

Survival and growth responses of eight Everglades tree species along an experimental hydrological gradient on two tree island types

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Abstract

Questions: How are the early survival and growth of seedlings of Everglades tree species planted in an experimental setting on artificial tree islands affected by hydrology and substrate type? What are the implications of these responses for broader tree island restoration efforts?

Location: Loxahatchee Impoundment Landscape Assessment (LILA), Boynton Beach, Florida, USA.

Methods: An experiment was designed to test hydrological and substrate effects on seedling growth and survivorship. Two islands – a peat and a limestone-core island representing two major types found in the Everglades – were constructed in four macrocosms. A mixture of eight tree species was planted on each island in March of 2006 and 2007. Survival and height growth of seedlings planted in 2006 were assessed periodically during the next two and a half years.

Results: Survival and growth improved with increasing elevation on both tree island substrate types. Seedlings' survival and growth responses along a moisture gradient matched species distributions along natural hydrological gradients in the Everglades. The effect of substrate on seedling performance showed higher survival of most species on the limestone tree islands, and faster growth on their peat-based counterparts.

Conclusions: The present results could have profound implications for restoration of forests on existing landforms and artificial creation of tree islands. Knowledge of species tolerance to flooding

and responses to different edaphic conditions present in wetlands is important in selecting suitable species to plant on restored tree islands

Keywords: Ground and surface water dynamic; Plant–soil interaction; Soil–water interaction; Substrate type; Tree islands; Wetland restoration.

Nomenclature: Wunderlin (1998).

Abbreviations: CERP = Comprehensive Everglades Restoration Plan; RE = Relative elevation; LILA = Loxahatchee Impoundment Landscape Assessment; SFWMD = South Florida Water Management District.

Introduction

In the broadest sense, tree islands are clumps of woody vegetation embedded in a matrix of contrasting vegetation type (Tomlinson 1980). However, most often the term has been applied where the surrounding matrix is freshwater marsh, in places such as the Florida Everglades (Wetzel et al. 2005), the Okavango Delta (Gumbrecht et al. 2004) and the Pantanal of Brazil (Prance & Schaller 1982). Tree islands in these ecosystems occupy modestly elevated locations in slightly inclined, flooded landscapes over which surface water has flowed slowly in a consistent direction for centuries, at least prior to any human modification of the hydrological regime. The presence of tree islands in such systems, despite divergent climatic and sedimentary conditions, raises questions about common biological and physical mechanisms in their formation and maintenance (Wetzel 2002a). During the early stages of tree island development, facilitative processes by which biological agents, such as nurse trees (Duarte et al. 2006) or termitaria (McCarthy et al. 1998), serve as nucleation sites may be critical. Concurrently, the biogeochemistry of the rooting environment, which emerges from the interaction of substrate with local hydrology, exerts an overriding influence on tree growth and forest composition. Hydrological conditions can influence chemical and physical properties such as nutrient availability,

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degree of substrate anoxia, sediment properties and pH (Mitsch & Gosselink 2007), which, in turn, have a direct effect on wetland plants. Experiments have demonstrated that competition from neighbors of similar or different growth form can exert a significant influence upon plant performance (Keddy 2000), as the growth of individuals rises toward limits imposed by their own physiology when competition is reduced.

Among the most distinctive features of the Everglades landscape, tree islands were described in some detail by early explorers, naturalists, and ecologists (Willoughby 1898; Harshberger 1914; Harper 1927). Tree islands can form on flat limestone surfaces, or above depressions or outcrops in the bedrock, but in most cases soil-forming processes cause surfaces to build up tens or hundreds of centimeters above the surrounding terrain. Several modes of tree island formation have been noted. Battery islands, common in the Loxahatchee National Wildlife Refuge, Florida, USA, form when a large peat mat detaches and rafts downstream, finally attaching to form a local high point favorable to colonization by woody plants (Gleason & Stone 1994). In most of the Everglades, however, tree islands form in place, in edaphic and physiographic settings that favor woody plant establishment and survival (Sklar & van der Valk 2002). Once formed, accretionary processes within the tree islands modify the substrate on which they became established. Everglades tree island soils display high variability, with sediments in the center of the drainage and along its immediate flanks ranging from nearly pure peats to highly calcareous mucks.

Sharp declines in the number and area of tree islands have been reported for some portions of the Everglades (Wetzel et al. 2005; Hofmockel et al. 2008). Tree island loss has generally been attributed to management-related changes in hydrological regime, either prolonged periods of high water, which can cause death in all but the most flood-tolerant woody species, or excessively dry conditions, which increase the likelihood of catastrophic peat fires. The less dramatic hydrologic influences, for example effects on stand composition or forest productivity, are pervasive. Several studies have described the hydrological affinities of woody species common to Everglades tree islands, based on their field distributions (Armentano et al. 2002; Wetzel 2002b) or their performance under experimental conditions (Gunderson et al. 1988; Jones et al. 2006). One element absent from the above studies was an explicit consideration of the underlying soils, which may shape species responses to hydrology through their

capacities to store water or nutrients, or to supply them to plants. More recently, van der Valk et al. (2007) tested the effect of elevation and substrate on seedling survival and growth in a field experiment.

In 2006, we established mixed tree communities on artificially created islands in the Loxahatchee Impoundment Landscape Assessment (LILA) site, where van der Valk et al. (2007) had performed their earlier experiment. The replicated design and controlled hydrology of the LILA site allowed us to investigate the initial development of these forests in a robust experimental framework. Our research objective was to analyse the effects of water levels and soils on seedling growth and survivorship during the first 2.5 yr of stand development.

Methods

Experimental design

The LILA project examines ecosystem processes in an experimental landscape constructed at the Arthur R. Marshall Loxahatchee National Wildlife Refuge (LNWR) in Boynton Beach, Florida, USA. LILA was created through a partnership between the South Florida Water Management District, the US Fish and Wildlife Service and the US Army Corps of Engineers. It consists of four identical, 8.1-hectare 'macrocosms' that were established in 2002-2003 from existing LNWR impoundments. In each macrocosm, a landscape comprising the key features of the interior Everglades (i.e. ridges, sloughs and tree islands) was constructed. Water within LILA is managed by a large electric pump ($1.84 \text{ m}^3 \cdot \text{s}^{-1}$), a series of water control structures and recording stage gauges, allowing scientists to manage water levels and flow rates within each macrocosm. LILA serves as a landscape-scale physical model of the Everglades and allows investigators to precisely measure environmental responses to restoration strategies as hydrology and other critical processes are controlled and replicated.

At LILA, tree island construction began in October 2002 and was completed by February 2003. Two islands were constructed in each macrocosm: a peat-based island that mimicked the 'battery' islands common in LNWR (Gleason & Stone 1994), and a limestone-core island that represented the 'fixed' islands that form around bedrock highs throughout the Everglades. Referred to hereafter as peat and limestone islands, both types were $71 \text{ m} \times 43 \text{ m}$, with a flat center portion elevated 0.9 m above the surrounding slough surface. Peat islands

were constructed from the organic surface sediments that characterized the pre-construction marshes, while the core of the limestone island consisted of a 49 m × 14 m strip of locally mined limestone along the central axis, capped throughout with ca. 0.3 m of peat. The slopes from the central plateau of both island types were graded to 16:1 along the long north and south sides, and 12:1 along the shorter east and west edges.

The islands were planted initially in 2004, but survival was <10% for all but three of the eight species planted, and survivors were harvested after 18 mo (van der Valk et al. 2007). By 2006, infra-structural changes allowed for improved planting success. Herbicide applications (glyphosate 2%), followed by prescribed fire, were used to prepare the islands for planting. An irrigation system was installed to mitigate seedling moisture stress during the first 3 mo after planting. Seedlings were watered three times a week during the first month, and twice a week through the remainder of the establishment period. Nuisance vegetation was treated periodically for 18 mo after planting, through a combination of herbicide and manual treatments.

A planting scheme was implemented on each island that included four densities, with trees arranged along rectangular lattices at spacings of 1.00, 1.66, 2.33 and 3.00 m. Each quadrant of the plantable area was randomly assigned to one of the four planting densities. Buffers of 2 m (E-W direction) or 3 m (N-S direction) were retained between density treatments, which provided space for the irrigation system, groundwater wells and foot traffic. To ensure representative placement in all hydrological environments, eight species common to Everglades tree islands were randomly assigned to planting locations within the relatively high, interior 18 m × 10 m of each quadrant, and the lower surrounding areas separately. The planting arrangement called for 89 trees of each species per tree island. Planting stock was from local seed sources, grown for about 9 mo in 1-gallon (3.785) pots at a local commercial nursery prior to outplanting in March of 2006 (macrocosms M1 and M4) and 2007 (macrocosms M2 and M3) (Fig. 1). Our analyses in this paper focus on the responses of the 2006 cohort, comprised of following species: *Annona glabra*, *Acer rubrum*, *Bursera simaruba*, *Chrysobalanus icaco*, *Ficus aurea*, *Ilex cassine*, *Morella cerifera* and *Persea palustris*.

Survival and total height of each planted seedling was assessed at 2-mo intervals during the first year after planting, and subsequently at 6-mo intervals. During May–July 2006, new seedlings were replanted at ca. 50 locations where the originally

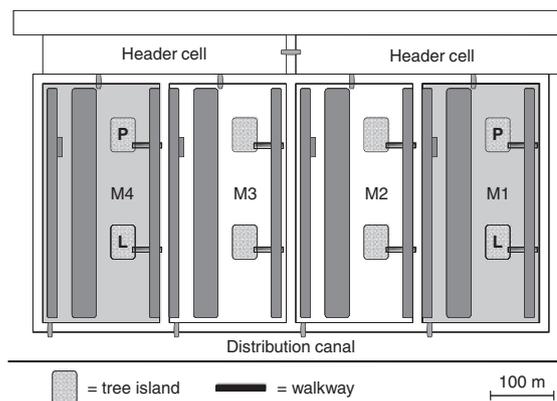


Fig. 1. Schematic of the Loxahatchee Impoundment Landscape Assessment (LILA) site.

planted individual had died soon after planting. Replanted individuals were not included in the survival and growth analyses from the first 2 yr, but were included thereafter.

Hydrological and soil data

A continuous record of surface and ground-water stage was available for the period May 2007–Aug 2008. Surface water level at each island was derived from stage recorders maintained by the South Florida Water Management District (SFWMD) at the east and west ends of each macrocosm. Stages for each tree island were estimated from a linear interpolation between water level at the western (Input) and eastern (Output) ends.

Tree island elevations were established by (1) surveying with an auto-level (3 mm accuracy) from vertical control benchmarks established by the SFWMD in each macrocosm to a temporary benchmark established in the center of each island, (2) surveying from the temporary benchmark to the base of approximately 150 newly planted trees of known horizontal location, (3) developing a contour plot of elevation from these data through ARC-GIS 9.2, and (4) applying the Spatial Analyst Extension in ARC-GIS to determine an elevation for each planted tree. The relative elevation (RE; i.e., cm above or below the mean surface water adjacent to the island) over the period 01.05.2007 to 30.04.2008, was calculated for each tree as an indicator of its position along the hydrologic gradient.

Groundwater monitoring wells were also installed at the center of each island. Wells were cased at the top with Schedule-40, 3.8 cm diameter PVC pipe, and along the bottom 0.6 m with 0.010 slotted well screen. Mean (\pm SD) well depth was

1.34 ± 0.15 m. The top of each well was surveyed from the benchmark established at the center of each island, and groundwater levels were recorded at 15-min intervals through an In-Situ 500-Troll™ pressure transducer (accuracy ± 3.5 mm) fixed in the well. Two of the pressure transducers (M1E and M4E) failed for short periods of time, which led to a 6% loss in data. Of this lost data, 71% was estimated using a linear regression ($R^2 = 0.98$) relationship between the data collected in the center well and a nearby well on the same tree island. The groundwater levels were then normalized to interpolated surface water levels. Monthly means of the relative groundwater levels were calculated for each island. The monthly mean of the two wells in each island type were then combined to calculate a mean monthly relative water level by type. Surface water levels were managed at LILA to mimic the temporal pattern of surface water in the Everglades, where seasonal precipitation typically causes levels to decline from the end of Nov to the end of May, then rise from Jun through Nov. Precipitation data from the SFWMD's Loxahatchee weather station (26°29'56.257"N, 80°13'20.159"W), located approximately 1.13 km north east LILA, was used to relate large changes in groundwater levels with rain events from May 2007 through Aug 2008. In addition, a 30-yr mean monthly precipitation value was calculated from data collected at SFWMD's LWD weather station (26°28'14.261" N, 80°12'18.158" W) located 2.38 km south west of LILA.

Data analysis

The effects of RE and underlying substrate type (peat or limestone) on species survival and growth in height were analysed throughout the first two and a half years after planting. The effect of planting density was not examined because individuals were too small to have interacted meaningfully during at least the early part of the study period. Logistic and linear regressions were applied to explore the effects of RE on cumulative species survival and total height through Sep 2008 (i.e. 2.5 yr after planting, in limestone and peat tree islands). A 2 and analysis of variance (one-way ANOVA) test were used to assess the effect of substrate on species survival and growth, respectively. In this case, analysis was restricted to trees planted in the high, flat 14 m-wide central strip, because this was the only area underlain by limestone in islands of that type. This limitation in the elevational range of limestone substrate also prevented us from examining the substrate × RE interaction. Compliance with the assumptions of least-square regression were

examined through normal probability plots of residuals, plots of standard residuals versus predicted values, and plots of standardized residuals against fitted values of independent variables. All analyses were done in STATISTICA (version 7.1, StatSoft Inc., Tulsa, OK, USA).

Results

Substrate type

Sediment profiles at the centers of peat and limestone islands are illustrated in Fig. 2. Both island types featured an underlying sand unit at 70–80 cm depth, extending down through at least 1.4 m. The substrate above this unit differed in limestone and peat islands. The peat horizon at the surface of the limestone-core islands averaged only 11 cm depth. Below it, the limestone used in construction extended down to the sand layer. In the peat-based islands, the peat substratum extended from the surface to the sand unit.

Groundwater–surface water interactions

Mean daily surface water level in the adjacent sloughs ranged about 0.7 m over the 17-mo period (Fig. 3). The high water period of Sep–Jan matches the seasonal pattern found in much of the Everglades, as does the low water period of Mar–Jul. Several interruptions (in the cycle of flooding and recession (e.g. Aug 2007, Jan and Mar 2008) were operational artifacts of short wildlife experiments at LILA.

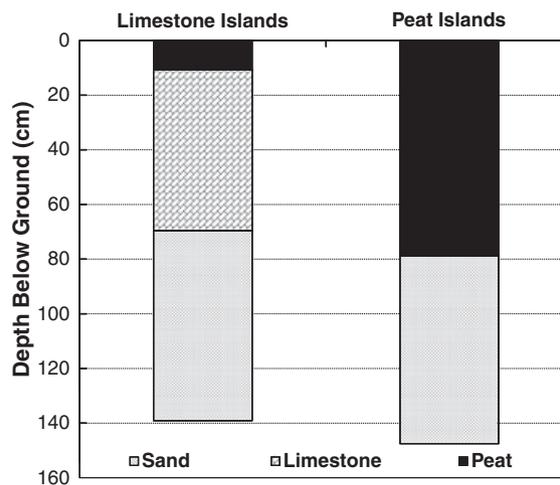


Fig. 2. The average below-ground depth (m) of sediment detected at the center of the peat and limestone tree islands when the groundwater wells were installed.

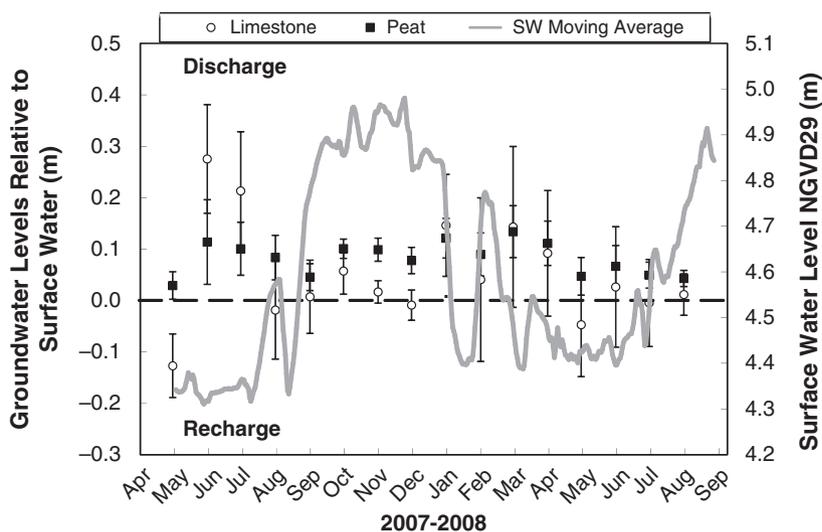


Fig. 3. Mean monthly relative groundwater levels and standard deviation for the peat (black) and limestone (open) based tree islands compared to the mean daily surface water levels (gray) from May 2007 to Aug 2008.

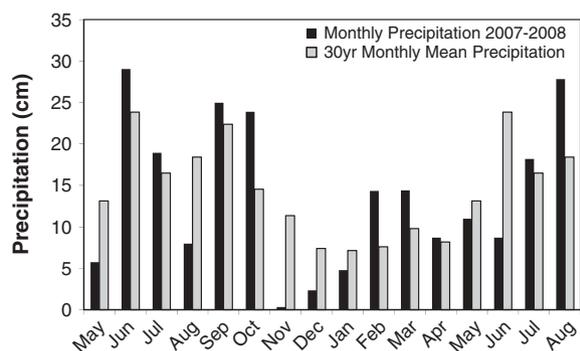


Fig. 4. Mean monthly and 30-yr mean monthly precipitation from May 2007 to Aug 2008.

During the period of study, within- and among-month variation in groundwater levels were both greater in limestone tree islands than peat islands (Fig. 3). Mean monthly relative groundwater levels in the limestone islands varied from 27.5 cm above the surface water to 12.7 cm below it. In these islands, groundwater was recharged by surface water in May 2007, despite surface water levels being very low and a monthly precipitation input of only 5.74 cm (Fig. 4). During the next 2 mo, monthly mean relative groundwater levels in limestone islands rose sharply to their highest relative position, more than 20 cm above surface water. Although surface water in Jun–Jul 2007 remained low, high rainfall that typifies early summer in the area, totaled 47.95 cm over the 2-mo period (Fig. 4), raised groundwater levels in the tree islands above the surface water, thereby causing groundwater to dis-

Table 1. Logistic regression coefficients (β_1) and *P*-values of relative elevation on survival through Sep 2008. NS = Not significant.

Species	Limestone		Peat	
	β_1	<i>P</i>	β_1	<i>P</i>
<i>Annona glabra</i>	0.01	NS	0.0004	NS
<i>Acer rubrum</i>	0.04	<0.05	0.03	NS
<i>Bursera simaruba</i>	0.20	<0.01	-0.0009	NS
<i>Chrysobalanus icaco</i>	0.06	<0.01	-0.02	<0.05
<i>Ficus aurea</i>	0.18	<0.01	0.02	NS
<i>Ilex cassine</i>	0.03	<0.01	0.006	NS
<i>Morella cerifera</i>	0.07	<0.01	0.007	NS
<i>Persea palustris</i>	0.20	<0.01	0.04	<0.01

charge to the surface water. In peat islands, groundwater levels were elevated (by 2.0–13.4 cm) relative to surface water year-round. From Oct to Dec the monthly mean relative groundwater levels in the peat-based islands were significantly greater than in the limestone islands (Fig. 3).

Survival

Survival of all species except *A. glabra* showed a significant response to RE on limestone tree islands (Table 1); the positive regression coefficients indicate a trend of increasing survival with increasing RE. On peat islands, only *C. icaco* and *P. palustris* showed a survival response to RE. The *C. icaco* survival rate decreased as RE increased, while *P. palustris* survival was higher at higher elevations. Especially on limestone islands, the magnitudes of

Table 2. The χ^2 (P -values) of survival percentages on limestone and peat substrates through Sep 2008. NS = Not significant.

Species	Survival (%)		P
	Limestone	Peat	
<i>Annona glabra</i>	85	48	<0.01
<i>Acer rubrum</i>	98	100	NS
<i>Bursera simaruba</i>	45	25	<0.05
<i>Chrysobalanus icaco</i>	86	55	<0.01
<i>Ficus aurea</i>	63	24	<0.01
<i>Ilex cassine</i>	85	91	NS
<i>Morella cerifera</i>	98	80	<0.01
<i>Persea palustris</i>	97	86	<0.05

Table 3. Linear regression coefficients (b) and P -values of relative elevation on height through September 2008. NS = Not significant.

Species	Limestone		Peat	
	b	P	b	P
<i>Annona glabra</i>	0.19	NS	1.76	<0.01
<i>Acer rubrum</i>	-0.44	NS	1.56	<0.01
<i>Bursera simaruba</i>	-0.25	NS	1.09	NS
<i>Chrysobalanus icaco</i>	1.19	<0.01	1.31	<0.01
<i>Ficus aurea</i>	-1.86	NS	1.36	NS
<i>Ilex cassine</i>	0.65	<0.01	1.16	<0.01
<i>Morella cerifera</i>	1.15	<0.01	2.29	<0.01
<i>Persea palustris</i>	-0.10	NS	1.96	<0.01

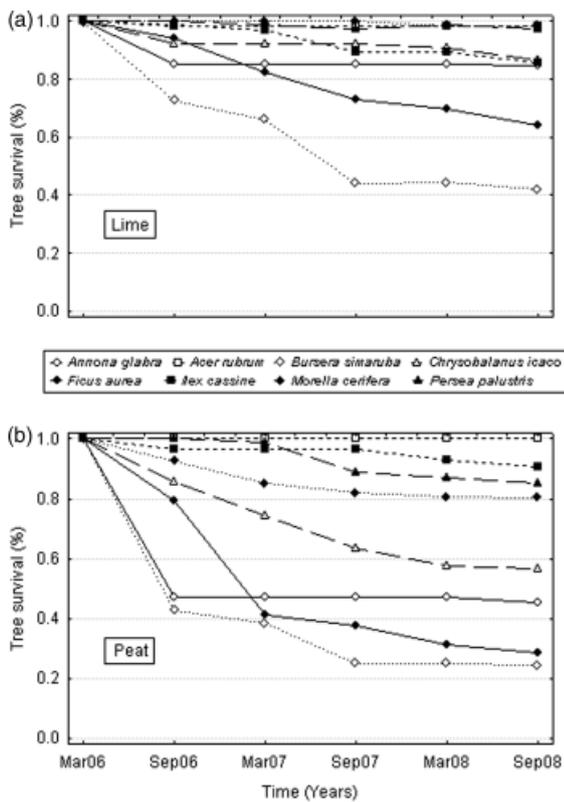


Fig. 5. Mean (\pm SE) survival of all tree species in (a) limestone and (b) peat tree islands.

the coefficients of the logistic regression models are notable. The high coefficients (β_1) in the *B. simaruba*, *P. palustris* and *F. aurea* models indicate that the most positive responses to RE were associated with species typically found in the more well-drained portions of tree islands. Among species characteristic of more hydric settings, *M. cerifera*, *C. icaco*, *A. rubrum* and *I. cassine* responses to RE were less marked and *A. glabra* was unaffected.

Results comparing species survival in limestone and peat tree islands through Sep 2008 are shown in Table 2. All species except *A. rubrum* and *I. cassine*

Table 4. ANOVA (P -values) of tree heights (cm) 2.5 yr after outplanting on limestone and peat tree islands.

Species	Limestone		Peat		P
	n	Mean \pm SD height (cm)	n	Mean \pm SD height (cm)	
<i>Annona glabra</i>	50	165 \pm 48	31	211 \pm 39	<0.01
<i>Acer rubrum</i>	55	150 \pm 55	71	253 \pm 58	<0.01
<i>Bursera simaruba</i>	31	129 \pm 41	16	225 \pm 66	<0.01
<i>Chrysobalanus icaco</i>	55	150 \pm 38	32	183 \pm 51	<0.01
<i>Ficus aurea</i>	42	160 \pm 61	16	227 \pm 51	<0.01
<i>Ilex cassine</i>	50	127 \pm 35	50	168 \pm 53	<0.01
<i>Morella cerifera</i>	65	198 \pm 56	54	236 \pm 66	<0.01
<i>Persea palustris</i>	70	130 \pm 71	56	213 \pm 74	<0.01

showed significantly higher survival on limestone than peat substrate. The dynamics of survival from time of planting through Sep 2008 is illustrated for limestone and peat tree islands in Fig. 5. Mortality of many species was concentrated during the spring-summer period (Mar–Sep); an outbreak of eastern lubber grasshoppers (*Romalea guttata*) in 2006 was responsible for extremely high mortality among newly planted *B. simaruba*, *A. glabra* and *F. aurea* on peat tree islands.

Height growth

The effect of RE on height growth was most pronounced on peat tree islands, where six species were significantly taller at higher elevations (Table 3). The high mortality experienced by *B. simaruba* and *F. aurea* on peat islands (Fig. 5b) contributed to their non-significant responses by reducing the number of individuals in the sample. Three species exhibited significantly greater height growth with increasing RE on limestone islands, but

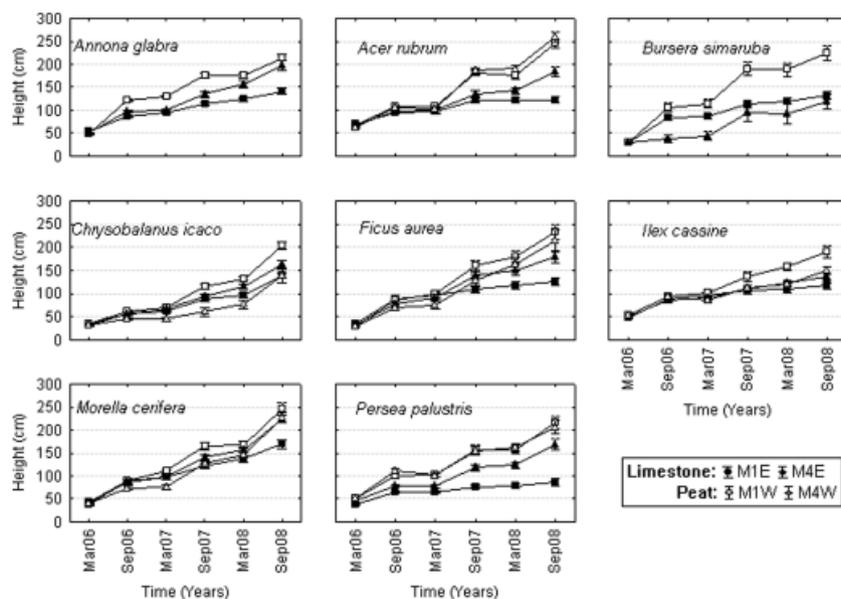


Fig. 6. Mean plant height (\pm SE) of eight species in two peat and two limestone tree islands, Mar 2006-Sep 2008.

slope coefficients for all species were lower than on peat islands.

The effect of substrate type on the height achieved by individuals during the 2.5-yr study period is illustrated in Table 4. All species were significantly taller on peat than on limestone tree islands. Changes in mean height from time of planting to September 2008 are shown for all species across all islands in Fig. 6. As some individuals were eliminated by mortality, these means are not based on precisely the same set of stems, and therefore the progression between sampling periods only approximates growth *per se*. However, the figure demonstrates that tree growth was concentrated in March-September, the season in which most mortality was also experienced (Fig. 5).

Discussion

Hydrology has been recognized as the main driver of landscape organization in the Everglades ecosystem through its direct effect on vegetation dynamics and its influence on edaphic patterns and processes (Gunderson 1994). The relationship of hydrology and vegetation is mediated by interactions with dynamic environmental factors, including soil characteristics and disturbance regime (Duever et al. 1986; Olmstead & Armentano 1997). Hydrological changes have been cited as the primary cause of the reduction in tree island size and number in south Florida, especially in the central and northern Everglades (Wetzel et al. 2005; Hofmockel et al. 2008). In

response to tree island loss, many restoration projects have been proposed under the Comprehensive Everglades Restoration Plan (CERP) framework, spanning from the replanting of islands that have suffered structural degradation owing to prolonged flooding, fire or exotic invasion, to the wholesale creation of functioning tree islands where they no longer exist. Whatever the goal, restoring tree island communities requires a more comprehensive understanding of the factors that interact with hydrology to shape and maintain ecosystem structure. Primary among these are the interactions between hydrology and soil variables, which are fundamental to tree island restoration efforts.

The two types of LILA tree island represent physiographic types common in the Everglades: those composed purely of peat and those in which predominantly organic soils build up around a central limestone core. At LILA, these two types displayed clear differences in hydrology, driven by the composite effect of their substrates on the local water table, relative to the surface water surrounding them. The peat islands consistently maintained water levels several centimeters above the surrounding surface water, while the water table in the limestone islands, which appeared to be more rapidly drained and quicker to rise in response to large precipitation events, was generally lower and hovered near surface water level. In the latter case, the limestone core presumably provided little capacity to store water, while serving as a near-direct conduit for precipitation to recharge the porous sand unit below. Organic soils such as those present on the

peat islands generally hold more water than mineral soils, and prevent water from passing through rapidly (Mitsch & Gosselink 2007). The result was a higher water table and, very likely, wetter soils within the rooting zones of the planted trees.

On both island types, survival and growth improved with increasing elevation. Flooding is usually the primary stress on bottomland forest tree species of the USA (Mitsch & Rust 1984) as well as on swamp forest species in the Everglades (Gunderson et al. 1988; Guerra 1997; Jones et al. 2006). However, in the modern, drained and compartmentalized Everglades, flooding is rare on the most elevated islands in some portions of the wetland. For example, in Everglades National Park, the heads of islands 80-100 cm above marsh surface were not completely inundated even in 1995, when water levels reached their highest point in the last two decades. In such islands, drought may represent a more pressing limit to the growth and survival of recruits. Drought stress was moderated by experimental conditions at LILA, where groundwater generally remained within 0.5 m of the surface, even at the highest slope positions, and supplemental irrigation in Year 1 prevented soils from becoming entirely desiccated.

In this study, we were able to test the effect of substrate on seedling performance only at relatively high elevations in the centers of the islands, but responses within these elevated settings also reflected the influences of flooding and soil moisture. On the upper platform of the limestone islands, the combination of lower and more variable groundwater levels and the coarse materials used in island construction would likely have resulted in drought conditions within the plant rooting zone during much of the year. With a higher water table and greater moisture-holding capacity, deep organic soils in the peat islands would have been saturated or near-saturated for a longer period. We found higher survival of most species on the limestone tree islands, and faster-growing trees on their peat-based counterparts. The LILA growth responses may be understood within the context of a formulation of the subsidy-stress hypothesis (Odum 1979) expressed by Mitsch & Rust (1984) and Megonigal et al. (1997). In this formulation, wetland production is viewed as a balance between the costs of physiological stress (flooding or drought) during an unfavorable season with the benefits of resource subsidy (enhanced moisture or nutrient availability) during a favorable one. In the LILA experiment, the primary stress was flooding during the peak of the wet season, which resulted in elevated mortality

rates on peat islands. Flooding and soil saturation lead rapidly to oxygen deficiency and the accumulation of toxic metabolites in wetland roots or rhizosphere, increasing susceptibility to disease organisms and often resulting in plant death (Kozlowski 1997; Mendelssohn & Batzer 2006). Individuals on the LILA peat islands that survived the stress of the flooding period were 'subsidized' during the remainder of the growing season by an abundant supply of water, which may have contributed to rapid above-ground growth and production (Gosselink et al. 1981; Megonigal et al. 1997). More persistent groundwater inflow may also act as a hydrological pathway that brings nutrients into the system. Ground-water upwelling has been suggested as a possible source of phosphorus (P) in Everglades tree islands (Wetzel et al. 2005; Ross et al. 2006). Even on the young LILA sediments, soil P content in the surface 10 cm was higher in peat (9.01 g.m^{-2}) than limestone tree islands (7.33 g.m^{-2}) (L. Scinto, LILA soil scientist, June 2009, pers. comm.).

Our data also suggest that hydrology may also have influenced the performance of planted seedlings, especially their survival, through indirect pathways. One mechanism was via the competition between the trees and ruderal vegetation. Although efforts were made to control these plants, their response between treatments and after the cessation of herbicide treatment remained a factor that may have contributed to cross-island variation in seedling survival. Field observations and aerial photos from the LILA site both demonstrated that the cover of ruderal herbs and shrubs was considerably less in the centers of limestone tree islands than in similar positions on peat tree islands – a likely result of the contrast in soil moisture conditions on the two island types discussed above. Tree seedlings planted on the limestone islands therefore grew without serious competitors for light, while competition from ruderal species was an issue on the peat islands. The importance of competition from neighbors in controlling species distributions in wetlands has been demonstrated experimentally (Keddy 2000). Another indirect factor was herbivory from lubber grasshoppers, which were more prevalent on peat tree islands, leading to extensive mortality among preferred species. Irrigation probably played a positive role in limestone tree islands by mitigating seedling moisture stress, but in peat tree islands supplementary water may have created wetter conditions that made seedlings more susceptible to disease (Kozlowski 1997).

Most species planted at LILA showed better survival with increasing RE. Moreover, on

limestone islands, where high and low RE's were associated with very different soil moisture conditions, the slope coefficients of the logistic regression models approximate species' realized niches in the Everglades, although they do not match perfectly (Table 1). *Ficus aurea* and *B. simaruba*, two species with very high positive coefficients, are typically restricted to the elevated 'heads' of tree islands. In contrast, *M. cerifera* and *A. glabra*, with low coefficients indicative of low sensitivity to flooding, are characteristic of the wetter, downstream environments in the tree island 'tails' (Armentano et al. 2002; Conner et al. 2002; Sah 2004). In the same sources, the hydrological distributions of *Persea borbonia* (a close relative of *P. palustris*), *C. icaco*, *I. cassine* and *A. rubrum* in the Everglades are reported as intermediate or are not included. Other experimental trials with the same species generally support the survival-based hydrological rankings from LILA. Gunderson et al. (1988) ranked *F. aurea*, *C. icaco*, *I. cassine* and *M. cerifera* from least to most tolerant to flooding. Jones et al. (2006) ranked the species in order of increasing flood tolerance (increasing water depth): *B. simaruba*, *P. palustris*, *I. cassine*, *C. icaco*, *M. cerifera* and *A. glabra*. van der Valk et al. (2007) defined two broad flooding tolerance classes: less flood tolerant (*A. rubrum* and *C. icaco*) and most flood tolerant (*A. glabra*, *I. cassine* and *M. cerifera*). Although our results differ in detail for a few species, especially *P. palustris*, one should not expect perfect agreement among experiments employing different methods, or between experiments and field distributions that represent a long history of disturbance, inter-specific competition, and changing environmental conditions.

Conclusions: Implications for Conservation

The primary objective of this research was to link seedling survival and growth to hydrology and soil conditions over a prolonged period. In order to ensure that tree survival in the first few months after planting was sufficient to achieve our research objective, we used a more aggressive tree establishment protocol than used by van der Valk et al. (2007). By planting larger seedlings, irrigating for the first few months, and controlling weeds for 1.5 yr, we achieved much better early survival than if we had allowed local environmental conditions to entirely dictate initial tree survival. The amount of labor required to manage nuisance vegetation and irrigate newly planted seedling in the remote Everglades may not prove to be unmanageable, given the importance placed on restoring tree island vegetation

on individual high-value sites where it has disappeared because of unnatural water conditions.

The results of the present study showed that survival and growth responses of seedlings along a moisture gradient during the first two and a half years after planting matched species distributions along natural hydrological conditions in the Everglades. Knowledge of relative species tolerance could be useful in the selection of suitable species assemblages to replant damaged tree islands or to initiate new ones. The dependence of species responses to hydrology on soil conditions, particularly their capacity to store water or nutrients, is a major contribution of the present study. This knowledge could have profound implications for the restoration of existing landforms and artificial creation of tree islands. At early stages of development and especially during dry periods, limestone tree islands may provide a more beneficial environment for seedling survival, with less competition than peat tree islands. However, the latter seem to offer better conditions for growth. Nevertheless, both substrate types may be affected by flooding stress so that it becomes critical to anticipate any hydrological modification in that direction to avoid planting failure or tree island loss. Restoring the natural water flow patterns, one of the major goals of CERP, would become essential for the preservation of the remaining tree islands by reducing prolonged flooding or drought. Tree island creation has not been included as a CERP objective but complete restoration of the Everglades may require restoring lost tree islands in order to reinstate the original landscape complexity (Sklar et al. 2004).

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References

- Armentano, T.V., Jones, D.T., Ross, M.S. & Gamble, B.W. 2002. Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas. In: Sklar, F.H.

- & van der Valk, A. (eds.) *Tree islands of the Everglades*. pp. 225–282. Kluwer Academic, Dordrecht, NL.
- Conner, W.H., Doyle, T.W. & Mason, D. 2002. Water depth tolerances of dominant tree islands species: what do we know? In: Sklar, F.H. & van der Valk, A. (eds.) *Tree islands of the Everglades*. pp. 207–223. Kluwer Academic, Dordrecht, NL.
- Da Silva Duarte, L., Dos-Santos, M.M.G., Hartz, S.M. & De Patta Pillar, V. 2006. Role of nurse plants in Araucaria forest expansion over grassland in south Brazil. *Austral Ecology* 31: 520–528.
- Duever, M.J., Carlson, J.E., Meeder, J.F., Duever, L.C., Gunderson, L.H. & Riopelle, L.A. 1986. *The big cypress national preserve*. National Audubon Society, New York, NY, US.
- Gleason, P.J. & Stone, P. 1994. Age, origin, and landscape evolution of the Everglades peatland. In: Davis, S. & Ogden, J.C. (eds.) *Everglades: the ecosystem and its restoration*. pp. 149–197. St Lucie Press, Delray Beach, FL, US.
- Gosselink, J.G., Bayley, S.F., Conner, W.H. & Turner, R.F. 1981. Ecological factors in the determination of riparian wetland boundaries. In: Clark, J.R. & Benforado, J. (eds.) *Wetland of bottomland hardwood forests*. pp. 197–219. Elsevier, New York, NY, US.
- Guerra, R. 1997. Impacts of the high water period of 1994–95 on tree islands in Water Conservation Areas. In: Armentano, T. (ed.) *Ecological assessment of the 1994–1995 high water conditions in the southern Everglades*. pp. 47–58. South Florida Management and Coordination Working Group, Miami, FL, US.
- Gumbrecht, T., McCarthy, J. & McCarthy, T.S. 2004. Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surface Processes and Landforms* 29: 15–29.
- Gunderson, L.H. 1994. Vegetation of the Everglades: determinants of community composition. In: Davis, S.M. & Ogden, J.C. (eds.) *Everglades: the ecosystem and its restoration*. pp. 323–340. St Lucie Press, Delray Beach, FL, US.
- Gunderson, L.H., Stenberg, J.R. & Herndon, A.K. 1988. Tolerance of five hardwood species to flooding regimes. In: Wilcox, D.A. (ed.) *Interdisciplinary approaches to freshwater wetlands research*. pp. 119–132. Michigan State University Press, East Lansing, MI, US.
- Harper, R.M. 1927. *Natural resources of southern Florida*. Florida State Geological Survey Eighteenth Annual Report. Tallahassee, FL, US.
- Harshberger, J.W. 1914. The vegetation of south Florida south of 27 37' north, exclusive of the Florida Keys. *Transactions of the Wagner Institute of Science of Philadelphia* 7: 51–189.
- Hofmockel, K., Richardson, C.J. & Halpin, P.N. 2008. Effects of hydrologic management decisions on Everglades tree islands. In: Richardson, C.J. (ed.) *The Everglades experiments: lessons for ecosystem restoration*. pp. 191–214. Springer, New York, NY, US.
- Jones, D.T., Sah, J.P., Ross, M.S., Oberbauer, S.F., Hwang, B. & Jayachandran, K. 2006. Responses of twelve tree species common in Everglades tree islands to simulated hydrologic regimes. *Wetlands* 26: 830–844.
- Keddy, P.A. 2000. *Wetland ecology: principles and conservation*. Cambridge University Press, Cambridge, UK.
- Kozłowski, T.T. 1997. *Tree physiology monograph no. 1*. Heron Publishing, Victoria, CA.
- McCarthy, T.S., Ellery, W.N. & Dangerfield, J.M. 1998. The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes and Landforms* 23: 291–316.
- Megonigal, J.P., Conner, W.H., Kroeger, S. & Sharitz, R.R. 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis. *Ecology* 78: 370–384.
- Mendelsohn, I.A. & Batzer, D.P. 2006. Abiotic constraints for wetland plants and animals. In: Batzer, D.P. & Sharitz, R.R. (eds.) *Ecology of freshwater and estuarine wetlands*. pp. 82–114. University of California Press, Berkeley, CA, US.
- Mitsch, W.J. & Gosselink, J.G. 2007. *Wetlands*. 4th edn. John Wiley & Sons Inc., New Jersey, US.
- Mitsch, W.J. & Rust, W.G. 1984. Tree growth responses to flooding in a bottomland forest in northeastern Illinois. *Forest Science* 30: 499–510.
- Odum, E.P. 1979. Ecological importance of the riparian zone. In: Johnson, B.R. & McCormick, J.F. (eds.) *Strategies for protection of floodplain wetlands and other riparian ecosystems. [General Technical Report WO-12]*. pp. 2–4. U.S. Forest Service, Washington, DC, US.
- Olmstead, I. & Armentano, T.V. 1997 *Vegetation of Shark Slough, Everglades National Park*. South Florida Natural Resource Center Technical Report 97-001. Everglades National Park, Homestead, Florida, USA.
- Prance, G.T. & Schaller, G.B. 1982. Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia* 34: 228–251.
- Ross, M.S., Mitchell-Bruker, S., Sah, J.P., Stothoff, S., Ruiz, P.L., Reed, D.L., Jayachandran, K. & Coultas, C.L. 2006. Interaction of hydrology and nutrient limitation in the Ridge and Slough landscape of the southern Everglades. *Hydrobiologia* 569: 37–59.
- Sah, J.P. 2004. Vegetation structure and composition in relation to the hydrological and soil environments in tree islands of Shark Slough. In: Ross, M.S. & Jones, D.T. (eds.) *Tree islands in the Shark Slough landscape: interactions of vegetation, hydrology, and soils*. Final Report to Everglades National Park on Study EVER 00075, pp. 85–114. Everglades National Park, Homestead, FL, US.
- Sklar, F.H. & van der Valk, A. 2002. Tree islands of the Everglades: an overview. In: Sklar, F.H. & van der Valk, A. (eds.) *Tree islands of the Everglades*. pp. 1–18. Kluwer Academic, Dordrecht, NL.
- Sklar, F.H., Coronado, C. & Crozier, G. 2004. *Ecological Effects of Hydrology*. South Florida Water

- management District. Everglades Consolidation Report, Chapter 6. West Palm Beach, FL, US.
- Tomlinson, P.B. 1980. *The biology of trees native to tropical Florida*. Harvard University Printing Office, Allston, MA, US.
- van der Valk, A.G., Wetzel, P., Cline, E. & Sklar, F.H. 2007. Restoring tree islands in the Everglades: experimental studies of tree seedling survival and growth. *Restoration Ecology* 16: 281–289.
- Wetzel, P.R. 2002a. Tree islands ecosystems of the world. In: Sklar, F.H. & van der Valk, A. (eds.) *Tree islands of the Everglades*. pp. 19–69. Kluwer Academic Publishers, Dordrecht, NL.
- Wetzel, P.R. 2002b. Analysis of tree islands vegetation communities. In: Sklar, F.H. & van der Valk, A. (eds.) *Tree islands of the Everglades*. pp. 357–389. Kluwer Academic Publishers, Dordrecht, NL.
- Wetzel, P.R., van der Valk, A.G., Newman, S., Gawlik, D.E., Gann, T., Coronado-Molina, C.A., Childers, D.L. & Sklar, F.H. 2005. Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key. *Frontiers in Ecology and Environment* 3: 370–376.
- Willoughby, H.L. 1898. *Across the Everglades: a canoe journey of exploration*. Florida Classics Library, Port Salerno, FL, US.
- Wunderlin, R.P. 1998. *Guide to the vascular plants of Florida*. University Press of Florida, Gainesville, FL, US.

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