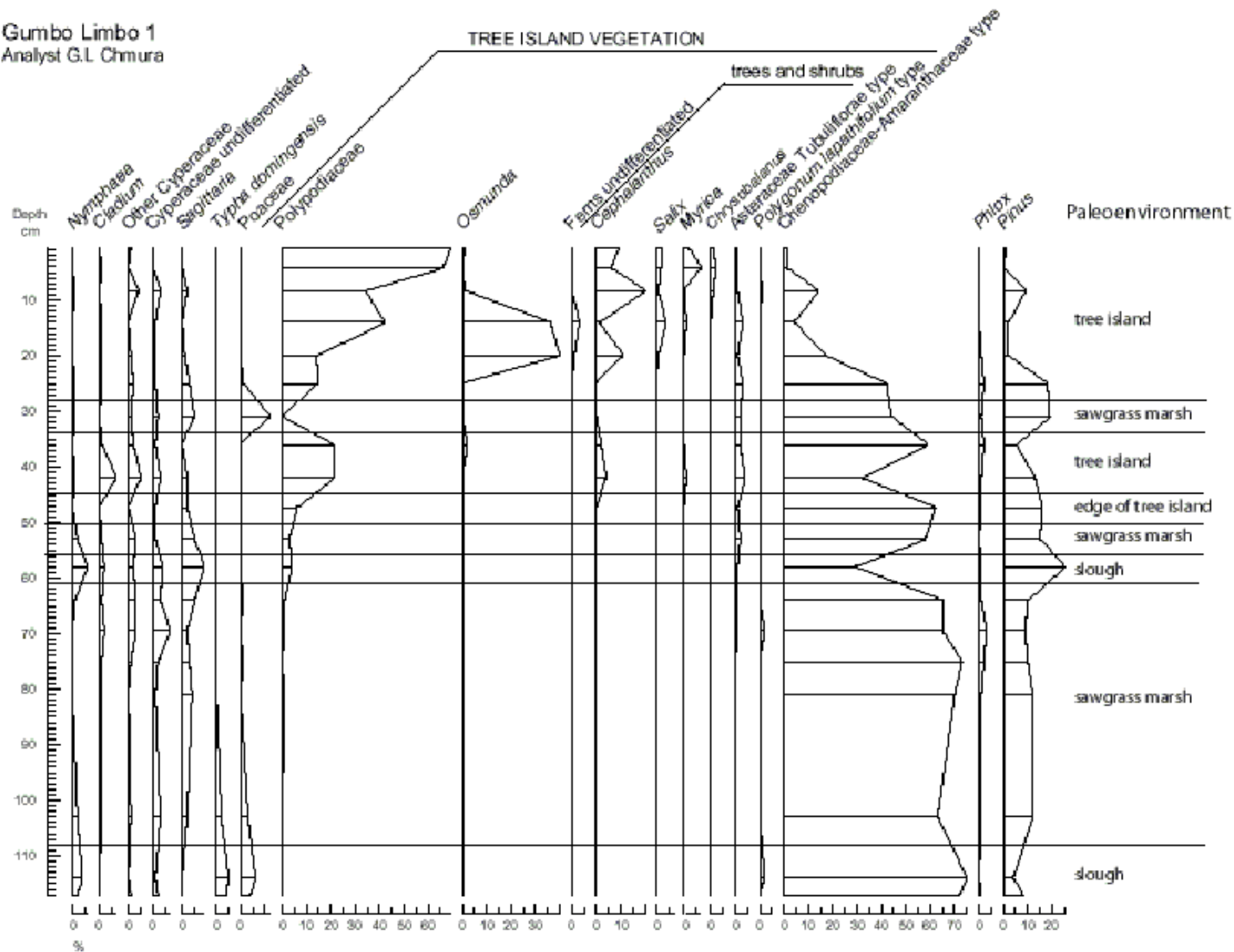


Figure 3: Percent pollen and plant spores from soil core taken at Gumbo Limbo Hammock, Shark River Slough, Everglades National Park, FL, USA. Original data and figure from Stone and Chmura (2004).

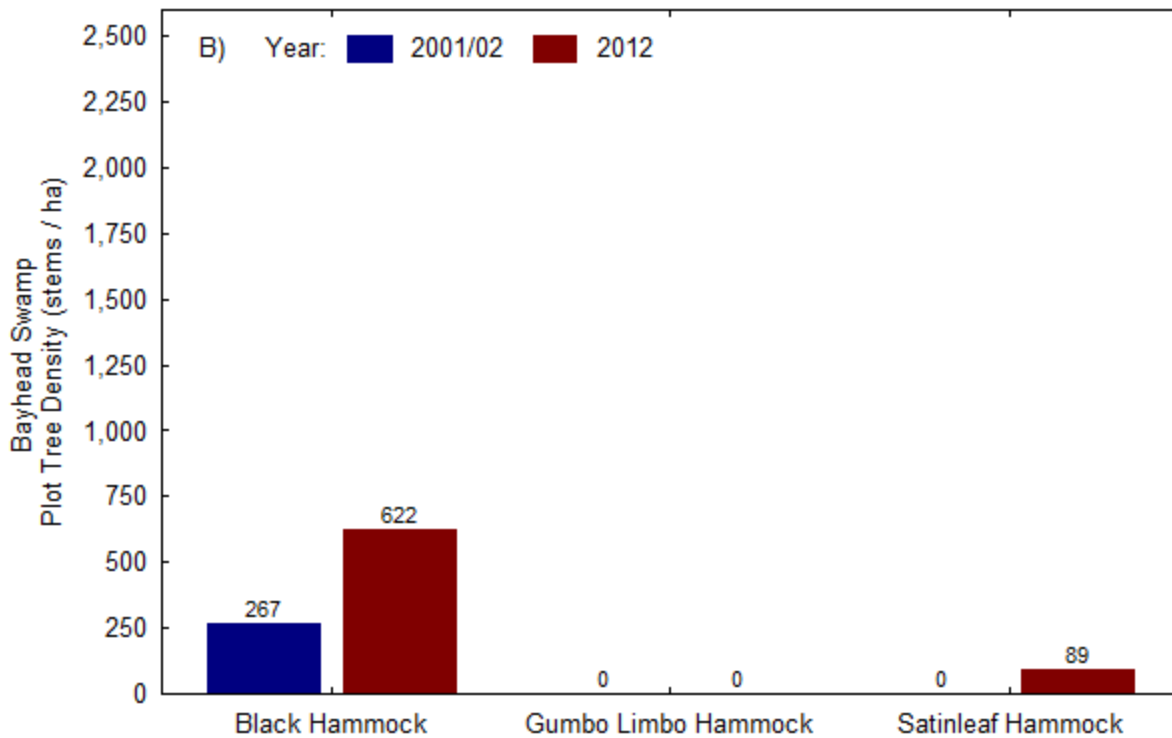
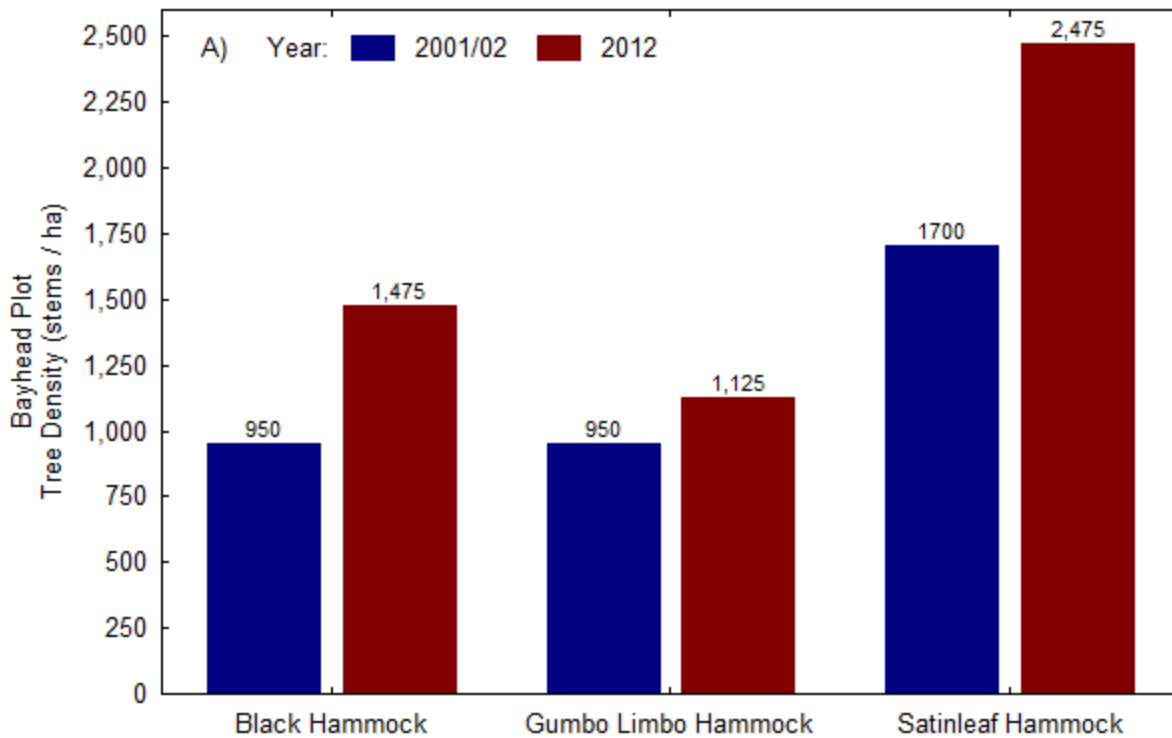


Figure 4: Tree density within the (A) Bayhead Forest and (B) Bayhead Swamp plots located on Black Hammock, Gumbo Limbo Hammock, and Satinleaf Hammock.

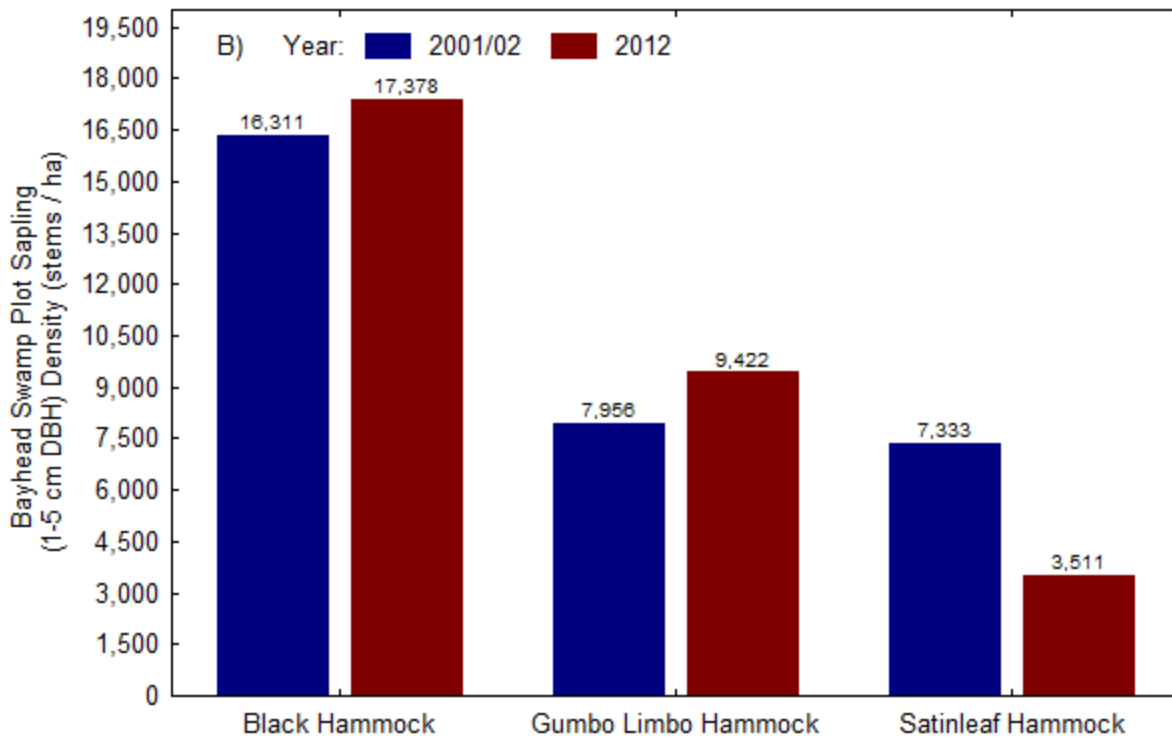
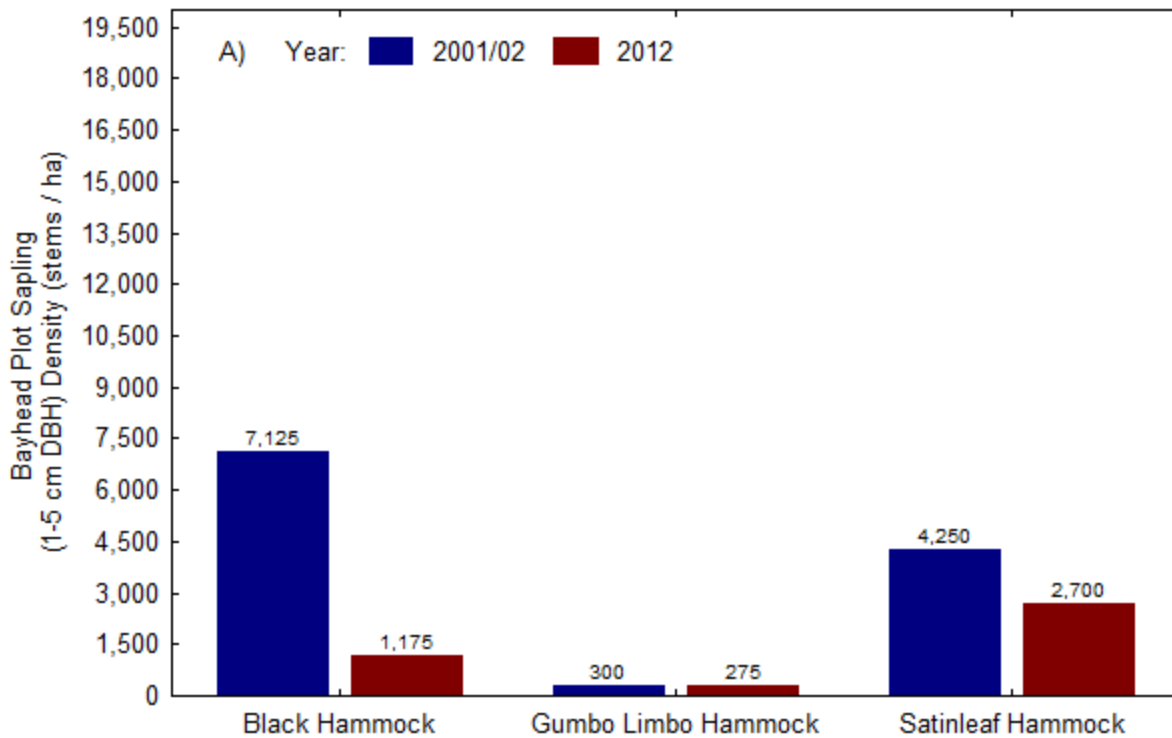


Figure 5: Sapling density within the (A) Bayhead Forest and (B) Bayhead Swamp plots located on Black Hammock, Gumbo Limbo Hammock, and Satinleaf Hammock.

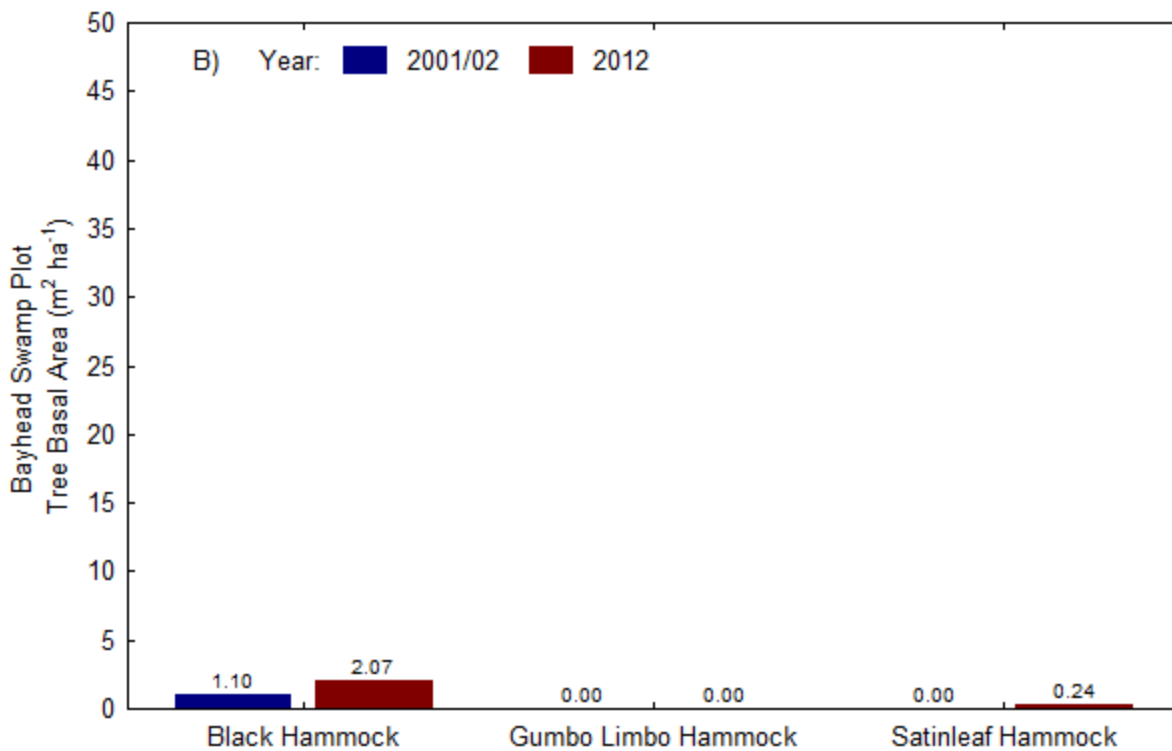
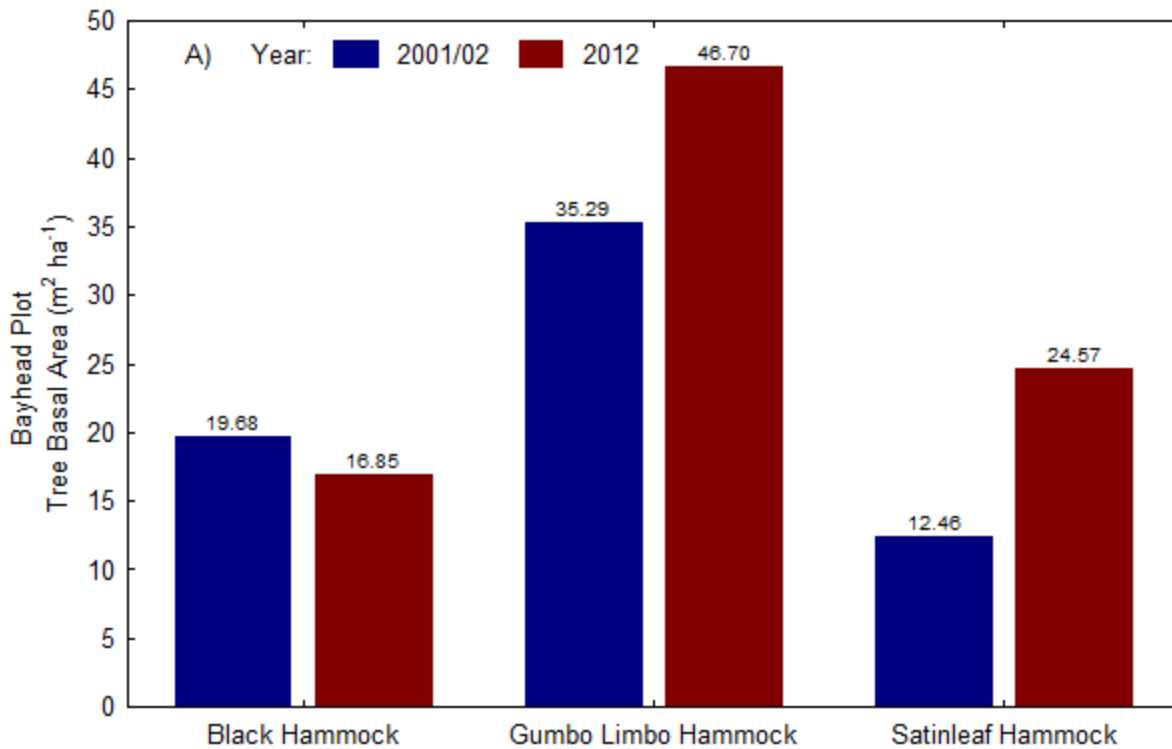


Figure 6: Tree basal area within the (A) Bayhead Forest and (B) Bayhead Swamp plots located on Black Hammock, Gumbo Limbo Hammock, and Satinleaf Hammock.

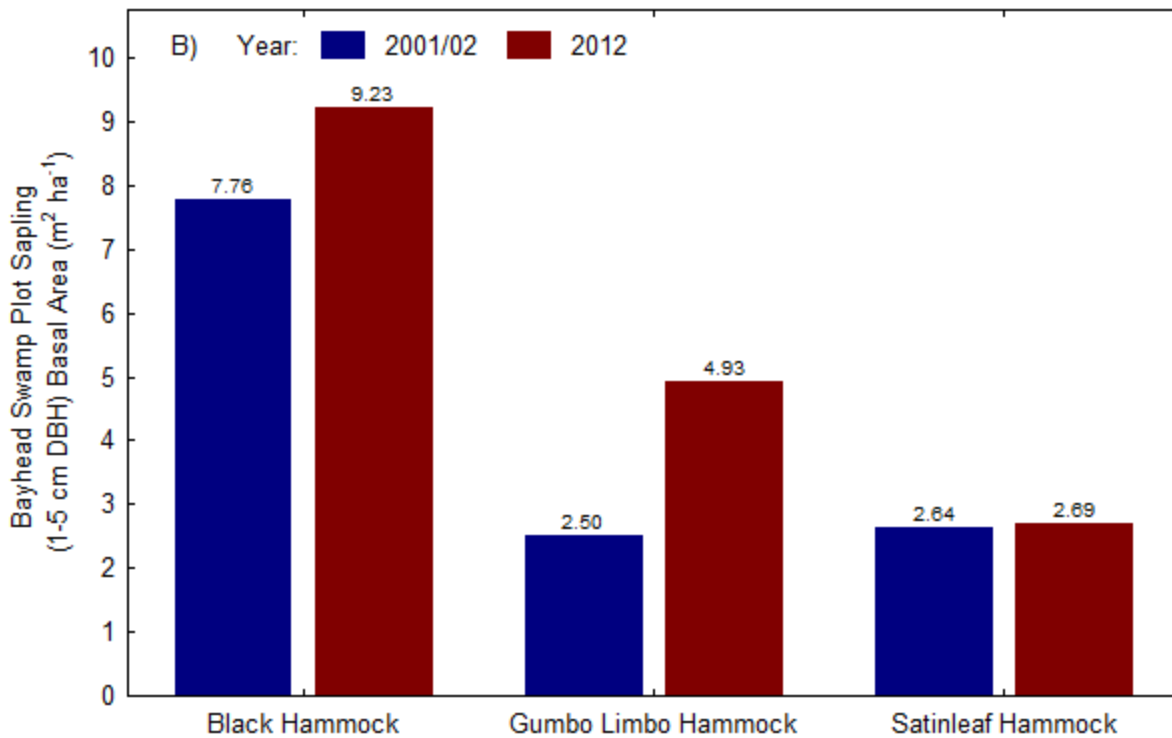
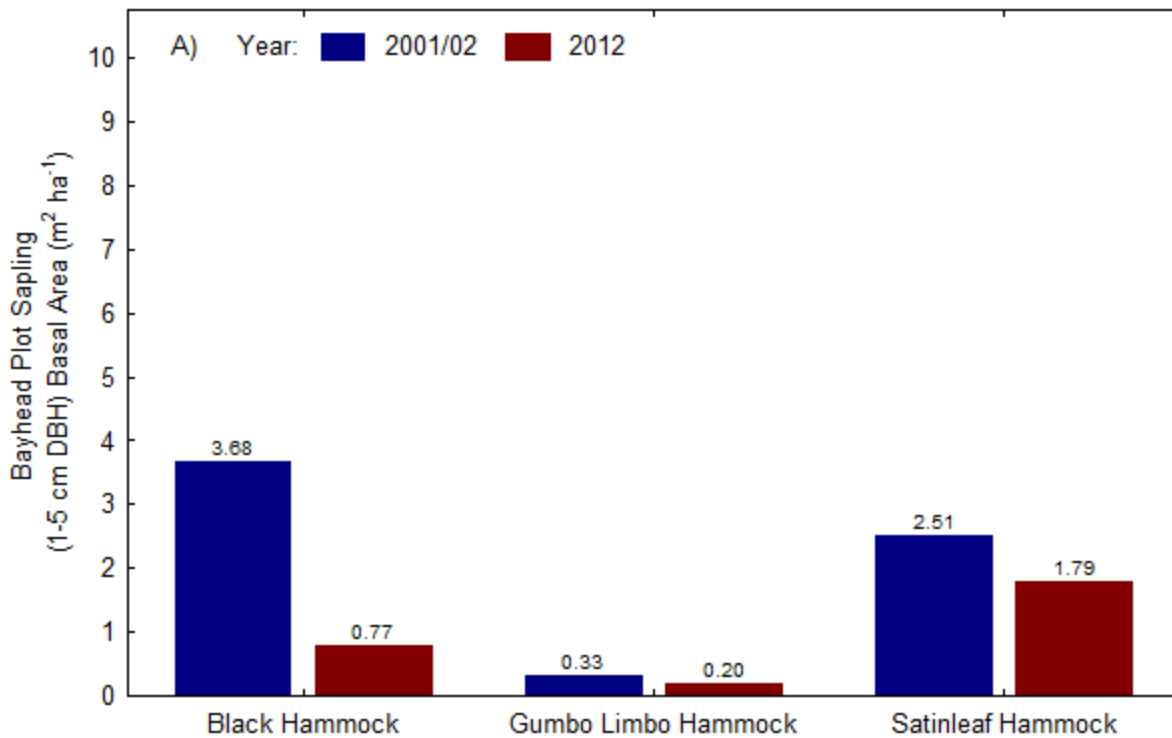
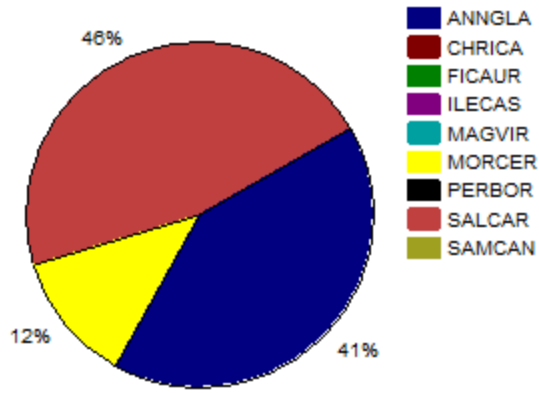


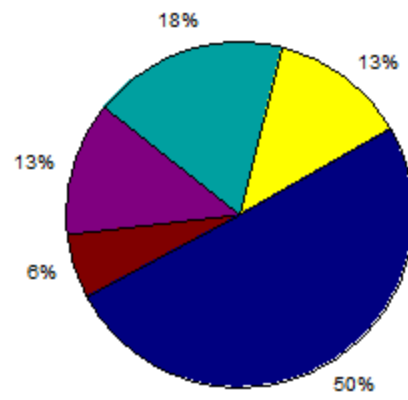
Figure 7: Sapling basal area within the (A) Bayhead Forest and (B) Bayhead Swamp plots located on Black Hammock, Gumbo Limbo Hammock, and Satinleaf Hammock.



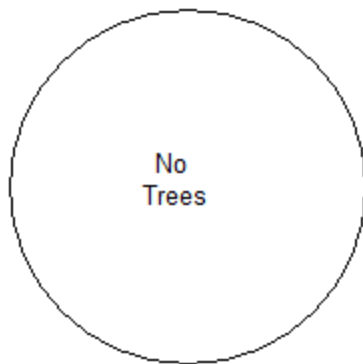
Figure 8: Tree species importance value (IV) across all bayhead plots between 2001/02 and 2012.



a) Black Hammock Bayhead Swamp Plot (2001/02)



b) Black Hammock Bayhead Swamp Plot 2012



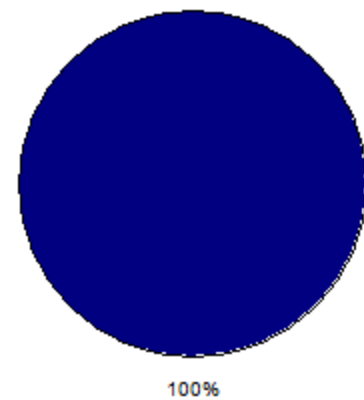
c) Gumbo Limbo Hammock Bayhead Swamp Plot (2001/02)



d) Gumbo Limbo Hammock Bayhead Swamp Plot (2012)



e) Satinleaf Hammock Bayhead Swamp Plot (2001/02)



f) Satinleaf Hammock BHS Plot (2012)

Figure 9: Tree importance value (IV) across all Bayhead Swamp plots between 2001 /02 and 2012.

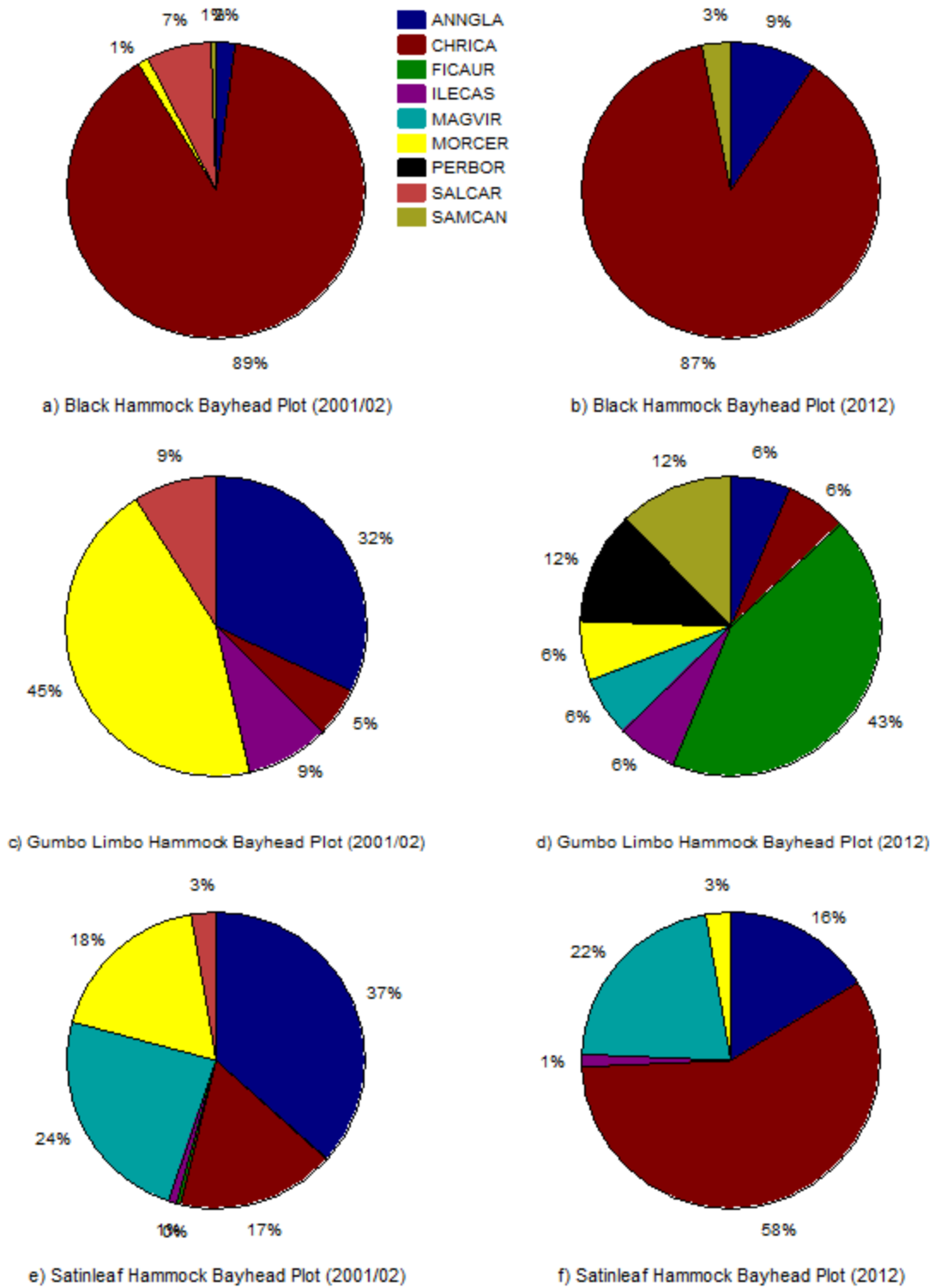


Figure 10: Sapling importance value (IV) across all Bayhead Forest plots between 2001/02 and 2012.

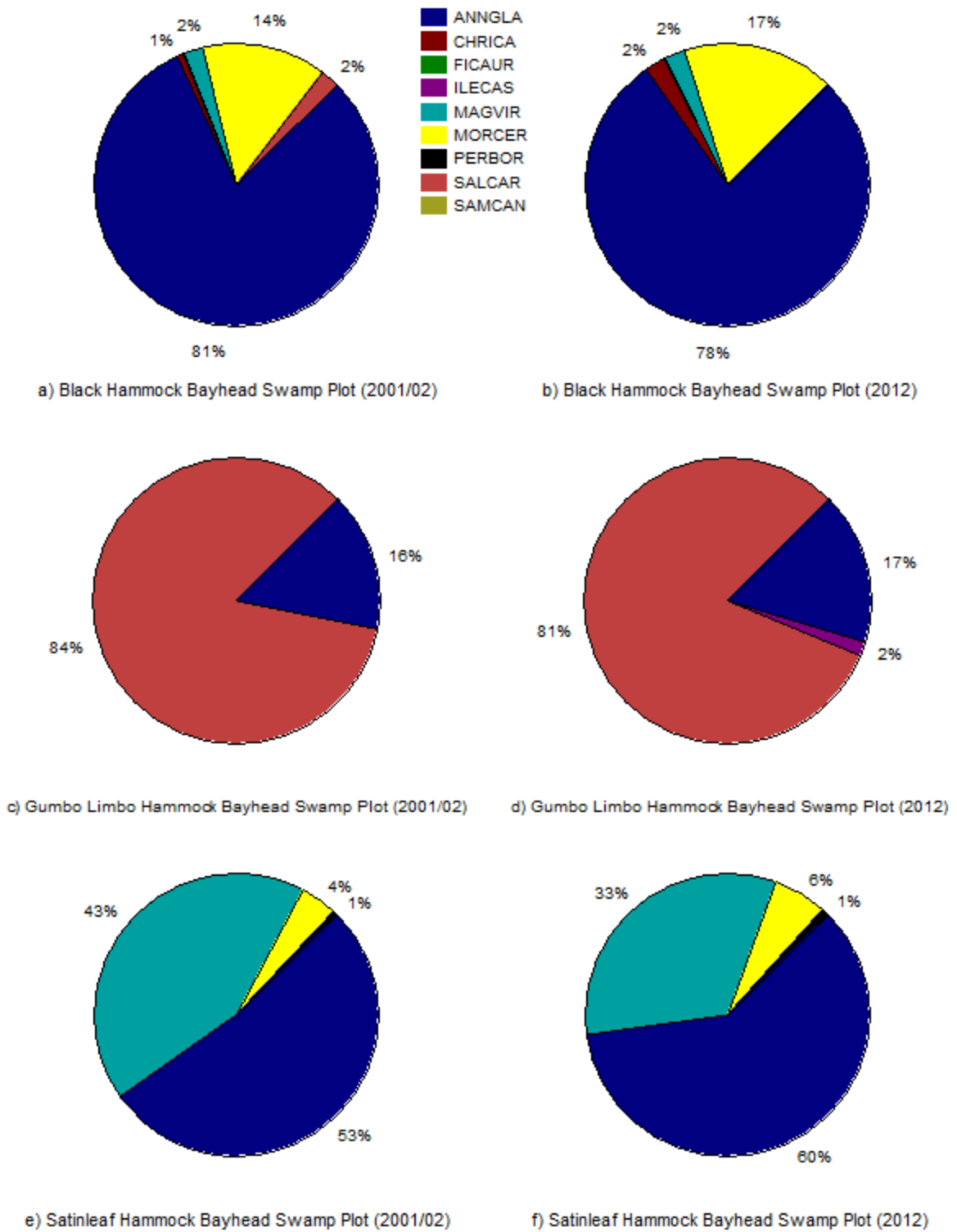


Figure 11: Sapling species importance values (IV) across all Bayhead Swamp plots between 2001/02 and 2012.

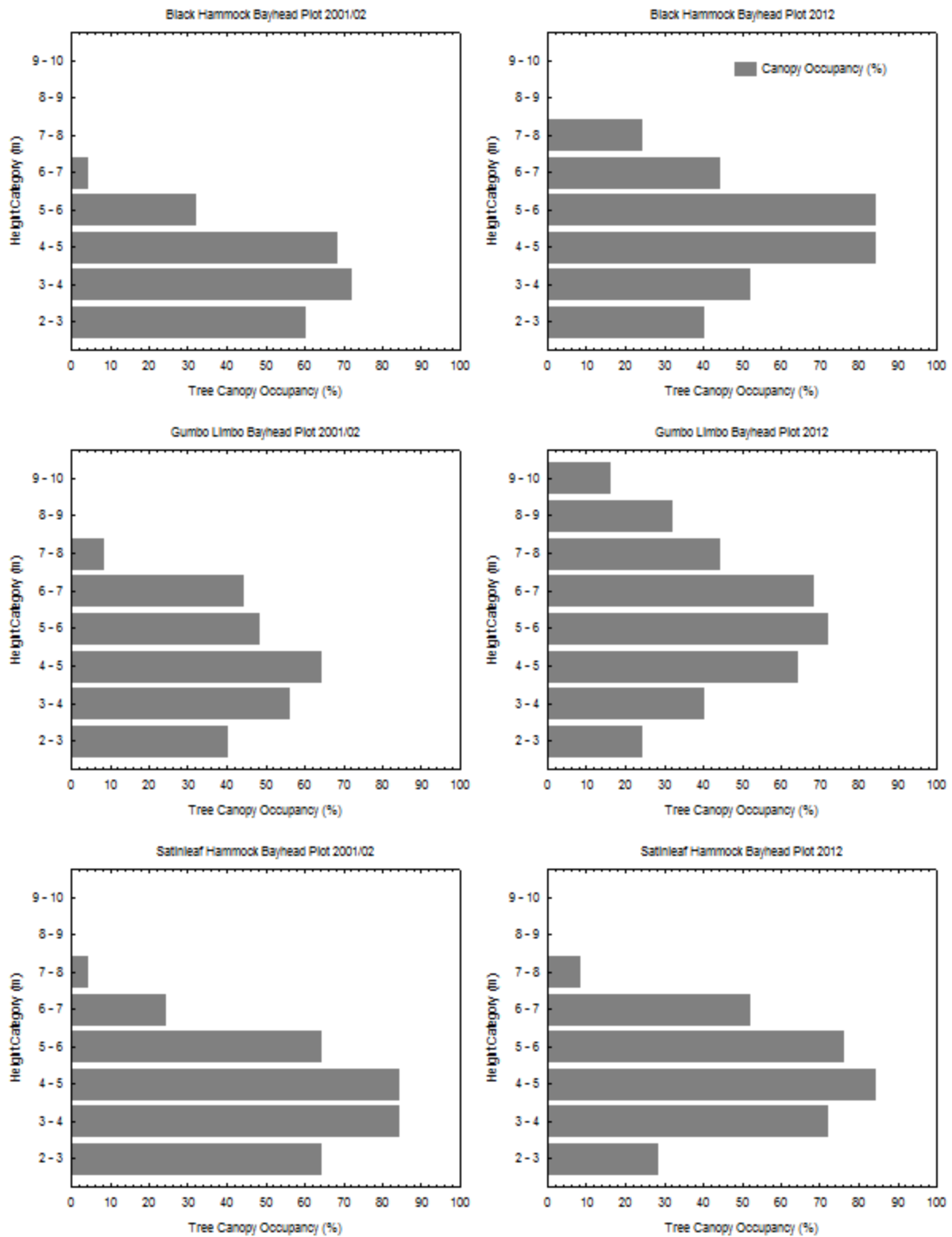


Figure 12: Decadal variation in the vertical canopy profile of the three Bayhead Forest plots.

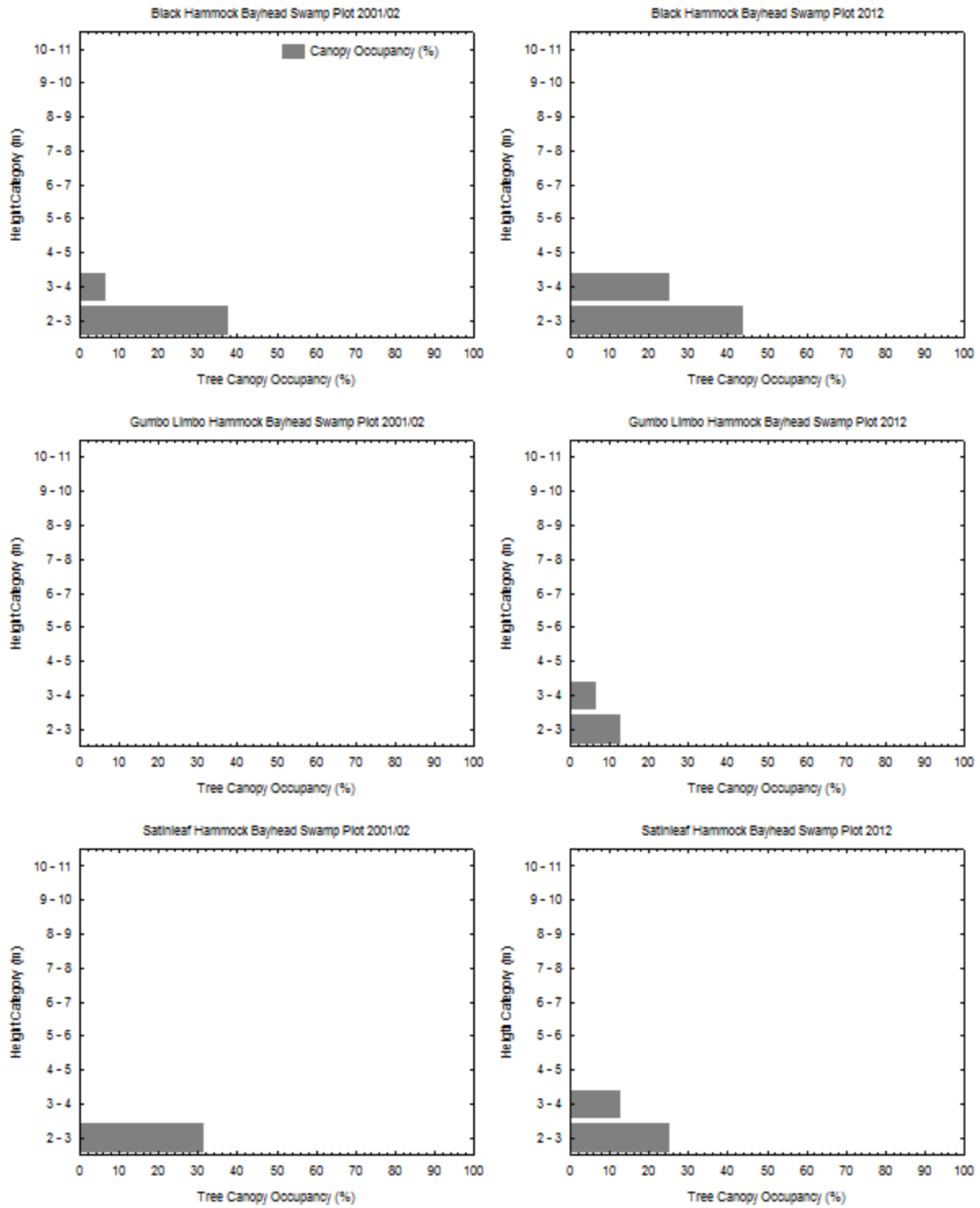


Figure 13: Decadal variation in the vertical canopy profile of the three Bayhead Swamp plots.

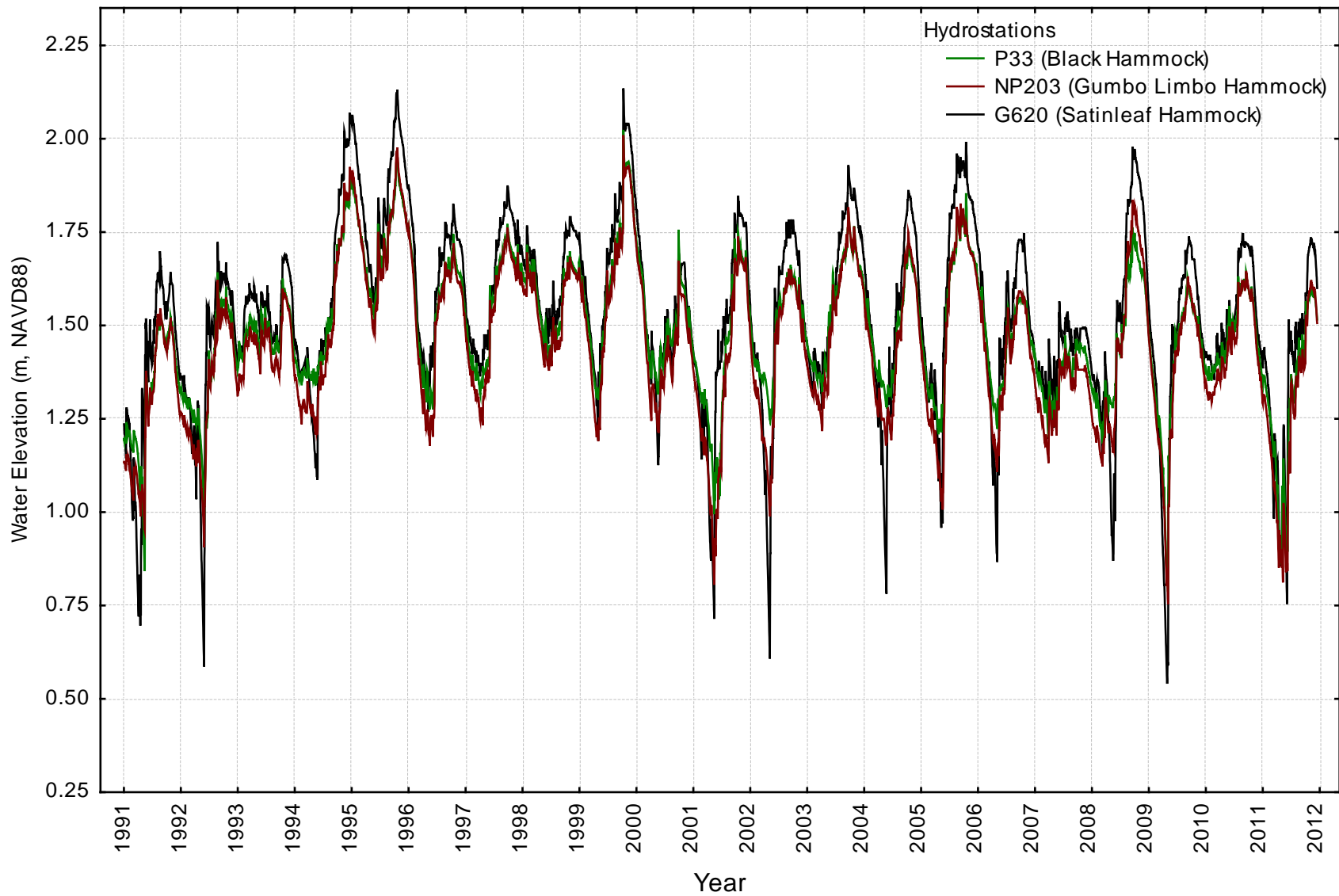


Figure 14: Twenty-one year hydrograph for the three stage recorders (P33, NP203, and G620) used to calculate individual plot hydroperiods.

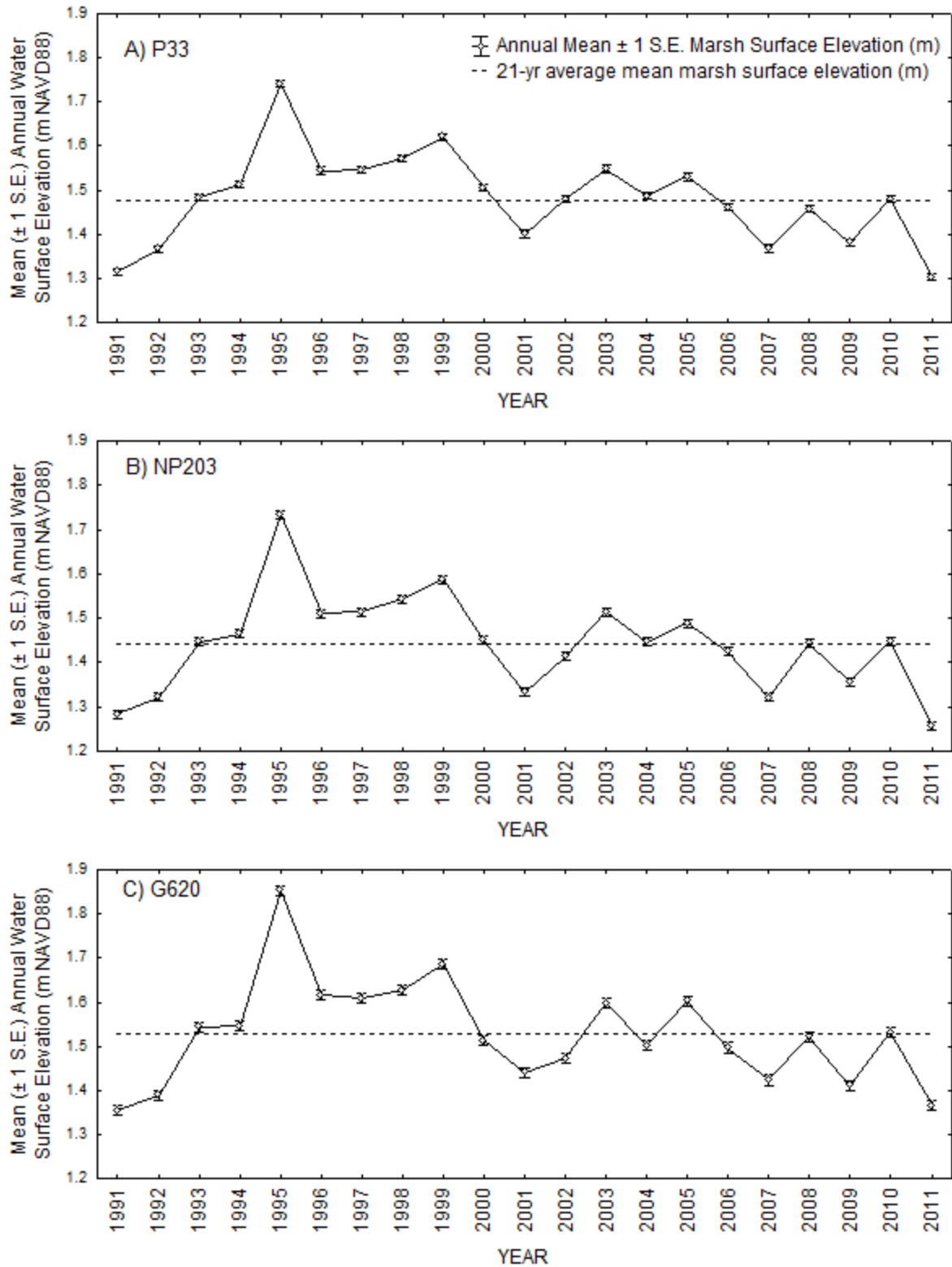


Figure 15: Mean (± 1 S.E.) annual marsh water surface elevation for (A) P33, (B) NP203, and (C) G620 between 1991 and 2011.

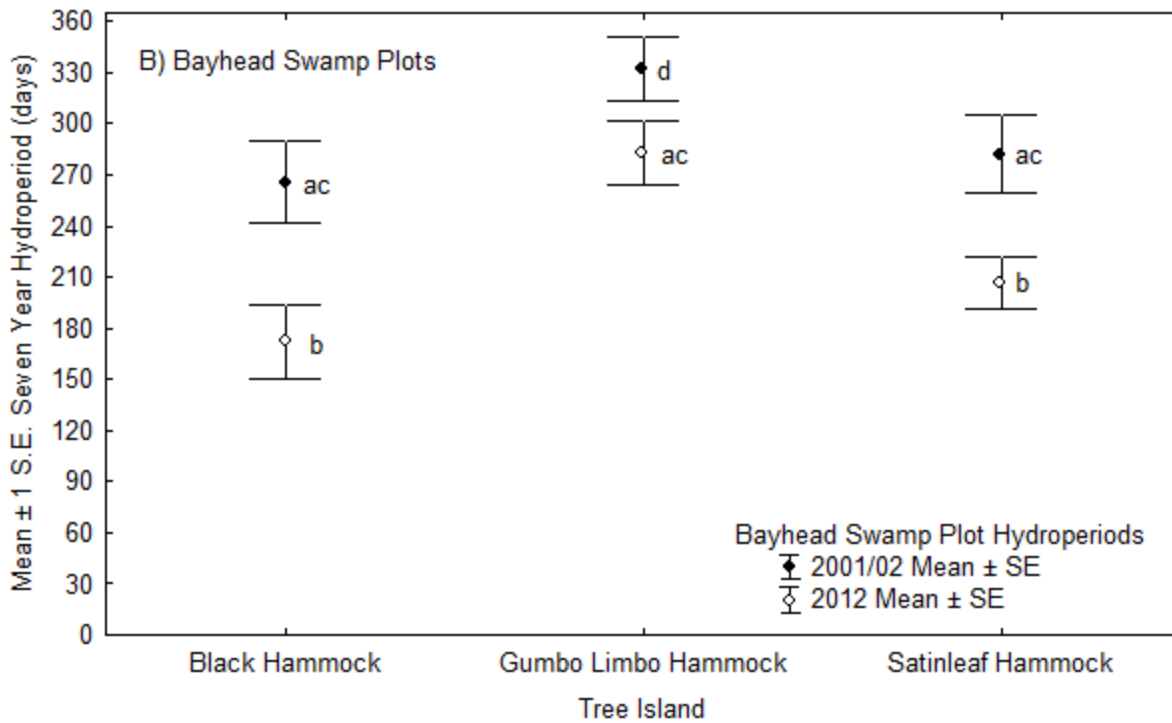
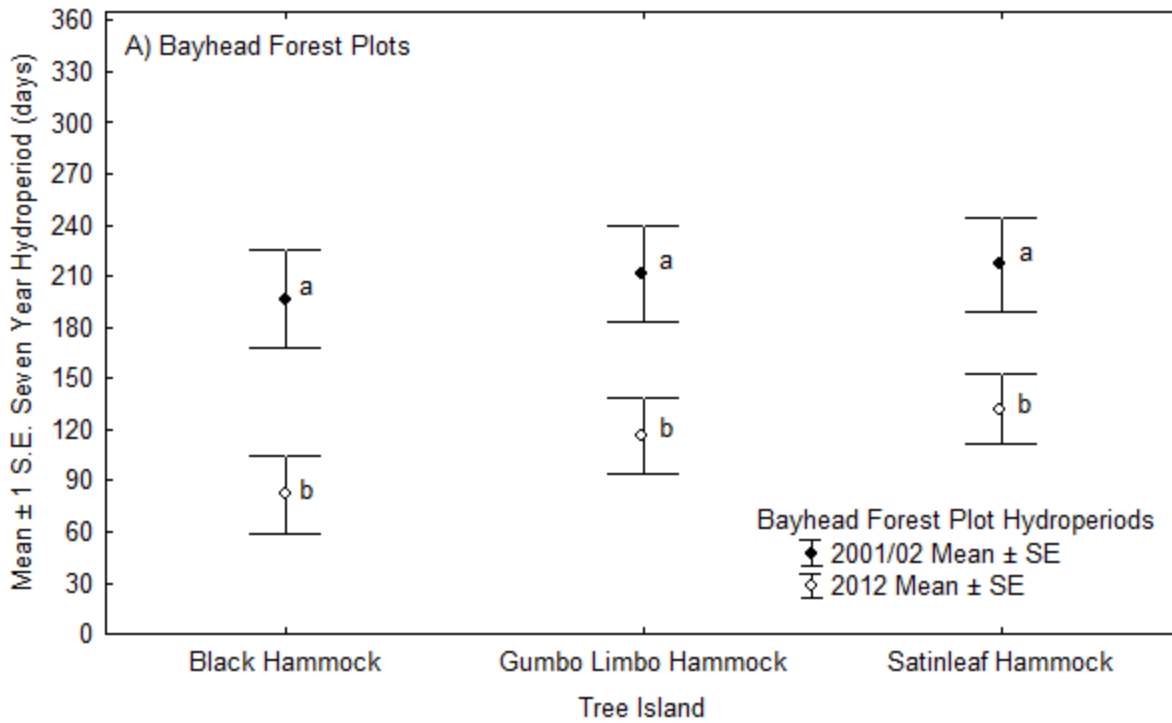


Figure 16: Differences in mean (± 1 S.E.) seven year average hydroperiod for A) Bayhead Forest and B) Bayhead Swamp plots between 2001/02 and 2012. Means with same superscript do not differ at $P < 0.05$.

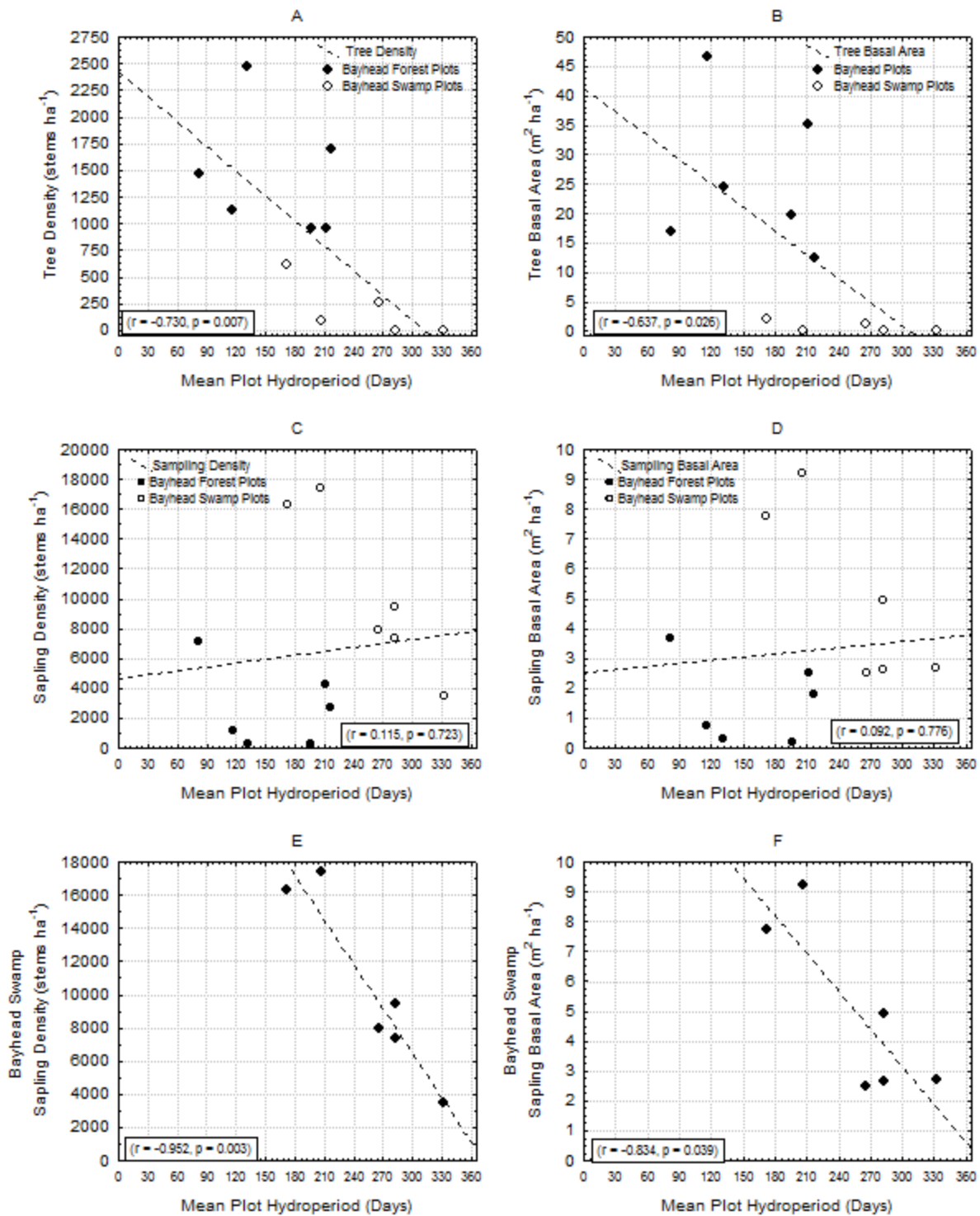


Figure 17: Correlation between combined mean plot hydroperiod (2001/02 and 2012) and tree (A) density and (B) basal area; sapling (C) density and (D) basal area; and Bayhead Swamp (only) sapling (E) density and (F) basal area.