



# Willow-shrub encroachment affects physicochemical properties differently in two subtropical freshwater marshes

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**Abstract** Shrub encroachment has been increasing at unprecedented rates worldwide and a knowledge gap exists regarding how nutrient dynamics differ in shrub-encroached wetlands compared to marshes. This study evaluated physicochemical property differences in the soil, water, and vegetation of willow (*Salix caroliniana*) plots, marsh plots adjacent to willows, and control marsh plots in two wetlands within the St. John's River watershed, FL. In both wetlands, Moccasin Island and Lake Apopka, willow leaves ( $484 \pm 7 \text{ g kg}^{-1}$ ) contained more carbon (C) than sawgrass ( $442 \pm 3 \text{ g kg}^{-1}$ ) and cattail ( $468 \pm 4 \text{ g kg}^{-1}$ ) leaves. At Moccasin Island, soil nutrient (C, nitrogen, phosphorous) concentrations were doubled in willow and adjacent plots compared to marsh plots, while 37% less soil C was observed in willow plots than marsh plots at Lake Apopka. These results demonstrate willow-encroached marshes have unique properties relative to non-encroached marshes, but the direction and magnitude of the differences are site-specific.

**Keywords** Shrub encroachment · Carbon · Nitrogen · Soil · Water

## Introduction

Wetlands provide important ecosystem services, such as regulating carbon (C) storage and removing excess dissolved nutrients (Mitsch and Gosselink 2007). Vegetation shifts can impact primary productivity and physicochemical properties, potentially altering wetland functions (Critchley et al. 2002). Shrub encroachment, or the transition from graminoid herbaceous plants to woody shrubs, has become a global management issue in the last century as physiological differences between shrubs and herbaceous plants can change primary productivity, nutrient storage, and sedimentation (Knapp et al. 2008). In general, shrub encroachment results in fertility, resource, and/or hydrologic islands due to the redistribution of nutrients and water into shrub canopies from the surrounding regions (Schlesinger et al. 1996). In response to resource competition, shrub encroachment can promote bare or unvegetated interspaces between shrub canopies (Darrouzet-Nardi et al. 2006). Greater nutrient export from excess bioavailable nutrients in the water column have been observed in shrub interspaces, increasing soil heterogeneity in shrub-encroached grasslands (Schade and Hobbie, 2005). However, most previous research has been

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conducted in terrestrial systems; it is unclear whether wetland shrub encroachment will result in similar changes. This represents an important knowledge gap considering the global scale of wetland shrub encroachment (Knickerbocker et al. 2009; Saintilan and Rogers 2014).

Subtropical marshes constitute a large portion of the world's total C sequestration and have become increasingly shrub encroached in the last century due to hydrological alterations, nutrient enrichment, and fire suppression (Lee et al. 2005; Knapp et al. 2008; Mitsch et al. 2012; Quintana-Ascencio et al. 2013). In particular, willow (*Salix* spp.) encroachment has become a major land management issue due to willows' ability to alter plant community structure and soil properties and its resilience to management practices (Hall 2017). Within the St. Johns River watershed alone (FL, USA), shrub coverage of willow (predominately *Salix caroliniana* Michx.) has increased from 6 to 89% depending on the region, in the last century (Hall 2017). Although this may mimic natural succession of native species, the potential for altered ecosystem processes and services remains important at local and regional scales. For example, lower decomposition and higher evapotranspiration rates have been reported in willow-encroached areas, suggesting that willow may alter biogeochemical cycling (carbon storage and water exchange) (Duffy 2014; Budny and Benschoter 2016), while also suppressing fire due to their high water-holding capacity and limitation of herbaceous species necessary to provide fuel for fire (Quintana-Ascencio et al. 2011; Hall 2017). However, it is unclear whether reported changes in willow-encroached marshes are similar worldwide, or even within the same watershed (Maestre et al. 2016).

The purpose of this study was to characterize soil and water physicochemical properties in two willow-encroached subtropical marshes within the same watershed to determine if encroached wetlands have different properties than marshes, which may lead to unique ecosystem functions and services. Ecosystem properties such as C:N ratios, soil moisture and litter quality have all been associated with important wetland processes such as nutrient storage (Britson et al. 2015; Xu et al. 2016; Xiong et al. 2018). This study did not attempt to understand why shrub encroachment occurred or elucidate if shrubs directly caused physicochemical property differences or

characterize seasonal variability. Rather, the goal was to provide critical initial data on how ecosystem services (e.g., nutrient storage) may differ between willow-encroached and non-encroached marshes. A secondary objective was to see if differences detected in the study were synonymous within the same watershed or similar to findings of terrestrial shrub encroachment studies.

## Materials and methods

### Site description

The two study regions, Moccasin Island and Lake Apopka, are located within the St. Johns River watershed (32,000 km<sup>2</sup>) in east-central Florida (USA), a low elevation gradient blackwater river that flows south to north (SJRWMD 2018). The watershed's climate is warm and wet with mean annual temperature and precipitation ranges of 21–22 °C and 1120–1160 mm (SJRWMD 2018). Moccasin Island marsh (28.2359° N, 80.8212° W), historically sawgrass (*Cladium jamaicense*) dominated, was hydrologically altered in the early 1900s with flood control levees, producing unvegetated moist soils ideal for willow seed germination (SJRWMD 2018). Hydrological restoration during the 1980s removed the levees, providing mature willows water needed for further expansion (Quintana-Ascencio et al. 2013). Over time, willows continued to replace areas previously occupied by sawgrass communities, possibly due to willow's longer life span, greater resilience, and shading effects (Scholes and Archer 1997). Presently, Moccasin Island's hydroperiod mimics the St. Johns River, resulting in seasonal flooding. Willow areal coverage ranges from 30 to 90% with expansion attributed to extended dry periods (Hall 2017).

Lake Apopka North Shore (28.6946° N, 81.6586° W) is 130 km downstream of Moccasin Island and was used for muck-farming in the early 1900s, resulting in nutrient enrichment and hydrological alterations (Murphy 2005). The soils are highly compacted, with floodplain marsh typically > 1 m below lake level, resulting in permanent flooding (Coveney 2016). Beginning in the 1980s, restoration commenced with the removal of levees, canals, and exotic species, as well as nutrient management through gizzard shad harvest and agricultural discharge reductions. Cattail

(*Typha latifolia*) appeared following nutrient enrichment in the early 1900s and persists as the dominant marsh species. Willows covers approximately 44% of the shoreline (Murphy 2005).

### Study design

A stratified random sampling approach was employed in each study region to determine if differences exist in physicochemical properties in willow-encroached marshes, relative to non-encroached marsh. Aerial photography was used to identify 50 potential research plots (4 × 4 m each) as either shrub or herbaceous vegetation (SJRWMD 2018). Each potential research plot was split into nine quadrats and vegetation type (herbaceous vs. shrub) was field-verified by confirming > 80% of quadrats within a sampling plot were dominated by the specified vegetation (shrub-willow, herbaceous-sawgrass or cattail). The verified herbaceous plots (~ 30) were further separated as adjacent marsh (< 1 m from willows) or marsh (> 10 m from willows) plots. Adjacent marsh plots were established to test for effects beyond the willow canopy (equivalent to interspaces in terrestrial shrub-encroachment studies; Darrouzet-Nardi et al. 2006). The result was three plot types designated based on vegetation type and willow proximity: willow (> 80% willow), adjacent marsh (> 80% herbaceous and < 1 m from willow), and marsh (> 80% herbaceous and > 10 m from willow). Sampling occurred twice, once in the dry season (February–March) and once in the wet season (July–August), as determined by the temporal distribution of rainfall in the region, to capture annual temperature and hydrologic variability in each region. Moccasin Island was only flooded during the wet season while Lake Apopka was permanently flooded. During sampling, five of each plot type were randomly selected from each region using a random number generator.

### Soil sampling and analysis

Three 0–15 cm soil cores were collected in every plot (five of each type, in each region) using the push core technique and extruded in the field. Samples were placed on ice, transported back to the lab, homogenized, and stored at 4 °C until analysis. Soil surface redox potential and temperature (1 cm depth) were measured at every sampling point using a platinum-

tipped electrode, volt meter, and calomel reference electrode for redox, and a Fisherbrand long-stem digital thermometer for temperature. In the lab, a subset of the field moist sample was dried in a ThermoFisher Heratherm oven (ThermoFisher Scientific, Waltham, MA) at 70 °C for 72 h and weighed for gravimetric moisture content and bulk density. Porosity was calculated as the % pore space = 1 – (bulk density/2.65 g cc<sup>-1</sup>) (Boyd 1995). Oven dried samples were then ground to a fine powder (SPEX Sample Prep Mixer Mill 8000 M, Metuchen, NJ). A subset of the dried, ground sample (~ 5 mg) was analyzed on the Elementar Vario Micro Cube (Elementar Americas Inc., Mount Laurel, NJ) for total C and nitrogen (N). Dried, ground subsamples were ashed for 4 h at 550 °C in a ThermoFisher Isotemp muffle furnace (ThermoFisher Scientific, Waltham, MA) for soil organic matter content. The ashed subsamples were digested with 50 mL of 1 M HCl at 150 °C for 30 min after Andersen (1976) and analyzed for total phosphorus (P) on an AQ2 Discrete Analyzer (Seal Analytical, Mequon, WI) using EPA method 134-A Rev. 5. Additionally, a subset of the wet sample (~ 5 g) was extracted with 2 M KCl for extractable nitrate (NO<sub>3</sub><sup>-</sup>), ammonium (NH<sub>4</sub><sup>+</sup>), and orthophosphate on an AQ2 Discrete Analyzer (Seal Analytical, Mequon, WI; methods AGR-231, AGR-210, and EPA-118 respectively). Extractable N was the sum of extractable NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>.

### Leaf tissue sampling and analysis

Plots were split into 9 quadrats and ~ 10 live mature leaves from the dominant species (willow, cattail, or sawgrass) were haphazardly collected at eye level in each quadrat. All leaves were brought back to the lab and rinsed with deionized water to remove sediment, larvae, and pollen. Samples were dried and ground to a fine powder for total C, N, and P analysis, as described above. Cell wall lignin (CWL) content was determined by the acetyl bromide method (Moreira-Vilar et al. 2014) and analyzed at 280 nm on an HTX Synergy MicroPlate Reader (Biotek Instruments, Winooski, VT).

### Statistical analyses

Due to the unique histories and hydrologies of the two study regions, they were analyzed individually. Paired

*t*-tests indicated no significant differences in any study parameter between seasons. Therefore, seasonal data were pooled, and all data presented had an  $n = 10$  for each plot type, and each region. Statistical analyses were performed in R Statistics (R Foundation for Statistical Computing, Vienna, Austria). All data sets were first tested for normality (Shapiro–Wilk) and homogeneity (Levene’s test). Data that did not meet the assumptions were log transformed. Differences between plot types and physicochemical properties were analyzed using a one-way ANOVA (stats package). To account for multiple comparisons, a Bonferroni correction was applied, adjusting the  $\alpha$ -value to 0.02. A Tukey’s post-hoc test was used to identify plot-level differences (lsmeans package). All results are the untransformed means  $\pm$  standard error (SE); *p*-values shown are from ANOVA models.

## Results

### Soil physicochemical properties

At Moccasin Island, encroached plots (willow and adjacent marsh plots) had greater porosity ( $p < 0.001$ ;  $82 \pm 2\%$ ) than marsh plots ( $67 \pm 4\%$ ). Resultantly, lower soil compaction ( $p < 0.01$ ) and greater soil moisture content ( $p < 0.001$ ) were observed in encroached plots ( $0.45 \pm 0.03 \text{ g cc}^{-1}$ ;  $83 \pm 2\%$ ) than in marsh plots ( $0.98 \pm 0.21 \text{ g cc}^{-1}$ ;  $52 \pm 9\%$ ). Redox potential was lower ( $p < 0.01$ ) in encroached plots ( $9 \pm 17 \text{ mV}$ ) compared to marsh plots ( $82 \pm 13 \text{ mV}$ ). Soil temperatures were greater in adjacent marsh plots ( $30.4 \pm 0.7 \text{ }^\circ\text{C}$ ) than in willow ( $28.0 \pm 0.6 \text{ }^\circ\text{C}$ ) and marsh plots ( $28.1 \pm 0.6 \text{ }^\circ\text{C}$ ). Greater soil nutrient (OM, C, N, and P) concentrations and higher C:N were observed in encroached marsh soils compared to control marsh soils ( $p < 0.01$ ; Table 1). Bulk extractable nutrients did not differ significantly between plot types.

At Lake Apopka, soil properties (soil porosity, redox potential, bulk density, and soil nutrient content) did not significantly differ by plot type (Table 1). In general, encroached plots had less soil moisture than control marsh plots ( $p = 0.03$ ). Willow plots generally ( $p = 0.03$ ) contained less total C ( $162 \pm 30 \text{ g kg}^{-1}$ ) than herbaceous plots ( $253 \pm 32 \text{ g kg}^{-1}$ ).

### Leaf tissue chemical composition

At Moccasin Island, willow leaf tissue had greater total C content ( $p < 0.001$ ;  $479 \pm 10 \text{ g kg}^{-1}$  leaf tissue) than sawgrass ( $442 \pm 3 \text{ g kg}^{-1}$  leaf tissue). Marsh and adjacent marsh plots contained the same vegetation composition, but greater N content was observed in sawgrass leaves in adjacent marsh plots ( $p < 0.001$ ; Table 1). Consequently, sawgrass leaves in adjacent marsh plots contained the highest quality (lowest C:N) and willow leaves contained the lowest quality ( $p < 0.001$ ). Total P and CWL content did not differ by plot type.

Similarly, at Lake Apopka, greater ( $p < 0.01$ ) total C content was observed in willow leaves ( $488 \pm 4 \text{ g kg}^{-1}$  leaf tissue) compared to cattail leaves ( $469 \pm 5 \text{ g kg}^{-1}$  leaf tissue). No significant differences in CWL, total N, total P, or C:N were detected (Table 1).

## Discussion

Physicochemical properties differed significantly by plot type in the two willow-encroached marshes (Fig. 1). For example, soil nutrient concentrations were two times greater in willow and adjacent marsh plots at Moccasin Island, while willow plots at Lake Apopka generally had lower C concentrations and soil moisture than marsh and adjacent marsh plots. This data indicates encroached marshes may function differently than non-encroached marshes, but the direction and magnitude of the difference is site-specific (Britson et al. 2015; Xu et al. 2016; Xiong et al. 2018). Therefore, localized studies risk making inaccurate generalizations regarding wetland shrub encroachment effects on regional or global scales.

Directional differences in properties between our study regions may be influenced by the identity of the dominant herbaceous vegetation (sawgrass or cattail). Both cattail and sawgrass are common in subtropical wetlands but have vastly different life histories (Mitsch and Gosselink 2007). Cattail can have greater nutrient requirements and leaf nutrient allocation than sawgrass, resulting in quicker turnover of cattail detritus and greater nutrient storage (Miao and DeBusk 1999). Cattail is also thought to have greater stomatal conductance, evapotranspiration, and radial oxygen loss than willow and sawgrass (Miao and

**Table 1** Mean  $\pm$  SE nutrient concentrations for each region by plot type

Soil						
Study Region	Plot Type	SOM (g kg <sup>-1</sup> soil)	Total C (g kg <sup>-1</sup> soil)	Total N (g kg <sup>-1</sup> soil)	Total P* (g kg <sup>-1</sup> soil)	C:N
<i>Moccasin Island</i>						
	Marsh	518 $\pm$ 89 <sup>a</sup>	241 $\pm$ 41 <sup>a</sup>	21 $\pm$ 4 <sup>a</sup>	5 $\pm$ 1 <sup>a</sup>	11.6 $\pm$ 0.1 <sup>a</sup>
	Adj	792 $\pm$ 24 <sup>b</sup>	400 $\pm$ 124 <sup>b</sup>	33 $\pm$ 1 <sup>b</sup>	7 $\pm$ 1 <sup>b</sup>	12.2 $\pm$ 0.4 <sup>b</sup>
	Willow	831 $\pm$ 29 <sup>b</sup>	399 $\pm$ 95 <sup>b</sup>	32 $\pm$ 1 <sup>b</sup>	8 $\pm$ 1 <sup>b</sup>	12.4 $\pm$ 0.2 <sup>b</sup>
<i>Lake Apopka</i>						
	Marsh	445 $\pm$ 140 <sup>a</sup>	269 $\pm$ 57 <sup>a</sup>	18 $\pm$ 5 <sup>a</sup>	4 $\pm$ 1 <sup>a</sup>	14.7 $\pm$ 2.0 <sup>a</sup>
	Adj	293 $\pm$ 63 <sup>a</sup>	226 $\pm$ 29 <sup>a</sup>	16 $\pm$ 3 <sup>a</sup>	4 $\pm$ 1 <sup>a</sup>	14.4 $\pm$ 1.3 <sup>a</sup>
	Willow	277 $\pm$ 74 <sup>a</sup>	136 $\pm$ 21 <sup>a</sup>	10 $\pm$ 1 <sup>a</sup>	4 $\pm$ 0 <sup>a</sup>	13.9 $\pm$ 0.7 <sup>a</sup>
Leaf tissue						
Study Region	Plot Type	Total C (g kg <sup>-1</sup> leaf)	CWL (g kg <sup>-1</sup> leaf)	Total N (g kg <sup>-1</sup> leaf)	Total P (g kg <sup>-1</sup> leaf)	C:N
<i>Moccasin Island</i>						
	Marsh	442 $\pm$ 3 <sup>a</sup>	33 $\pm$ 7 <sup>a</sup>	26 $\pm$ 2 <sup>b</sup>	2 $\pm$ 0 <sup>a</sup>	17.2 $\pm$ 1.4 <sup>b</sup>
	Adj	443 $\pm$ 3 <sup>a</sup>	33 $\pm$ 2 <sup>a</sup>	35 $\pm$ 1 <sup>c</sup>	2 $\pm$ 0 <sup>a</sup>	12.6 $\pm$ 0.3 <sup>a</sup>
	Willow	475 $\pm$ 10 <sup>b</sup>	47 $\pm$ 11 <sup>a</sup>	18 $\pm$ 3 <sup>a</sup>	2 $\pm$ 0 <sup>a</sup>	26.0 $\pm$ 1.3 <sup>c</sup>
<i>Lake Apopka</i>						
	Marsh	467 $\pm$ 5 <sup>a</sup>	21 $\pm$ 3 <sup>a</sup>	22 $\pm$ 2 <sup>a</sup>	1 $\pm$ 0 <sup>a</sup>	21.3 $\pm$ 2.6 <sup>a</sup>
	Adj	470 $\pm$ 4 <sup>a</sup>	11 $\pm$ 2 <sup>a</sup>	23 $\pm$ 5 <sup>a</sup>	2 $\pm$ 0 <sup>a</sup>	20.4 $\pm$ 3.7 <sup>a</sup>
	Willow	488 $\pm$ 4 <sup>b</sup>	44 $\pm$ 14 <sup>a</sup>	20 $\pm$ 3 <sup>a</sup>	1 $\pm$ 0 <sup>a</sup>	24.4 $\pm$ 4.0 <sup>a</sup>

Superscript letters represent significantly different means by Tukey's HSD test at  $p < 0.02$

\*Statistical analyses for Lake Apopka's total soil P were ran using log-transformed data, but untransformed results are shown for interpretation

DeBusk 1999), which was observed as lower soil moisture ( $\mu = 49\%$ ) and higher redox potentials ( $\mu = 67$  mV) at cattail-dominated Lake Apopka, compared to sawgrass-dominated Moccasin Island ( $\mu = 59\%$ ;  $\mu = 25$  mV). Greater soil nutrient content was observed in Moccasin Islands' encroached plots compared to its sawgrass-dominated control marsh plots, possibly due to willows' ability to act as sediment traps. Cattail can also act as sediment traps which may explain why soil nutrient concentrations were more homogenous at Lake Apopka than at Moccasin Island.

Hydroperiod differences may also contribute to the dissimilar directional shift of soil physicochemical properties between regions. Permanent flooding (Lake Apopka) can reduce the amount of litterfall reaching the soil surface in willow plots, decreasing soil C content. In contrast, seasonally flooding (Moccasin

Island) permitted direct litterfall deposition onto the soil surface during the dry season. The differences in soil nutrients between sites aligns with terrestrial shrub encroachment studies where drier sites captured more organic C, while wetter sites lose organic C (Schlesinger et al. 1996; Jackson et al. 2002; Schade and Hobbie 2005). Secondly, soil nutrient differences were more apparent at Moccasin Island than at Lake Apopka. Permanent flooding could increase litter hydrologic transport, resulting in homogenization of soil nutrients across the landscape. The force of inundation is important as well, which can alter sediment retention and should be considered in future studies. In summary, wetland hydroperiod may play a key role in determining the unique properties and potentially, the functions of shrub-encroached marshes. Furthermore, the results from the seasonally flooded marsh (Moccasin Island) more closely

		<u>Moccasin Island</u> (Seasonally flooded)		<u>Lake Apopka</u> (Permanently flooded)	
		 Adj.	 Willow	 Adj.	 Willow
Soil Properties		↑ Moisture**	↑ Moisture**		
		↑ OM**	↑ OM**		
		↑ TC, N & P**	↑ TC, N & P**		
Leaf Tissue			↑ TC*		↑ TC
			↓ TN**		

**Fig. 1** Key physicochemical property differences in willow and adj. plots compared to marsh plots by region. \*Represents physicochemical properties that significantly differed between

adj. marsh and willow plots compared to marsh plots ranging from  $p < 0.05$ ,  $p < 0.01$  (\*),  $p < 0.001$  (\*\*)

resemble the findings from terrestrial studies that indicate shrubs create islands of fertility and water (Schlesinger et al. 1996), while the permanently flooded conditions produced contrary results.

#### Management implications

Physicochemical properties are linked to important biogeochemical processes such as C storage and N cycling (Hartman et al. 2008), making them important to land managers. Based on this study, willow-encroachment at the seasonally flooded Moccasin Island site can result in greater soil nutrient and moisture storage, which may be a desirable outcome for land managers seeking to optimize a wetland's C, nutrient, and water retention capacity. On the contrary, greater dissolved N and DOC concentrations in encroached plots at Lake Apopka could pose a eutrophication risk (Coveney 2016). Overall, the detection of physicochemical differences in this study supports the need for future studies on how biogeochemical processes (decomposition and denitrification) are altered in willow-encroached landscapes to help land managers make informed decisions based on valued wetland functions.

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