

Trees: a powerful geomorphic agent governing the landscape evolution of a subtropical wetland

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Abstract *Transpiration-driven ion accumulation* in soil has been invoked as a biological and physical feedback mechanism in wetlands that governs topographic differences by regulating soil accretion—with greater transpiration, ion accumulation and soil accretion occurring on tree islands as compared to the surrounding marsh. The strength of this mechanism is hypothesized to be controlled by the ratio of

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E. Cline · T. W. Dreschel · F. H. Sklar Everglades Systems Assessment Section, South Florida Water Management District, West Palm Beach, FL, USA evapotranspiration (ET) to precipitation (P), where under greater ET to P conditions soil accretion may move from organic to mineral in nature. We tested the existence of this mechanism on tree islands in a subtropical wetland, determined if it supports mineral soil formation, and assessed its control on the development of nutrient resource contrasts (tree islandsmarsh). To test our hypotheses, biannual measurements of groundwater, surface water and aboveground biomass were made from 2007 to 2012. Water samples were analyzed for water isotopes, concentrations of major ions, and total and dissolved nutrients on constructed tree islands. We found that tree transpiration led to the advective movement of water and associated ions toward the center of the tree islands. supporting CaCO₃ precipitation. CaCO₃ accretion on the tree islands was estimated at roughly 1 mm per decade, and represented 5 % of the total soil accretion since the islands' planting. We also observed depletion in groundwater nutrient concentrations as tree biomass accumulated, indicative of tight nutrient cycling. This work provides direct evidence that trees can act as powerful geomorphic agents in wetland systems, forming mineral soils that support landscape heterogeneity on time scales of centuries to millennia.

Keywords Weathering · Soil formation · Tree islands · Plant-groundwater–surface water interactions · Everglades

Introduction

Trees play a critical role in shaping the earth surface through both chemical and physical weathering. Specifically, they govern subsurface moisture dynamics, and thus water-mineral interactions, simply through root-water uptake to meet transpiration demands but also by altering soil porosity and hydraulic conductivity as their extant root systems push soils and release organic matter into the subsurface (Angers and Caron 1998; Pawlik 2013). Often trees are associated with a weakening or loss of the soil fabric through enhanced mineral dissolution (Berner 1998) while biomechanical weathering such as tree uprooting (i.e., tree-throw) or root rock cracking also acts in concert to move soil on the landscape, creating the pit-and-mound topography in the case of treethrow. Conversely, trees also help to stabilize soils on the landscape as roots can promote mineral formation (Monger and Gallegos 2000), enhance soil cohesion and often anchor soils to the bedrock (Roering et al. 2003), all of which reduce erosion. As trees mediate the breakdown, transport and accretion of soils they act as important geomorphic agents shaping the surface of many ecosystems (Marston 2010; Pawlik 2013).

Often times in wetland systems, it is small changes in topography (10-100 cm) that support landscape heterogeneity. The landscape patterns of some of the world's largest wetland areas, such as the Okavango delta and West Siberian Basin, has been attributed to a transpiration-driven ion accumulation mechanism (Eppinga et al. 2008; McCarthy et al. 1993, 1998). In these examples, trees on the hummocks are postulated to have elevated transpiration rates compared to vegetation within the hollows. This elevated use of water then leads to the advective movement of water and associated ions from surrounding hollows toward the center of the hummock. Ions are then concentrated either through ion exclusion by vegetation or ion cycling through the mineralization of leaf litter and subsequent return to the underlying hummock groundwater. Over time, nutrient gradients develop between the hummock and hollow as access to greater nutrient resources leads to more productive hummocks, while the lack of resources inhibits production in the adjacent hollows (Eppinga et al. 2010; Rietkerk et al. 2004). The strength of the transpiration-driven ion accumulation mechanism in wetlands is hypothesized to be governed by the evapotranspiration (ET) to precipitation (P) ratio, where ET:P ratios of 0.6 or greater trigger a stronger positive feedback. In cool climates, where the ET:P ratio ranges from 0.6 to 1.0, such as those in the West Siberian Basin, the greater productivity of hummocks is associated with greater organic-rich soil accretion compared to hollows and is invoked to be one of the mechanisms that maintains the topographic difference between these landscape features (Eppinga et al. 2010). In hot climates, where ET:P ratio is much greater, such as in the case of the Okavango delta (ET:P = 4:1), this transpiration driven ion accumulation mechanism has also been invoked to maintain topographic differences and the lateral growth of tree islands through the formation of mineral soils, specifically calcite (CaCO₃) precipitation (McCarthy et al. 1993). While these examples demonstrate that the transpiration-driven ion accumulation mechanism can persist at fairly extreme wetland conditions, if and how it regulates organic and/or mineral soil formation in subtropical wetlands is only now emerging.

Over the last decade evidence from the subtropical Everglades, where annual evapotranspiration to precipitation rates nearly equate (Sullivan et al. 2014c; Saha et al. 2012), suggests transpiration-driven ion accumulation may be one mechanism supporting the presence of tree islands (Wetzel et al. 2005; Ross et al. 2006; Sullivan et al. 2011). Specifically, this mechanism has been suggested, in part, to explain the presence of petrocalcic horizons (dominated by CaCO₃) found in several tree island soils (Chmura and Graf 2011; Coultas et al. 2008; Graf et al. 2008) and the extremely high phosphorus concentrations in the groundwater and soil of many Everglades' tree islands (commonly one to three orders of magnitude greater than the adjacent marsh; Gann et al. 2005; Ross et al. 2006). Detailed estimates of the hydrogeochemical fluxes on a tree island in Everglades National Park (ENP) revealed that transpiration-driven ion accumulation supported groundwater geochemical conditions that favored the formation of calcium carbonate minerals (CaCO₃; Sullivan et al. 2014a). These data were corroborated by another detailed hydrogeochemical tree island study in the Water Conservation Area just north of ENP (WCA-3; Troxler et al. 2014). Here again, groundwater pumping by the overlying trees was associated with groundwater geochemical conditions that favored the formation of CaCO₃, which also

coincided with elevated soil phosphorus concentrations. Together, these data indicate that trees may create a hydrogeochemical condition under healthy tree islands that drives the accretion of $CaCO_3$ and maintains the topographic difference between tree islands and the adjacent marsh, yet determining the time period when and conditions under which this ecohydrogeochemical process initiates and the rate at which it operates remains elusive.

To mechanistically determine biological and physical feedbacks critical to maintaining tree islands and the overall health of the Everglades, a large physical ecosystem model of the Everglades, known as the Loxahatchee Impoundment Landscape Assessment (LILA; Aich et al. 2011; Fig. 1), was established in 2002. Containing eight constructed tree islands, planted in 2006 and 2007, and characterized by variable underlying lithology, LILA provides the experimental platform needed to elucidate the hydrogeochemical response of tree islands to early tree growth.

Utilizing continuously measured groundwater (28 wells) and surface water levels across the eight tree

islands, Sullivan et al. (2011) developed a conceptual model of the response of groundwater flow to early tree growth (Fig. 2). Immediately after planting, when the trees were small, the groundwater table was domed (mirroring topography) and groundwater flowed from the center of the islands toward the edges. By year three the aboveground biomass on the islands had increased twofold to eightfold and the groundwater table formed a depression in the center of the islands resulting in groundwater flow from the edges of the island toward the center. Groundwater levels further suggested that the magnitude of change was greater on islands underlain by limestone than those underlain by peat. These data indicated that within 3 years of growth, the tree islands at LILA had developed hydrodynamic functions similar to natural tree islands, yet the establishment of tree island hydrogeochemical function-defined as transpiration-driven ion accumulation and mineral precipitation-was unexplored.

Our goal in this paper is to utilize groundwater geochemistry to examine the evolution of tree island hydrogeochemical function during early forest development. Specifically we tested three hypotheses



Fig. 1 Left The Loxahatchee Impoundment Landscape Assessment (LILA) is located at the northeastern edge of the Everglades (grey), on the boundary of Water Conservation Area 1 (WCA-1). Center At least nine groundwater wells (circles) were located on each tree island. Surface (grey box) and groundwater were sampled on the peat (black circle) and limestone (white circle) at LILA. Right, top Aerial schematic of

sampled well locations on each island; the two EDGE wells sampled were located at a lower ground elevation (*lowland*), while the one (Limestone Center, LC) to two (Peat Center, PC) CENTER wells and the one DEEP (PC) well sampled were located in the center of the island at a higher elevation (*upland*). *Right, bottom* Profile schematic depicts the well locations and depths across each tree island derived from this LILA conceptual model on tree island hydrodynamics and from observations of present day groundwater geochemical conditions from natural tree islands (Sullivan et al. 2014a; Troxler et al. 2014):

Hyp1 Transpiration governs the hydrodynamics of tree islands during early stand development and results in the advective movement of groundwater and accumulation of ions towards the center of the islands.

Hyp2 Transpiration driven ion accumulation on tree islands supports $CaCO_3$ precipitation at early stages in tree island development, representing a meaningful contribution to soil accretion and thus tree island geomorphology. However, the degree of soil accretion will be mediated by the underlying geochemical conditions with peat having lower rates of $CaCO_3$ accretion given its a greater ability to store water (porosity) and generally lower pH as compared to limestone.

Hyp3 The accumulation of biomass during stand development governs ion accumulation and nutrient uptake in a manner consistent with the formation of resource contrasts between tree islands and the surrounding marsh system.

Testing these hypotheses will elucidate the impact of early stand development and aboveground biomass accretion on tree island groundwater-surface water interactions (Hyp1), the evolution of groundwater biogeochemistry on the islands and control on CaCO₃ formation (Hyp2), and the development of tree island– marsh nutrient contrasts (Hyp3). To test these hypotheses we collected surface water and groundwater and estimated aboveground biomass over 5 years on eight tree islands. We did not measure transpiration directly but instead we used aboveground biomass as a proxy for water loss, given that during early stand development, leaf area, and thus the total amount of photosynthesis and stomatal surface area, increased.

Materials and methods

Study area

LILA is located within the Loxahatchee National Wildlife Refuge (LWNR) in Boynton Beach, Florida (Fig. 1). Spanning over 34 ha, LILA consists of four, 8 ha macrocosms, each of which contains two tree islands, one constructed predominately of peat and the other constructed of a limestone rubble center overlain by a thin layer of peat (Fig. 1; van der Valk et al. 2008). Thus lithologic differences occur in the islands center, while the surrounding edges primarily consist of peat. Approximately 0.90 m elevation separates the tops of the tree islands from the surrounding slough, with the edges of the tree islands sloped downward to meet the slough (Fig. 1). Four islands were planted with saplings (one-gallon pot size) in March 2006 (Planting 1, P1, two peat and two limestone islands). The remaining islands were planted in March 2007 (Planting 2, P2). Each island was planted across the topographic gradient with 717 trees of eight species common to the Everglades (Stoffella et al. 2010).

Nine wells were installed on each island, three in the center and six on the edges, with an average depth of 1.34 m (Fig. 1). One additional deep well was installed in the center of each peat tree island with an average depth of 2.00 m (Fig. 1; DEEP). All wells had a 50–60 cm screened interval at the bottom. Wells at the same depth are used to interpret horizontal water exchange, while wells at different depths are used to elucidate vertical water exchange.

Distinct wet and dry seasons drive surface water levels in the Everglades, with the majority of rainfall occurring between June and November. On average, 130–160 cm of rainfall occurs annually near the LWNR (Ali et al. 2000). Surface water levels at LILA were managed according to an operational hydrograph that mirrored the seasonal variations in Everglades surface water levels (specifically based on WCA-3a gauge 64 data from 1965 to 2000), where the highest level occurred between October/November and the lowest levels between April/June. The general trend in groundwater levels followed those of the surface water, reaching the soil surface in October/November (Sullivan et al. 2011, 2014b).

Monitoring and sampling design

Groundwater and surface water

From October 2007 through April 2012, 28 groundwater wells and eight surface water sites were sampled biannually in October (wet season) and April/May (dry season; Fig. 1) to determine the response of tree island geochemistry to the underlying geochemical condition, tree growth, and seasonal variation in precipitation. The only exception was in April 2011 when the wells went dry due to a prolonged regional drought (Serna et al. 2013). At least three wells were sampled per island with one well located in the center of the islands and two wells located on the edges. Wells located on the edges of the islands were referred to as EDGE wells (ground elevation ~ 4.70 m, NGVD29), while those in the center were termed CENTER wells (ground elevation of ~ 5.02 m, NGVD29). Wells in the CENTER could then be grouped according to underlying geologic conditions [Limestone Center (LC) and Peat Center (PC)]. Two additional wells were sampled in the center of each of the four peat tree islands, one at approximately the average depth and the other a DEEP well, with approximately 0.20 m vertically separating the two well screens. All groundwater and surface water sites were sampled with a peristaltic pump and each well was purged of three well volumes before sampling. Temperature, conductivity and pH were measured in the field with a relative accuracy of ± 0.1 °C, ± 0.1 µS/ cm, and ± 0.002 , respectively using a YSI Professional PlusTM. Three filtered (0.45 μ m) and two unfiltered samples were collected at each well and surface water location. Two each of the filtered and unfiltered samples was preserved with 10 % HCl, for cation, soluble reactive phosphorus (SRP) and total phosphorus (TP) analysis, respectively. The filtered unacidified samples were analyzed for major anion concentrations and water stable isotopes, while the unfiltered unacidfied sample was analyzed for total organic carbon (TOC). All samples were stored at 4 °C. The measurements serve as a platform to elucidate plantgroundwater–surface water interaction (Cl^{-} and ^{18}O), to evaluate the geochemical condition with respect to mineral dissolution and precipitation and assess the potential development of a nutrient gradient between the marsh and tree island.

Water isotope sampling of precipitation

To determine the effect of plant-groundwater–surface water interaction on the hydrogeochemical condition of tree island groundwater, water isotopes from incoming precipitation were also collected from January 2009 through July 2010. A total of 28 rainfall samples were obtained using a wet-dry collector (Areochem Metrics, Inc.). Samples were stored in a plastic screw-top Nalgene bottle to prevent evaporation. The total volume of rainfall per sampling event was measured to determine the volume-weighted isotopic composition of each sample and the volume-weighted average was used as the isotopic end-member of incoming rainfall into each of the islands.

Chemical analyses

Ion and nutrient analyses

Groundwater and surface water samples were analyzed for SRP, TP and TOC using an Alpkem 300 Series 4 Channel Rapid Flow Analyzer, an Alpkem Rapid Flow Analyzer with a 2-Channel ER Detector and a Shimadzu TOC-V, respectively. Groundwater and surface water samples were also analyzed for total alkalinity, anions and cations using a Brinkman Titrino 751/735 and a Dionex-120 Ion Chromatograph, respectively. Total alkalinity was determined by the inflection point titration method on 40 mL water samples with 0.1 M HCl. The change in volume of the sample that resulted from the addition of the titrant was not taken into account, as it was only a small portion of the total volume (<10 %). Total alkalinity was calculated as mg L^{-1} of HCO₃⁻ as the pH of the water samples were near neutral. The charge balance of the major cations and anions for each water sample was <5 %.

Given that in the Everglades CaCO₃ minerals aragonite and calcite are the most prevalent, and thus likely to form or be dissolved, the mineral saturation indices (SI) for both minerals was estimated for each water sample along with the partial pressure of carbon dioxide (pCO₂) using the geochemical model PHREEQC (Parkhurst and Appello 1999). The major ion concentrations (HCO₃⁻, Cl⁻, SO₄²⁻, Na⁺, K⁺, Mg^{2+} and Ca^{2+}) and field parameters (temperature, pH, and conductivity) of each water sample were inputs to PHREEQC. With respect to the given minerals, water samples with SI values of 0 ± 0.05 were considered at saturation (i.e., thermodynamic equilibrium), SI > +0.05 indicated that the water sample was supersaturated (i.e., precipitation was expected), while SI < -0.05 indicated an undersaturated condition (i.e., dissolution was expected).

Stable isotopes

All water samples collected were analyzed for hydrogen (δ D) and oxygen (δ ¹⁸O) stable isotopes using a DTL-100 Liquid–Water Isotopes Analyzer (LWIA) with an accuracy of 0.2 and 0.6 ‰ for δ ¹⁸O and δ D, respectively. A subset of samples were also analyzed on a Isotopic Ratio Mass Spectrometry to check for alcohol related interference.

Aboveground tree biomass

Aboveground tree biomass was estimated to assess the relationship between stand development and the hydrogeochemical condition of the tree islands. A mixed-species regression allometric biomass model derived solely from total tree height, developed by Stoffella et al. (2009, 2010), was used to derive aboveground biomass for each individual tree at LILA from the initial planting through March 2012. Tree height was measured biannually in March and September from 2007 through 2012. The aboveground biomass was determined on all trees within a 6 m radius of each well and normalized by the ground area to obtain the amount of aboveground biomass per hectare (t ha^{-1}). The total aboveground biomass was compared to chemical constituents of the underlying groundwater chemistry according to elevation and underlying geologic material [EDGE, Peat Center (PC), Limestone Center (LC)] and year of planting (P1 or P2).

Statistical analyses

The Shapiro–Wilk test ($\alpha = 0.01$) was utilized to determine if the data had a normal distribution. Nonnormally distributed data were transformed either using a logarithmic or reciprocal root (1/x^a) transformation to approximate normality (Shapiro–Wilk test; $\alpha = 0.01$). While repeated measures of the surface water and groundwater were taken over the study period, we do not expect carry-over between sampling events. Thus, one- and two-way analysis of variance (ANOVAs) were used to test hypotheses, instead of a Repeated Measures ANOVA or Mixed Effect General Linear Model. Post-hoc Tukey test ($\alpha = 0.05$) was then used to detect significant differences between groups.

Groundwater and surface water Cl^- and $\delta^{18}O$ were used to examine tree island hydrodynamics and transpiration driven ion accumulation. Here, an ANOVA was used to distinguish differences between CENTER, DEEP and EDGE groundwater and the surface water (Hyp1). Groundwater chemistry (Cl⁻, Na⁺, Mg²⁺, Ca²⁺) and mineral saturation indices from the EDGE and the center of the limestone (LC) and peat (PC) islands were compared to aboveground biomass to assess any significant responses of groundwater geochemical condition and potential for CaCO₃ formation to changes in aboveground biomass (Hyp2). Here, LC and PC were compared separately to distinguish the role of underlying lithology on the hydrogeochemical behavior of the islands. Significant differences in the response of groundwater geochemistry to aboveground biomass were then evaluated using an analysis of covariance (ANCOVA) with a post hoc Tukey test ($\alpha = 0.05$). Finally, groundwater nutrient concentrations (TOC, K, and TP) were compared to changes in aboveground biomass for islands planted in 2006 (P1) and 2007 (P2) to elucidate if the accumulation of biomass was driving the formation of resource contrasts between tree islands and the surrounding marsh system (Hyp3). The islands were separated by planting year to examine if the response was consistent regardless of climatic differences at different points during stand development. In addition, data from both the EDGE and CENTER were used to evaluate the entire island response.

Results

Water tracers indicate transpiration governs tree island hydrodynamics

Given that δ^{18} O and Cl⁻ are conservative tracers of water, meaning organic and mineral materials have negligible influence on the concentrations of these substances as they move through the environment (Kendall and Caldwell 1998; Schlesinger 1997), they can be used to trace the interaction between precipitation, surface water and groundwater. At LILA the δ^{18} O and Cl⁻ of the surface water and the groundwater at the EDGE and CENTER portions of the islands significantly differed with elevated Cl⁻ concentrations and depleted isotopic values detected in the CENTER (Table 1). In general this pattern reversed with decreased in Cl⁻ concentrations and enriched $\delta^{18}O$ values going from the DEEP to the EDGE groundwater and then finally to the surface water (SW; Fig. 3a). The isotopic values of the DEEP groundwater indicated that water flowed from the ground surface downward at the islands' CENTER and laterally from the EDGE toward the middle of the island (Fig. 3a) as the δ^{18} O and δ D values of the DEEP groundwater declined between the EDGE and CENTER groundwater compositions (except in April 2011). Precipitation, that is inputs from rainfall, represent the most depleted (or lightest) input of water isotopes into the system, and the CENTER wells, with depths of \sim 1.34 m, maintain a consistently depleted signature compared to both the EDGE and DEEP groundwater. As such the fluctuation in isotopic values in the DEEP groundwater (2.00 m deep) must arise from flow paths composed of waters contributed from vertically above and laterally adjacent to them. In other words the flow paths are likely driven by a sustained water table depression, which was initially observed 2.3-2.5 years after planting the tree islands at LILA (Sullivan et al. 2011).

Over the study δ^{18} O and Cl⁻ concentration were positively correlated in the SW (r² = 0.865, P < 0.001), indicative of evaporation as a dominant process governing the surface water chemistry; here, the lightest water isotopes are preferentially evaporated compared to the heavy, while Cl⁻ remains behind (Fig. 3a). Conversely, groundwater Cl⁻ concentrations increased while stable isotopic values remained relatively stable in the CENTER of the tree islands, indicating transpiration as a dominant process controlling the groundwater chemistry. Specifically,

Table 1 The mean and SE of Cl^- and $\delta^{18}O$ values in the marsh surface water and tree island groundwater in the EDGE, DEEP and CENTER wells

Units	Statistic	Surface water	EDGE	DEEP	CENTER	F values	P values
mmol L^{-1}	Mean	$0.90^{\rm a}$	1.17 ^b	1.41 ^{b,c}	1.85 ^c	23.95	< 0.001
	SE	0.04	0.04	0.17	0.11		
(‰)	Mean	2.19 ^a	0.60^{b}	0.16 ^{b,c}	-0.25°	80.257	< 0.001
	SE	0.19	0.08	0.14	0.09		
	Units mmol L ⁻¹ (‰)	Units Statistic mmol L ⁻¹ Mean SE (‰) Mean SE	UnitsStatisticSurface watermmol L^{-1} Mean 0.90^a SE 0.04 (‰)Mean 2.19^a SE 0.19	Units Statistic Surface water EDGE mmol L^{-1} Mean 0.90^a 1.17^b SE 0.04 0.04 (‰) Mean 2.19^a 0.60^b SE 0.19 0.08	Units Statistic Surface water EDGE DEEP $mmol L^{-1}$ Mean 0.90^a 1.17^b $1.41^{b,c}$ SE 0.04 0.04 0.17 (‰) Mean 2.19^a 0.60^b $0.16^{b,c}$ SE 0.19 0.08 0.14	Units Statistic Surface water EDGE DEEP CENTER $mmol L^{-1}$ Mean 0.90^a 1.17^b $1.41^{b.c}$ 1.85^c SE 0.04 0.04 0.17 0.11 (‰) Mean 2.19^a 0.60^b $0.16^{b.c}$ -0.25^c SE 0.19 0.08 0.14 0.09	Units Statistic Surface water EDGE DEEP CENTER F values $mmol L^{-1}$ Mean 0.90^a 1.17^b $1.41^{b.c}$ 1.85^c 23.95 SE 0.04 0.04 0.17 0.11 (‰) Mean 2.19^a 0.60^b $0.16^{b.c}$ -0.25^c 80.257 SE 0.19 0.08 0.14 0.09 0.09

A one-way ANOVA and post hoc Tukey test ($\alpha = 0.05$) was used to determine significant difference between locations

^{a,b,c} Significant differences between the surface water, EDGE, DEEP and CENTER

Fig. 3 a The average δ^{18} O compared to the Cl concentration for surface water (blue asterisks; light blue designates samples collected in wet season (Oct), dark blue designates samples collected in dry season (April/May), rainfall (orange) and groundwater at the CENTER (red) and EDGE (black) of island as well as in the DEEP (purple) groundwater. b The average δ^{18} O compared to the Cl⁻ concentration of groundwater at the EDGE (black/gray) and CENTER (red) of the islands from the 2007 to 2012 wet (open) and dry (closed) sampling events. (Color figure online)



transpiration does not result in δ^{18} O fractionation (Ehleringer and Dawson 1992) but can lead to the elevated ion concentrations (e.g., Cl⁻) through root ion exclusion during plant water uptake.

Groundwater isotopic values and Cl^- concentrations also provide a line of evidence that transpiration governed groundwater–surface water interactions (Fig. 3b). Specifically, the groundwater isotopic signature at the EDGE of the islands approached that of the average surface water composition. The only possible way to increase the oxygen composition but decrease the Cl^- composition is through the mixing of water; as such these data suggest water flowed from the marsh into the EDGES of the islands. The groundwater isotopic and Cl^- trends remained fairly consistent over time until a prolonged drought in April 2011 when the groundwater in both the CENTER and EDGES of the tree islands increased in both Cl⁻ and δ^{18} O values (Fig. 3b). These elevated isotopic values suggest a significant loss of soil water through evaporation during this extended drought, which resulted in the establishment of a new baseline within the groundwater system.

Transpiration driven ion accumulations supports CaCO₃ formation

Within 3 years of planting, the groundwater geochemistry on the LILA islands attained a similar hydrogeochemical function as mature tree islands within the Everglades (Sullivan et al. 2014a; Troxler et al. 2014). Aboveground biomass by this time averaged 3.6 t ha^{-1} at the EDGES and 10 t ha^{-1} in the CENTER of the islands. The average ion concentrations were significantly higher in the CENTER compared to the EDGE, but did not significantly differ between the two lithologies (Table 2). The transpiration loss supported by the aboveground biomass drove the advective movement of groundwater into the center of the islands and led to ion accumulation and the potential for CaCO₃ formation. Groundwater Cl⁻, Na⁺, Ca²⁺ and Mg²⁺ concentrations significantly increased in the center of both the peat (PC) and limestone (LC) islands as the aboveground biomass increased (Fig. 4a-d). Conversely, no significant changes in groundwater ion concentrations were detected at the EDGES of the islands as biomass increased, with the exception of Ca^{2+} (Fig. 4c). The rate of cation accumulation (e.g., Na⁺, Ca²⁺, and Mg^{2+}) was greater in the LC than the PC (Fig. 4b-d), while no difference was detected in Cl⁻ accumulation rates between the two different lithologies. These data elude that transpiration drives similar ion accumulation but that the groundwater geochemical processes that influence cation concentrations differs with lithology.

The general saturation state (as saturation index, SI, where positive values indicate supersaturation) of the groundwater with respect to calcite and aragonite also changed with the aboveground biomass in the center of the islands (Fig. 4e, only SI for calcite shown). In LC and PC, groundwater went from saturated and undersaturated, respectively, to supersaturated with respect to both minerals as the aboveground biomass increased. Interestingly, like the cation accumulation rate, the strength of this positive response in SI values to aboveground biomass was greater in the LC as compared to the PC (Fig. 4e).

Establishment of nutrient gradients

Over this 5-year study (2007–2012), aboveground biomass on the islands increased one order of magnitude for the P1 and P2 islands (Fig. 5). Concurrent with this increase in biomass was a significant increase in groundwater Cl⁻ and TOC concentrations while K and TP significantly declined. We attribute the significant increase in groundwater Cl⁻ to the transpiration driven ion accumulation phenomena (as discussed above), which we postulate was enhanced over time as a result of the substantial increase in biomass and thus water loss and root ion exclusion by transpiration. The increase in aboveground biomass requires the uptake

 Table 2
 The mean and SE of major ion and saturation indices with respect to calcite and aragonite in the Limestone Center (LC),

 Peat Center (PC) and EDGEs of the tree islands

Constituents	Units	Statistic	LC	PC	EDGE	F values	P values
Cl-	mmol L^{-1}	Mean	1.87 ^a	1.82 ^a	1.16 ^b	18.937	< 0.001
		SE	0.13	0.18	0.04		
Na ⁺	mmol L^{-1}	Mean	1.88 ^a	1.75 ^a	1.28 ^b	18.404	< 0.001
		SE	0.11	0.14	0.03		
Mg ²⁺	mmol L^{-1}	Mean	0.59 ^a	0.55 ^a	0.47 ^b	11.18	< 0.001
		SE	0.03	0.03	0.01		
Ca ²⁺	mmol L^{-1}	Mean	4.88^{a}	4.53 ^{a,b}	4.01 ^b	7.023	0.001
		SE	0.22	0.26	0.11		
SI calcite		Mean	0.19 ^a	-0.01^{b}	0.02^{b}	5.518	0.004
		SE	0.04	0.06	0.03		
SI argonite		Mean	0.05^{a}	-0.15^{b}	-0.12^{b}	5.489	0.005
		SE	0.04	0.06	0.03		

A one-way ANOVA and post hoc Tukey test ($\alpha = 0.05$) was used to determine significant difference between locations and underlying geologic condition

^{a,b,c} Significant differences between the LC, PC and EDGE

Fig. 4 Groundwater concentrations of a chloride, b sodium, c calcium and d magnesium and the groundwater, e saturation index (SI) compared to tree island aboveground biomass at the EDGES (black), Limestone Center (LC; red), and Peat Center (PC; green). Significant liner regressions are provided in each panel and asterisks indicate a significant difference between regressions lines using an ANCOVA $(\alpha = 0.05)$. (Color figure online)



of both K and phosphorus (as reflected in TP), and increase in belowground carbon as a result of belowground biomass production; we discuss these implications in detail in the discussion.

Discussion

Our results are consistent with those suggested in Wetzel et al. (2005), Ross et al. (2006) and Sullivan et al. (2011) where the unifying hypothesis is that transpiration by trees drives inward flow of regional groundwater into tree islands. Specifically we demonstrate that the accumulation of aboveground biomass during early stand development results in the accumulation of ions in groundwater. As biomass accretes on the islands, the build-up of ions alters the groundwater geochemical conditions to favor mineral formation (e.g., CaCO₃). Transpiration driven groundwater uptake and the aboveground biomass accretion at LILA further resulted in the uptake and subsequent storage of nutrients on the islands. Below we expand on how trees play a meaningful role in driving geomorphic and nutrient patterns found across this wetland system.

Biogenic CaCO₃ formation

To estimate the amount of $CaCO_3$ formation on the islands we used an inverse modeling approach, where the initial condition was represented by the ground-water just after the trees were planted. Specifically, we elucidate how evapotranspiration, cation exchange, and $CaCO_3$ formation govern the groundwater geochemical evolution of the islands by examining changes in the groundwater Cl^- , Na^+ , Mg^{2+} and Ca^{2+} concentrations overtime (Supplementary Material 1).



Fig. 5 The average aboveground biomass compared to the average groundwater water concentrations of **a** chloride, **b** TOC, **c** potassium (K^+), **d** total phosphorus (TP) in the Planting-1 (P1, *black*) and Planting-2 (P2, *open*) islands

Ion concentration by evapotranspiration

As Cl^- is a conservative tracer (i.e., little soil and vegetation interaction), variation in its concentration reflects hydrologic inputs and outputs. For example, a dilution of Cl^- often results from inputs of rainfall, while a concentrating effect occurs with loss of water through evapotranspiration, given Cl^- is not vaporized with water. Thus, we can infer that solutes whose concentration ratio to Cl^- remains constant with changes in Cl^- concentrations are also governed by the same hydrologic inputs and outputs.

Cation exchange

As the Na⁺ requirements by upland trees is minimal and Na⁺ mineral formation is unlikely in this carbonaceous setting, deviation in the ratio of Na⁺:-Cl⁻ (dashed line Supplementary Material 1b) can be inferred as exchange of cations from the mineral and organic soil surfaces. The observed decrease in the slope can be interpreted as cation adsorption and quantified as the difference between the predicted Na⁺:Cl⁻ from evapotranspiration and the observed concentration. Given Mg²⁺/Cl⁻, Ca²⁺/Cl⁻ and K⁺/Cl⁻ ratios also decreased with increased Cl⁻ concentration (Supplementary Material 1), we then used the amount of Na⁺ adsorption to estimate a proportional amount of Mg²⁺, Ca²⁺ and K⁺ also adsorbed by exchange sites. In the case of divalent cations (Mg²⁺ and Ca²⁺), we use a 1:2 ratio between divalent cations and Na⁺ to estimate cation adsorption.

CaCO₃ formation

Calcite and aragonite represent the two most abundant minerals able to precipitate or dissolve under these hydrogeochemical conditions. As such, we estimated the amount of Ca^{2+} removed from solution through $CaCO_3$ formation by the difference between the

predicted increase in Ca^{2+} based on evapotranspiration and the Ca^{2+} concentrations, corrected for cation adsorption. To estimate the amount of $CaCO_3$ precipitated, a proportional HCO_3^- removed from the groundwater was allotted to Ca^{2+} using the following reaction.

$$2\text{HCO}_3^- + \text{Ca}^{2+} \Leftrightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$$

Following the first 3 years of planting, groundwater concentrations of major ions mirrored the increase in Cl⁻, with little cation adsorption or mineral formation. In October 2010 and then following the drought in the spring of 2011, cation adsorption and CaCO₃ formation increased substantially (Fig. 6). The highest values of Na⁺ adsorption and CaCO₃ formation was estimated in April 2011, with average values of 0.41 and 1.03 mol Na⁺ m⁻³, and 1.53 and 3.81 mol CaCO₃ m⁻³ in the LC and PC, respectively.

Our estimates of $CaCO_3$ formation at LILA mirror those from natural Everglades tree islands if we use a very broad-brushed approach to estimate the biogenic $CaCO_3$ accretion rates from the published literature. Tree islands began to form on the Everglades landscape between 3500 and 1000 years BP (Willard et al. 2006) and of these at least 12 islands have been identified with enigmatic caliche layers 50–70 cm thick within the soil profiles (Graf et al. 2008). Based on groundwater geochemistry trends observed at LILA, the precipitation of $CaCO_3$ can initiate fairly quickly under today's climatic conditions. If we assume that these layers begin formation at an island's inception, that accretion rates are constant over time, that all CaCO₃ is derived from transpiration driven ion accumulation, and that no dissolution has taken place, then we can estimate caliche accretion rates at roughly 1–7 mm per decade. If we assume the bulk density of these caliche layers is 1.9 g m⁻³ (Hennessy et al. 1983), this accretion rate translates to 2.7–13.3 mol CaCO₃ m⁻³ year⁻¹, which is remarkably close to the amount estimated at LILA after the drought of 2011, which was 1.5 and 3.8 mol CaCO₃ m⁻¹.

In comparison to total soil accretion rates in LILA tree islands which was estimated at 7 mm year $^{-1}$ (Rodriguez et al. 2014), mineral formation only represents ~ 5 % of the total accretion. What has yet to be determined is the longevity of these tree-derived organic and inorganic carbon pools on the landscape. While mineral soil formation may be slow compared to that of organic soils, they represent ~ 33 % of the soil profile under tree islands, where caliche layers have been observed (Chmura and Graf 2011; Coultas et al. 2008; Graf et al. 2008). In this study we are taking modern day, nascent tree island soil profiles and the knowledge of today's accretions rates and hindcasting the evolution of tree island soil profiles, yet we still need to project forward in time how these will change with respect to restoration, rising sea level and a changing climate.

In addition, we know that PHREEQC (Parkhurst and Appello 1999) modeling supports the potential for CaCO₃ precipitation but rates estimated at LILA from



Oct-07 May-08 Oct-08 May-09 Oct-09 April-10 Oct-10 April-11 Oct-11 April-12

Fig. 6 Estimated weathering of CaCO₃ (g m⁻³), negative values indicate a mineral loss, while positive values indicate mineral gain

inverse modeling may represent an upper limit, as Ca^{2+} is a macronutrient for vegetation growth and thus is likely taken up by overlying trees. Continued groundwater geochemical measurements are needed at LILA to examine how CaCO₃ weathering rates respond to the reduced rates of biomass accretion as a mature forest develops and leaf litter mineralization establishes.

Drought and geological condition influence tree island groundwater geochemical behavior

The Cl⁻ and δ^{18} O values on the tree islands demonstrate that following drought conditions (April 2011), hydrogeochemical the groundwater behavior responded quickly and differed with the underlying geologic condition. Here, groundwater δ^{18} O values and Cl⁻ concentrations in the center of the islands increased and inverse modeling indicated a substantial increase in cation adsorption and mineral formation following this significant dry period. These data suggest drought may drive meaningful episodic CaCO₃ precipitation events on the islands. Interestingly the strength of the response was greater in the PC as compared to the LC, with higher ion concentrations observed and a greater prediction of cation adsorption and mineral formation in the PC. Together these data may provide insight into tree island evolution as tree island establishment is thought to occur during prolonged drought events (Willard et al. 2006). Given that caliche layers on natural tree islands in the Everglades have been identified between layers of peat (Schwadron 2006), it may be no surprise that soil mineral formation in the PC was four times that of the LC islands (Fig. 6), but geochemically this behavior is perplexing given limestone islands reside closer to CaCO₃ equilibrium conditions as compared to the peat. Here we must invoke total ion storage to explain the predicted trends in CaCO₃ formation. Specifically peat, which has a much higher porosity, can hold a greater ion load as compared to limestone (examined in detail in Sullivan et al. 2014b). In addition, this higher porosity likely gives rise to more effective capillary action-the upward wicking of groundwater and associated ions from the water table to the vadose zone by adhesion (Bear and Cheng 2010). Given that both island types (LC and PC) had fairly similar groundwater ion concentrations in the years preceding the drought, our data would suggest that under drying conditions, the loss of water resulted a much greater concentrating effect in the PC as compared to the LC and as such $CaCO_3$ precipitation occurred more readily within peat-based tree islands at LILA under drought conditions. We can infer that this process helps to maintain tree island soil elevation on peat islands in the face of drought driven organic matter oxidation.

Stand development governs island-marsh nutrient resource contrast

The trends in groundwater nutrient concentrations at LILA are supported by the accretion of live biomass and the establishment of a functioning forest microbial community. The concurrent increase in groundwater TOC with biomass can be explained by an increase in both root exudates and microbial activity that is associated with tree growth (Jones et al. 2004). An increase in root depth along with associated exudates and microbes may also explain the doubling of TOC in the groundwater on both P1 and P2 islands following the spring 2011 drought (Fig. 5b), a trend which was pronounced in the DEEP groundwater (data not shown).

Given that both K⁺ and phosphorus are essential for plant growth it is no surprise that they declined in solution over time as biomass accumulated. For example, K⁺ plays a key role in plant water relations and enzyme activation, as such it is the most abundant cation found in plant cells, comprising 2–10 % of plant dry weight (Leigh and Jones 1984). Thus, on the low end we would expect that at least 2.34×10^4 mol m⁻² of K⁺ (2 % dry weight potassium for an accretion of 6.6 t ha⁻¹ of biomass) was extracted from the soil and groundwater over the study period.

The decline in TP over time likely resulted from the microbial transformation of TP to SRP and the uptake of SRP by overlying trees, as SRP is a bioavailable form of phosphorus but only represented ~25 % of the TP at LILA. While other biotic pools (understory vegetation and/or microbes) are likely utilizing nutrients during this period, the decrease in TP and K concentrations can be explained through a simple mass-balance that incorporates the accumulation of overlying biomass. Considering phosphorus specifically, we constructed a rudimentary phosphorus budget by making five assumptions: (1) wood and foliar phosphorus concentrations were the same; (2)

the increase in belowground biomass was negligible; (3) the concentration of phosphorus in the recharge water (precipitation, surface water, regional groundwater) was negligible; (4) uptake of groundwater by trees was similar year-round; and (5) all the total phosphorus was available. By combining the average groundwater uptake by tree $(3-4 \text{ mm day}^{-1}; \text{Sullivan})$ et al. 2011), the average leaf total phosphorus from concentrations two tree species of (19–38 μ mol g⁻¹; Subedi 2011), and the increase in biomass at LILA, we estimated the phosphorus concentration in the groundwater should have decreased by 1.6–6.9 μ mol L⁻¹ over the study. Thus, the observed decrease in the groundwater phosphorus concentrations (average 3.2 μ mol L⁻¹) from 2007 to 2012 was within this estimated decrease based on the accumulation of aboveground biomass.

Note that the decrease in TP may also be a result of adsorption of phosphorus and/or co-precipitation with the predicted precipitation of CaCO₃, a common phenomenon observed with the formation of calcium carbonate in the Ca^{2+} rich water (Dodds 2003). While this phenomenon likely occurs, soil nutrient data from the LILA islands indicated the development of a new organic horizon (0-3 cm deep) that contained significantly higher (1.4-1.8 times) concentrations of TP, total nitrogen and total carbon compared to underlying soils (3-10 cm deep; Rodriguez et al. 2014). These elevated concentrations were inferred to indicate that plant activity, specifically groundwater uptake by overlying trees, drove nutrient accumulation. Here, we provide direct evidence of transpiration driven groundwater uptake and a concomitant decrease in groundwater nutrient concentrations that support a mechanism for nutrient cycling and the eventual development of a nutrient contrast between tree island and marsh groundwater.

While Sullivan et al. (2014a, b, c) demonstrated that present day hydrologic fluxes on the island could not account for the mass of extant phosphorus found in many tree island soils, data from LILA show that CaCO₃ formation, which has a high affinity for phosphorus adsorption, provides a mechanism for sequestering phosphorus that reaches the tree islands by other suspected mechanisms of transport, e.g., deposition of dust or bird guano (Irick et al. 2015). If we expand this reasoning, then the secondary mineral formation caused by transpiration-driven ion accumulation on tree islands in the Everglades can act as a phosphorus filter helping to maintain this wetland in an oligotrophic state.

Conclusions

Trees help to govern the geomorphic evolution of subtropical wetlands as their transpiration demands result in the accumulation of ions and nutrients that support greater soil accretion on tree islands as compared with the surrounding marsh. We provide evidence from constructed tree islands that demonstrate the increase in aboveground biomass during early stand development triggers transpiration-driven ion accumulation in soils and supports the formation of calcium carbonate (CaCO₃)-enriched soil. Under current climatic conditions, CaCO₃ accretion for these young tree islands (~ 5 years old) was predicted to be 1 mm per decade or approximately 5 % of the total soil accretion. Our results also indicate that the greatest amount of CaCO₃ accretion occurs following drought conditions and is enhanced on tree islands underlain by peat compared to those underlain by limestone. Finally, the observed depletion of nutrients (potassium and phosphorus) in the groundwater suggests a connection between the nutrient uptake and storage by the overlying trees and the initial development of a nutrient contrast between the tree islands and marsh. Given that trees can govern local water flow paths and the ability of that water to dissolve or form minerals, their role in governing soil formation and landscape evolution must be embraced from wetlands to upland watersheds.

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