VEGETATION AND ENVIRONMENTAL FACTORS OF INLAND SALINE WETLANDS IN THE UPPER ST. JOHNS RIVER BASIN, FLORIDA, U.S.A.

Alexander Lee Griffel Dalager

South Florida Water Management District
7345 Greenbriar Parkway
Orlando, Florida 32819, U.S.A.
agriffel@sfwmd.gov

ABSTRACT

Inland saline wetlands are a global ecosystem that rarely occur in humid climates. Along the upper St. Johns River Basin in the southeast coastal plain inland saline wetlands occur, formed by fossil saline groundwater. The goal of this study was to describe and evaluate the distribution of species along environmental gradients in the inland saline wetlands of the upper St. Johns River Basin. In June 2022, species composition and cover were assessed at 82, one square meter plots at the Buck Lake Conservation Area (BLCA) in Volusia County, Florida. Soil samples were collected from each plot and electric conductivity, pH, total carbon, total nitrogen, soil color, and soil type were analyzed. Elevation was estimated at each plot from a digital elevation model. Hierarchical agglomerative clustering and the silhouette method determined 9 optimum vegetation assemblages. The constrained correspondence analysis accounted for 22.5% of the variation in site by species distribution and CCA model permutation found that electric conductivity, elevation, soil color, soil type, and canopy closure were significant environmental variables.

RESUMEN

Los humedales salinos continentales son un ecosistema global que rara vez se da en climas húmedos. A lo largo de la cuenca alta del río St. Johns, en la llanura costera del sureste, existen humedales salinos interiores formados por aguas subterráneas salinas fósiles. El objetivo de este estudio era describir y evaluar la distribución de especies a lo largo de gradientes ambientales en los humedales salinos interiores de la cuenca superior del río St. Johns. En junio de 2022, se evaluó la composición y cobertura de las especies en 82 parcelas de un metro cuadrado en el Área de Conservación del Lago Buck (BLCA) en el condado de Volusia, Florida. Se recogieron muestras de suelo de cada parcela y se analizaron la conductividad eléctrica, el pH, el carbono total, el nitrógeno total, el color del suelo y el tipo de suelo. La elevación se estimó en cada parcela a partir de un modelo digital de elevación. La agrupación jerárquica aglomerativa y el método de la silueta determinaron 9 conjuntos óptimos de vegetación. El análisis de correspondencia restringido dio cuenta del 22,5% de la variación en la distribución de especies por sitio y la permutación del modelo CCA encontró que la conductividad eléctrica, la elevación, el color del suelo, el tipo de suelo y el cierre del dosel eran variables ambientales significativas.

Key Words: Wetlands, Inland Saline Wetlands, St. Johns River

INTRODUCTION

The distribution of plant communities and species along environmental gradients is a principal question of vegetation science, plant ecology, and wetland ecology (Whittaker 1967; Mitsch & Gosselink 2007; Austin 2013). Soil salinity is attributed as the driving factor for the distribution of plant species and community zonation within coastal systems (Adams 1962; Odum 1988; Pennings et al. 2005; Alvarez-Rogel et al. 2006; Wu 2020). However outside of coastal and desert ecosystems the importance of salinity within inland ecosystems including wetlands is underrepresented (Bui 2013). The main factors known to drive the distribution of plant species in inland saline wetlands are salinity, soil moisture, and hydrology (Ungar 1967; Ungar 1970; Ungar 1973; Burchill & Kenkel 1991; Pan et al. 1998; Ungar 1998; Eallonard & Leopold 2014).

Inland saline wetlands have been studied and described globally including North America, Europe, Asia, and Africa. In a boreal inland salt pan in Manitoba a constrained correspondence analysis (CCA) was conducted suggesting that salinity, which ranged from 3.9 to 20.1 mg mL^{-1}, explained the most variation but, elevation, soil organic matter, and pH also explained variation in plot distribution (Burchill & Kenkel 1991). Pan et al. (1998) used multivariate statistics to evaluate the role of environmental and spatial factors on the

J. Bot. Res. Inst. Texas 19(3): 241–254. 2025
https://doi.org/10.17348/jbrit.v19.i3.1426
Published online: 23 September 2025

structure of an inland saline wetland along the Hutubi River of Xinjiang China. Premutation tests of the CCA were significant and support the importance that soil moisture and salinity drive the structure of these community types (Pan et al. 1998). Inland saline wetlands (dominated by halophytic shrubs) in South Africa were clustered into 29 plant assemblages and ECe and soil wetness were the most important environmental variables (Sieben et al. 2016). A principal component analysis of Serbian inland saline wetlands, known from only two locations, suggested that chemical oxygen demand, carbonate, pH, and ECe were the main factors affecting species distribution (Ljevnaic-Masic et al. 2020). Moreover, a study of inland saline wetlands in central Türkiye found that pH, and the concentration of sodium and chloride ions were most important in explaining vegetation zonation (Tug et al. 2012).

In the continental United States Ungar provided some of the earliest studies of these ecosystems in arid and humid climates (Ungar 1967; Ungar 1968; Ungar 1970; Ungar 1973; Ungar 1998). Ungar et al. (1979) found that the salinity gradient determined the distribution of species of an inland saline marsh east of the Mississippi River in Ohio where electric conductivity ranged from 1.1 to 142.8 mmhos/cm. Prior work by Ungar occurred west of the Mississippi River and east of the Rocky Mountains where evapotranspiration exceeds precipitation. In New York and Michigan, Eallonardo and Leopold (2014) found that ECe (maximum 107 dS/m & 23 dS/m, respectively), flood duration, depth to water table, and total nitrogen were significantly different across inland saline wetland species assemblages. Furthermore, the authors found significant temporal variation in species composition within the New York inland saline marsh driven by annual variability in osmotic potential (Eallonardo & Leopold 2014). Inland saline wetlands have a limited extent in eastern North America. Eallonardo and Leopold (2014) estimated that inland saline wetlands in the northeast cover approximately 15 hectares, 5 of which have high natural quality.

In North American's southeastern coastal plain, the St Johns River Basin (SJRB) spans from the blue cypress swamp in Indian River County Florida north to the Atlantic Ocean in Duval County Florida. Near Jacksonville, Florida, the river is tidally influenced resulting in higher salinity and estuary communities with salt tolerant plant species such as *Juncus roemerianus* Scheele and *Spartina alterniflora* Loisel. (Montague & Wiegert 1990; Kinser et al. 2012). Under normal conditions a tide less than 0.5 ft typically reaches Lake George which is approximately 204.3 kilometers upriver (Kinser et al. 2012). Above the head of the tide in the upper SJRB, wetland communities consist primarily of palustrine forested swamps and palustrine emergent marshes dominated mostly by glycophytes (Lowe 1983; Lowe 1986). Still, halophytes, unvegetated salt pans and inland saline wetlands occur upriver of Lake George (Kinser et al. 2012). The Florida Natural Areas Inventory (FNAI) briefly described salt flat communities around Puzzle Lake (Volusia Co.) and Salt Lake (Brevard Co.) and suggested that soil salinity is the explanatory environmental gradient (FNAI 2006; FNAI 2010).

Water supply planning and hydrogeology studies conducted by the St. Johns River Water Management District (SJRWMD) determined that relict sea water (connate or fossil water) from the Floridan aquifer, an absent or thin confining unit (hawthorn formation), and a potentiometric surface 3–6 meters above the St Johns River result in ground water upwelling and is the cause of the oligosaline conditions in the surficial aquifer and formation of inland saline wetlands and salt barrens of the upper SJRB (Toth 1988; Belaineh et al. 2011). The highest chloride concentrations (5,000 –18,000 mgL-1) were observed south of Lake Harney and north of State Road 46 in the same location as this study and the highest concentration of salt barrens (Belaineh et al. 2011).

A formal study has not been carried out to explore fundamental questions of inland saline wetlands of the upper SJRB. The goal of this study is to describe and document the vegetation and environmental factors of an understudied and spatially limited wetland ecosystem. Objectives were to 1) voucher plant specimens for the community, 2) identify and describe floristic composition of inland saline wetlands through floristic and quantitative sampling, 3) evaluate soil characteristics, 4) describe the distribution and abundance of ground cover species across environmental gradients, and 5) describe plant assemblages/clusters.

MATERIALS AND METHODS

Wetlands were studied at Buck Lake Conservation Area (BLCA) in Volusia County Florida. A 244-hectare area was selected at BLCA to assess plant community composition and environmental variables (Fig. 1). A simple random sample using QGIS (version 3.12.3-Bucuresti) vector geoprocessing tools determined the location of 82 one-meter square plots (Fig. 2). Vegetation and soil sampling was conducted from June 30, 2022, through July 9, 2022. All groundcover stratum plant species within the plots were identified and aerial cover visually estimated by a single observer. A spherical concave densiometer was used to measure canopy closure at each plot. Plant collections made from July 2019 to March 2024 were deposited at the University of Florida Herbarium.

Soil Variables.—Soil samples were collected at each one-meter square plot within the rooting zone to a depth of 15 centimeter using a 5-centimeter diameter hand core. Electric conductivity (ECe) was measured with a Hanna Instruments HI763100 electric conductivity probe using a soil saturated paste extract (US Salinity Laboratory 1954). Soil pH was measured following Hanlon (2015) using a 2:1 water to soil solution with a Hanna Instruments pHep5 HI98128 pH tester. Total carbon (TC) and total nitrogen (TN) were analyzed by the University of Florida Geological Science Light Stable Isotope Mass Spectrometry Laboratory using a Costech ECS 4010 Elemental Combustion System elemental analyzer. The Munsell soil color chart quantified soil color and the near-saturated rub test determined organic from mineral soils (Vasilas et al. 2018). Using QGIS (version 3.12.3-Bucuresti) elevation was determined at each plot based on a digital elevation model from the SJRWMD.

Hydrology.—Two groundwater piezometers were installed to a depth of 1.5 meters with a 1.5 meter riser. One piezometer was installed in soil map unit 31-Malabar fine sand a mineral soil (Grossarenic Endoaqualfs) and the second in soil map unit 64-Tequesta Muck a histic glossaqualf. However, the dataset is incomplete because of frequent equipment failure, vandalism, and high-water levels from Hurricane Ian in 2022. Data was used to describe general qualitative patterns of the wetland hydropattern.

Statistical Methods.—Descriptive summary statistics were calculated for plant species and abiotic variables. Importance values (sum of relative abundance and relative frequency) were calculated for each species across all plots and within plant assemblages. Frequency was calculated as the percentage of plots that contained the species. R packages vegan and cluster were used to implement statistic functions (Maechler et al. 2021; Oksanen et al. 2020). Species abundances were square root standardized by the Hellinger standardization and the Bray-Curtis dissimilarity index was used to determine ecological resemblance of the site by species data matrix (Peet & Roberts 2013; Oksanen et al. 2020). Agglomerative hierarchical clustering with average linkage method was conducted on the site by species ecological resemblance matrix (Maechler et al. 2021). The agglomerative coefficient and correlation between the distance matrix and cophenetic cluster height was evaluated to determine if cluster structure was appropriate and the silhouette method determined the optimum number of clusters. Each cluster was validated by reviewing species fidelity. Constrained correspondence analysis was conducted on the transformed data (Oksanen et al. 2020; Palmer n.d.). The variation inflation factor was calculated to review the correlation between constraining variables in the CCA. Species abundance and environmental variables were square root transformed, and the data met parametric statistical assumptions of linearity, normality, and homogeneity. Anova like permutation tests of the CCA model residuals evaluated the significance of the full CCA, axes, and independent variables (Legendre et al. 2011; Maechler et al. 2021).

RESULTS

Across all plots 82 species were observed in 66 genera, and 35 families. Poaceae had the most species (21), followed by Asteraceae (15), and Cyperaceae (9). *Spartina bakeri* Merrill had the highest importance value (20.86), followed by *Sporobolus virginicus* (L.) Kunth (18.9), *Juncus roemerianus* (16.21), *Paspalum vaginatum* Sw. (10.96), *Sesuvium portulacastrum* (L.) L. (9.62), *Fimbristylis castanea* (Michx.) Vahl (9.2) and

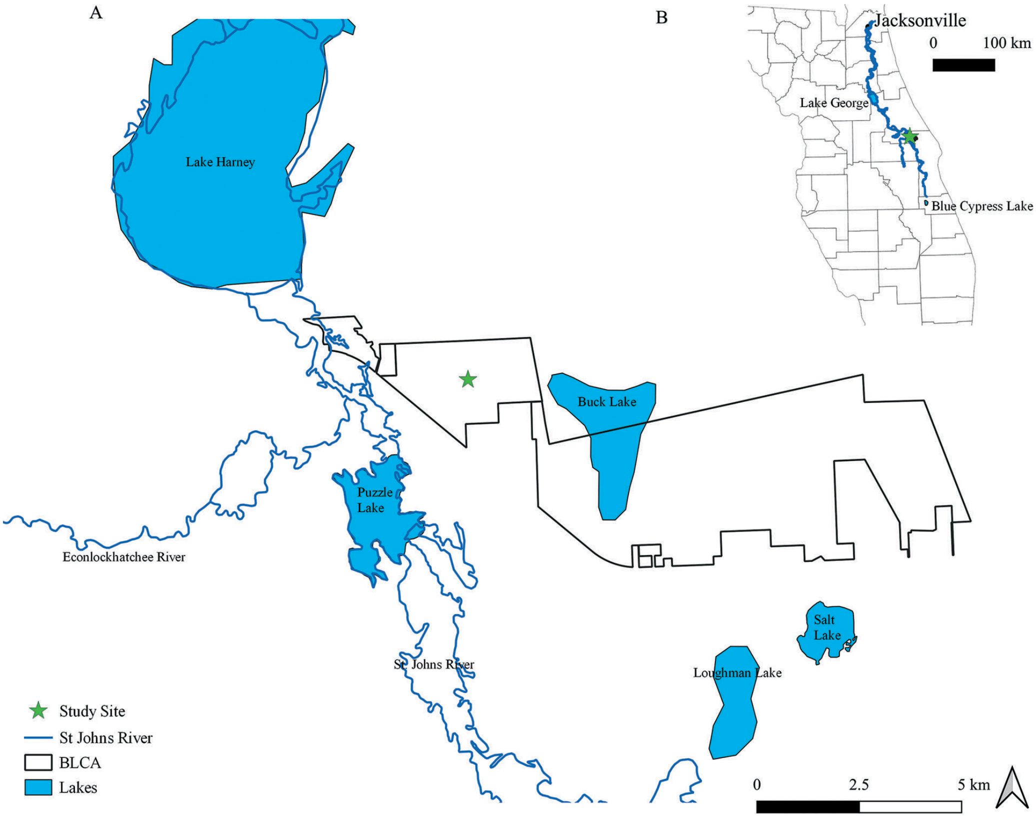

Fig. 1. Location of inland saline wetland study site in the upper SJRB. Part A displays the centroid of the study site (green star) at the BLCA and the regional landscape. Important lakes and rivers are displayed and labeled. Part B is an inset map which displays peninsular Florida, county boundaries, and the extent of the St. Johns River. The SJRB spans from the Blue Cypress swamp in Indian River County Florida north to the Atlantic Ocean in Duval County Florida

Telmatoblechnum serrulatum (Rich.) Perrie, D.J. Ohlsen, & Brownsey (9.02). All other species had importance values of 5 or less. Canopy closure ranged from 0% to 100% with an average of 11 ± 24.

Across all plots the electric conductivity ranged from 1.51 ds/m to 100.10 ds/m and the average was 26.61 ± 24.79 ds/m. The average pH across all plots was 5.51 ± 1.29 ranging from 3.22 to 8.24. Elevation ranged from 1.66 m to 3.02 m with an average of 2.25 ± 0.31 m. Soil total nitrogen by weight ranged from 0.01% to 2.57% with an average of 0.32 ± 0.52% across all plots. Total carbon by weight ranged from 0.06% to 43.60% and averaged 5.85 ± 9.89% across all plots. Soil color in the top 15 cm ranged in value from 2 to 7 with an average of 4 ± 2. Fourteen plots were identified as organic soil and 68 as mineral soil using the near saturated rub test.

Agglomerative Hierarchical Clustering.—The average agglomerative coefficient of the dendrogram was 0.67 and the correlation between the cophenetic height and the plot ecological dissimilarity was 0.908 (Fig. 3). At 9 clusters the maximum average silhouette width was 0.37 and the silhouette width for each cluster was positive (Fig. 3). Table 1 displays the importance value, relative abundance, and relative frequency for the top 5 species of each cluster. Cluster 1 contained 4 plots and 27 species. *Fimbristylis castanea* had an importance value of 0.81 and was the most important species occurring in all plots. Most species in the cluster occurred in only 1 plot. In cluster 2 bare ground had the highest importance value (1.11). *Sesuvium portulacastrum* had the second highest importance value (0.36), followed by *Salicornia ambigua* Mich. Twenty plots occurred in this cluster with a total of 8 species. Cluster 3 included 10 plots, 24 species, and *Sporobolus virginicus* was the most

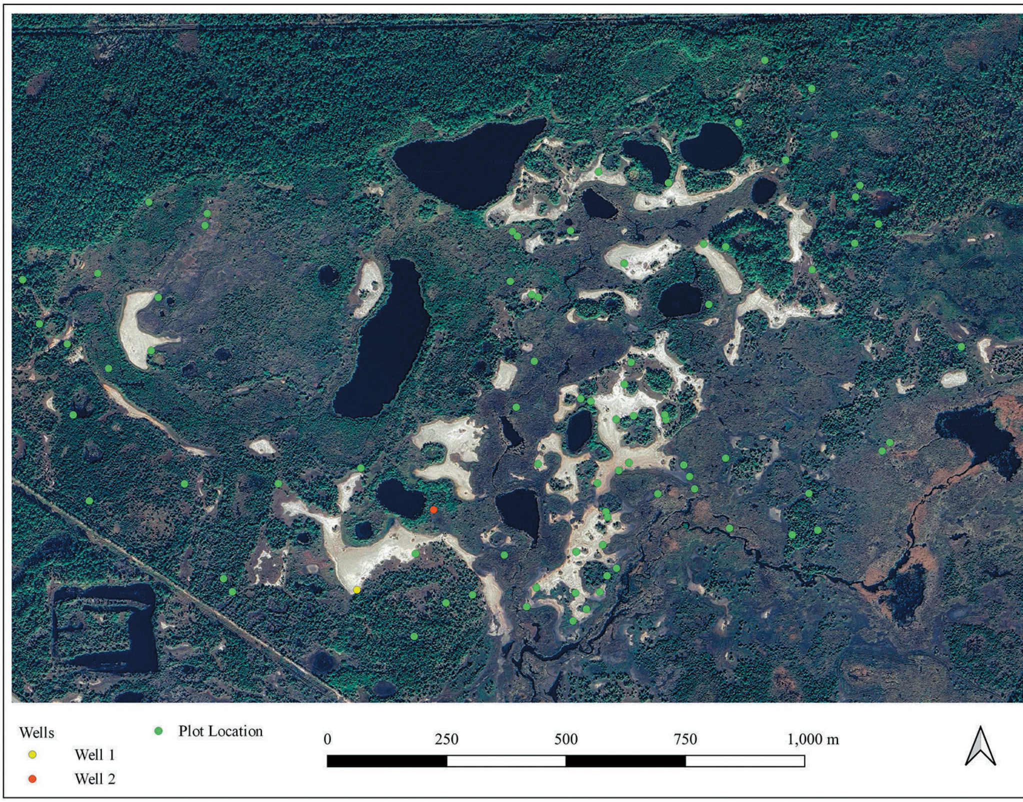

Fig. 2. Aerial of inland saline wetland displaying the location of one-meter square plots and well locations.

important (0.82), occurring in all 10 plots. Cluster 4 included 11 plots, 30 species, and *Juncus roemerianus* had the largest importance value (0.93). *Telmatoblechnum serrulatum* was the most important species in cluster 5 and occurred in all 6 of the plots. Cluster 6 was the second most diverse cluster, including 31 species and 16 plots: *Spartina bakeri* had the highest importance value (IV=0.86) followed by *Kosteletzkya pentacarpos* (L.) Ledeb. (0.14) and *Telmatoblechnum serrulatum* (0.09). Thirty-four species were identified in cluster 7, seven species had importance values over 0.10, and all importance values were less than 0.25. *Euthamia weakleyi* Nesom had the highest importance value (0.22). In cluster 8, *P. vaginatum* had the highest importance value (0.93) and occurred in all 7 of the plots. Fifteen species occurred in cluster 8. Finally, cluster 9 included 2 plots and four species. *Cladium jamaicense* Crantz was the most important (1.01) followed by *Cyclosorus interruptus* (Willd.) H. Ito (0.50). Other than cluster 2 and 7 the most important species occurred in all plots and had an importance value ranging from 0.5 to 0.82 higher than the second most important species.

Environmental Variables by Cluster.—Environmental variables of each cluster are displayed in Figure 4. Cluster 4 had the highest average elevation at 2.65 ± 0.19 m, followed by cluster 5, with an average of 2.54 ± 0.35 m. Cluster 8 had the lowest average elevation of 1.92 ± 0.30 m. Cluster 4 and 5 had the highest average canopy closure with 21.27 ± 19.2 and 67.33 ± 28.81, respectively. In general, most plots within the other clusters had little to no canopy closure (Fig. 4).

All clusters had an average electric conductivity over 4 ds/m. Cluster 5 had the lowest average (4.66 ± 2.63 ds/m) and cluster 2 had the highest average (64.54 ± 22.64 ds/m). Cluster 3 was the second most saline with an average of 21.52 ± 13.25 ds/m. Boxplots in Figure 4 display the range of electric conductivity across

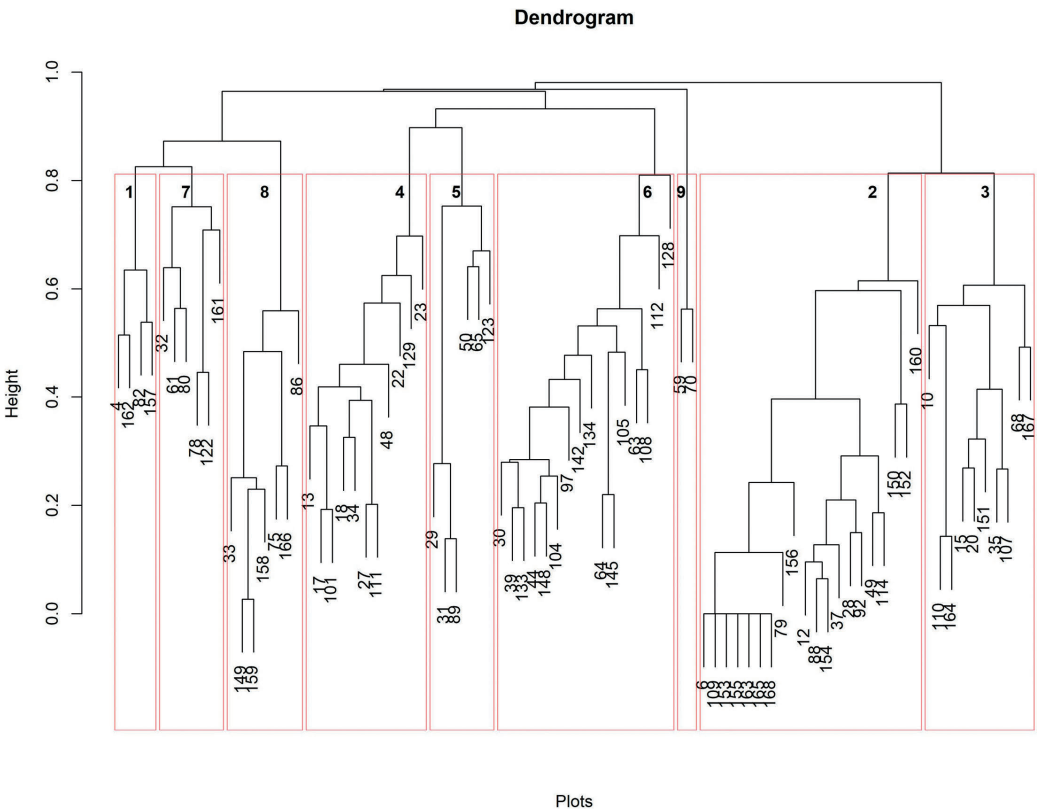

Fig. 3. Dendrogram of agglomerative hierarchical clustering with average linkage method. The y axis is the height or dissimilarity across plots. Nine optimum clusters were identified at a height of 0.809. Clusters are identified with red boxes and labeled: 1. *Fimbristylis castanea*, 2. Bare ground & *Sesuvium portulacastrum*, 3. *Sporobolus virginicus*, 4. *Juncus roemerianus*, 5. *Telmatoblechnum serrulatum*, 6. *Spartina bakeri*, 7. *Euthamia weakleyi*, 8. *Paspalum vaginatum*, and 9. *Cladium jamaicense*.

clusters. Cluster 2 had an average pH of 7.22 ± 0.86 and ranged from acidic (5.22) to alkaline (8.24). All other clusters had circumneutral to acidic pH. Cluster 5 had the lowest average pH of 4.1 ± 0.52.

Total carbon and total nitrogen have a strong linear positive correlation and display similar summary statistics by cluster ($r^2 = 0.99$). Both cluster 9 and 6 had the highest carbon (26.51%, 17.84%) and nitrogen (1.43%, 0.93%) by weight. Cluster 6 had more variation in the total carbon and nitrogen than other clusters. Generally, all other clusters had less than 10% carbon and less than 0.5% nitrogen. The soil in clusters 1, 2, 3, 5, 7, and 8 were mineral. In cluster 4 all but 1 plot was mineral. Eleven of the 16 plots in cluster 6 were organic and 5 plots were mineral. Both plots in cluster 9 were organic soil material. Representative photographs of the landscape and selected clusters are displayed in Figure 5.

Wetland Hydrology.—The hydrologic regime ranges across the site depending on elevation. Well one was installed at the edge of the salt barren at an elevation of 2.2 m and well two was installed adjacent to a *S. bakeri* slough at an elevation of 1.98 m (Fig. 2). At well one, the soil was seasonally saturated, to intermittently flooded (3 cm) for no more than a few days without a clear seasonal pattern. Generally, well two was temporarily to seasonally flooded up to 18 cm during the growing season and the water level was generally below the surface during the dry season. Stain lines were observed 90 to 130 cm above the ground surface across the site following Hurricane Irma in September 2017. Hurricane Ian (August 2022) caused greater depths, inundating the well risers (1.5 m).

TABLE 1. Relative abundance, relative frequency, and importance value, for the top 5 species by cluster. Importance value is the sum of the relative abundance and relative frequency.

Cluster	Species	Relative Abundance	Relative Frequency	Importance Value
1	*Frimbristylis castanea*	0.694	0.118	0.811
	Phyla nodiflora	0.091	0.059	0.149
	Centella erecta	0.016	0.059	0.074
	Mikania cordifolia	0.008	0.059	0.067
	Pluchea odorata (L.) Cass.	0.008	0.059	0.067
2	Bare ground	0.718	0.4	1.118
	Sesuvium portulacastrum	0.141	0.22	0.361
	Salicornia ambigua	0.069	0.12	0.189
	Sporobolus virginicus	0.050	0.12	0.170
	Distichlis spicata	0.015	0.06	0.075
3	*Sporobolus virginicus*	0.656	0.172	0.830
	Frimbristylis castanea	0.042	0.069	0.111
	Sesuvium portulacastrum	0.023	0.086	0.109
	Distichlis spicata	0.038	0.069	0.107
	Salicornia ambigua	0.070	0.034	0.104
4	*Juncus roemerianus*	0.721	0.212	0.932
	Anchistea virginica	0.068	0.038	0.106
	Telmatoblechnum serrulatum	0.028	0.077	0.105
	Sporobolus virginicus	0.025	0.058	0.083
	Acrostichum aureum	0.022	0.058	0.080
5	*Telmatoblechnum serrulatum*	0.486	0.222	0.708
	Andropogon glomeratus	0.157	0.037	0.194
	Dichanthelium strigosum var. *glabrescens*	0.075	0.111	0.186
	Euthamia weakleyi	0.036	0.111	0.147
	Panicum virgatum L.	0.060	0.037	0.097
6	*Spartina bakeri*	0.645	0.219	0.864
	Kosteletzkya pentacarpos	0.045	0.096	0.141
	Telmatoblechnum serrulatum	0.043	0.055	0.100
	Teucrium canadense L.	0.021	0.055	0.076
	Bacopa monnieri (L.) Pennell	0.038	0.027	0.065
7	*Euthamia weakleyi*	0.144	0.077	0.221
	Centella erecta	0.128	0.077	0.205
	Andropogon cretaceus	0.098	0.046	0.145
	Dichanthelium dichotomum	0.077	0.062	0.138
	Frimbristylis castanea	0.065	0.046	0.111
8	*Paspalum vaginatum*	0.717	0.219	0.936
	Mikania cordifolia	0.091	0.188	0.279
	Centella erecta	0.082	0.063	0.145
	Dichanthelium dichotomum	0.048	0.094	0.142
	Setaria parviflora	0.012	0.125	0.137
9	*Cladium jamaicense*	0.612	0.4	1.012
	Cyclosorus interruptus	0.306	0.2	0.506
	Acrostichum aureum	0.051	0.2	0.251
	Frimbristylis castanea	0.031	0.2	0.231

Results of Constrained Correspondence Analysis.—The CCA included ECe, pH, elevation, total carbon, canopy closure, soil color, and soil type (mineral or organic). The constrained variation accounted for 22.5% of the total variation. Figure 6 displays the tri-plot of the CCA, axis one accounted for 30.06% of the constrained variation and axis two accounted for 20.42% of the constrained variation. Permutation test of the CCA residuals indicated that the overall model is significant at $p < 0.001$. The F-statistic of the entire model is 3.06 and the probability that random values are greater than the observed statistic is 0.1%. A permutation test

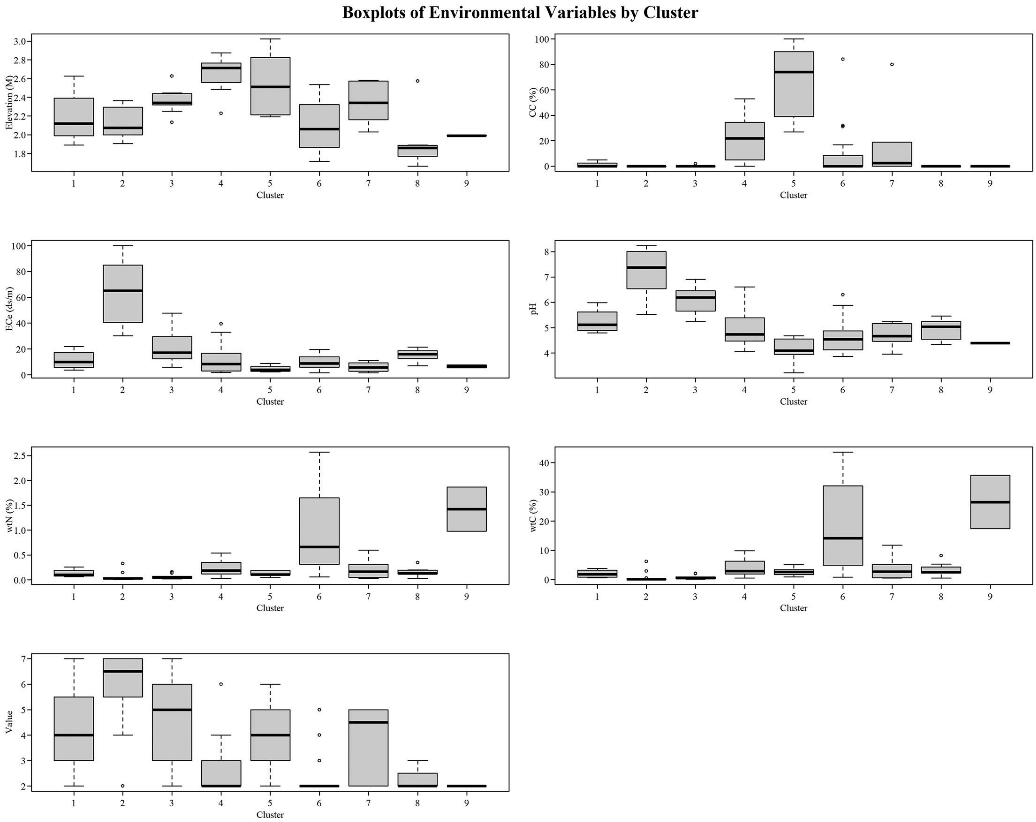

Fig. 4. Boxplots of environmental variables for the nine optimum clusters. CC is canopy closure, ECe is the electric conductivity of a saturated paste, wtN is total nitrogen by weight, and wtC is total carbon by weight.

of the axes indicated that CCA axis 1 through 5 were also significant. Table 2 lists the permutation test results for each environmental variable. The variation inflation factor for total carbon and total nitrogen was greater than 10 and total nitrogen was removed from the CCA.

Electric conductivity, pH, and soil value are all positively correlated (Fig. 6). Increasing total carbon was negatively correlated to increasing ECe, pH, and value but, total carbon had no relationship with increasing elevation. Canopy closure and total carbon have a positive correlation. Elevation and canopy closure are positively related, but canopy closure was negatively correlated with pH and ECe. Elevation was orthogonal to soil value, total carbon, ECe, and pH indicating no relationship.

The mineral soil type is centrally located in the plot and doesn't have a strong correlation with either axis. Organic soil type is in the top right side of the plot suggesting an association with increasing total carbon. Plots in cluster 2 and 3 are positioned on the left-hand side of Figure 6 and are associated with increasing ECe, pH, and value. These plots are also associated with decreasing amounts of total carbon. Cluster 1 and clusters 4 through 9 are on the right side of the plot and associated with decreasing pH, ECe, and soil value. Plots in cluster 4 and 5 are positioned on the bottom right of the plot and are associated with increasing elevation and canopy closure. Plots within cluster 6 are primarily associated with increasing carbon and declining elevation and are positioned on the top half of Figure 6. Many of the plots in cluster 6 are positioned closely to organic soil type. Clusters 8 and 1 are positioned along the top half of Figure 6 and are associated with declining elevation and canopy closure. Cluster 9 plots are located closely to and associated with the organic soil type.

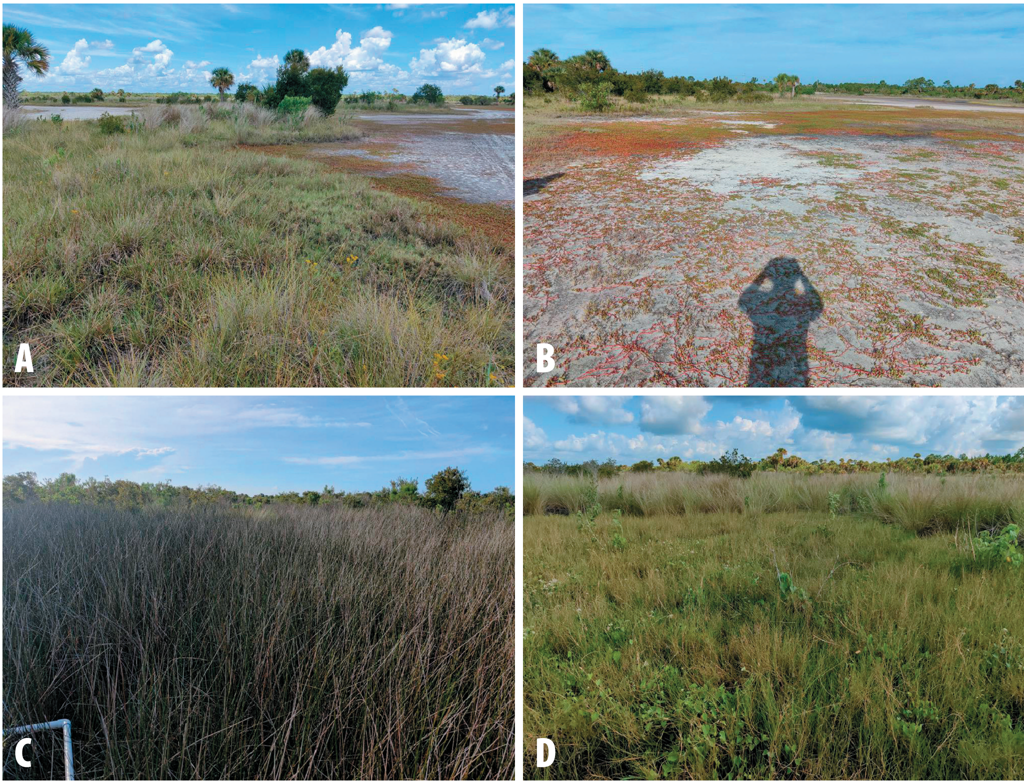

Fig. 5. Representative photos of inland saline wetlands of the upper SJRB. Part A displays *Fimbristylis castanea* in the left foreground, *Sporobolus virginicus* in the central foreground, in the background are a mosaic of bare ground and *Sesuvium portulacastrum* and discrete barrens. Part B displays a barren with a mosaic of *S. portulacastrum*. In the background *S. virginicus* makes up the groundcover. Part C displays an area dominated by *Juncus roemerianus*, and part D displays *Paspalum vaginatum* and *Mikania cordifolia* in the foreground and *Spartina bakeri* in the background.

Relationship between Species and Environmental Variables.—Halophytes including *Sesuvium portulacastrum*, *Salicornia ambigua*, *Sporobolus virginicus*, *Distichlis spicata* (L.) Greene, *Salicornia bigelovii* Torr., *Lycium carolinianum* Walter, and *Agalinis maritima* (Raf.) Raf. var. *grandiflora* (Benth.) Pennell are positioned along CCA1 and are associated with increasing pH, ECe, and soil value (Flowers & Colmer 2008). Bare ground is located along this increasing pH, ECe, and value gradient. Similarly, these species are negatively associated with increasing total carbon.

The highest ECe measured was 100.1 ds/m and vegetation was not present. *Distichlis spicata*, *Salicornia ambigua*, *Sesuvium portulacastrum*, and *Sporobolus virginicus* all occurred in very strongly saline soils and were observed in soils greater than 75 ds/m. *Acrostichum aureum* L., *Juncus roemerianus*, and *Paspalum vaginatum*, occurred in areas where ECe exceeded 25 ds/m. Additional species occurred beyond 12.25 ds/m such as *Centella erecta* (L.f.) Fernald, *Dichanthelium dichotomum* (L.) Gould, *Fimbristylis castanea*, *Kosteletzkya pentacarpos*, *Mikania cordifolia* (L.) Willd., *Phyla nodiflora* (L.) Greene, *Spartina bakeri*, and *Setaria parviflora* (Poir.) Kerguélen, *Andropogon cretaceus* Weakley & Schori, *Andropogon glomeratus* (Walter) Britton, Sterns, & Poppenb., *Cyclosorus interruptus, Cladium jamaicense, Dichanthelium strigosum* (Muhl. ex Elliott) Freckmann var. *glabrescens* (Griseb.) Freckmann, *Euthamia weakleyi*, and *Telmatoblechnum serrulatum*, did not occur beyond 12.25 ds/m. *Telmatoblechnum serrulatum* primarily occurred in plots with salinity less than 4 ds/m. Of the species with the highest importance values only *Anchistea virginica* (L.) C. Presl did not occur in plots above 4.0 ds/m (maximum ECe 2.9 ds/m). Three hundred and seventy-two species observations were made in

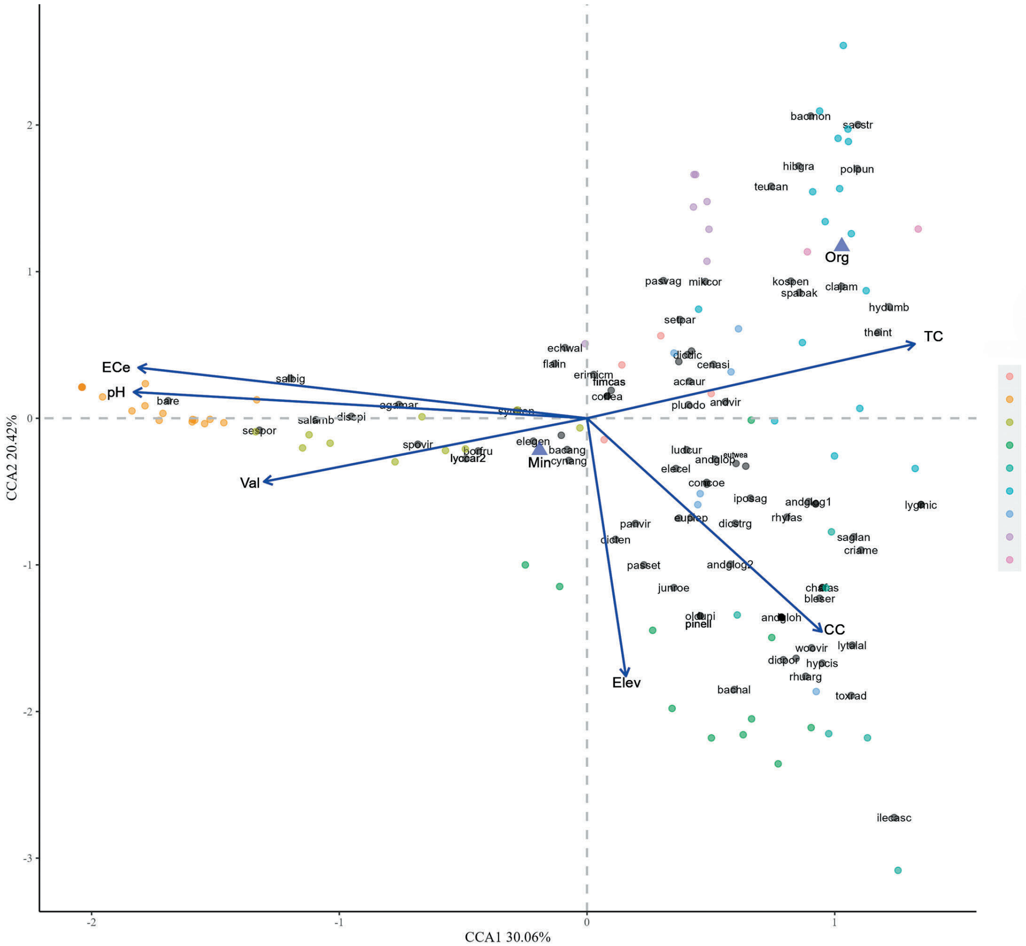

Fig. 6. Tri-plot of constrained correspondence analysis. CCA1 explains 30.06% of the constrained variation and the y axis is CCA2 explaining 20.42% of the constrained variation. Grey circles are species labeled by acronym, colored circles are plots categorized by the nine optimum clusters, continuous environmental variables are blue vectors, and categorical environmental variables are blue triangles. Elev. is elevation, CC is canopy closure, TC is total carbon, Org is organic soil type, Min is mineral soil type, ECe is electric conductivity of a saturated soil paste, and Val is soil value.

the 82 sampling quadrats and 86% occurred at or below an ECe of 21.8 ds/m, 13.9% occurred above 21.8 ds/m, and 7.5% occurred below 2 ds/m. No species occurred in plots with ECe greater than 88.1 ds/m.

Species along the right-hand side of Figure 6 are associated with increasing carbon such as *Cyclosorus interruptus*, *Cladium jamaicense*, and *Hydrocotyle umbellata* L. These same species in addition to *Kosteletzkya pentacarpos* and *Spartina bakeri* are clustered around soil type organic. Species located on the bottom right of Figure 6 are associated with increasing elevation like *Baccharis halimifolia* L., *Juncus roemerianus*, and *Pinus elliottii* Engel. Species associated with increasing canopy closure are found on the bottom right of Figure 6 such as, *Anchistea virginica*, *Ilex cassine* L., and *Telmatoblechnum serrulatum*. Conversely, those located on the top half and close to CCA2 are associated with declining elevation and canopy closure for instance, *Echinochloa walteri* (Pursh) Heller, *Flaveria linearis* Lag., *Mikania cordifolia*, and *Paspalum vaginatum*.

DISCUSSION

Inland saline wetlands of the upper SJRB are dominated predominantly by salt tolerant graminoids and forbs and canopy closure was limited. Nine optimum clusters were suggested based on the ecological resemblance

TABLE 2. Permutation results of the CCA model for environmental variables.

	Df	ChiSquare	F	Pr(>F)
ECe	1	0.2387	1.8582	0.001***
wtC	1	0.2057	1.6011	0.016*
Elevation	1	0.3723	2.8979	0.001***
pH	1	0.1400	1.0895	0.317
CC	1	0.3108	2.4191	0.001***
Value	1	0.2568	1.9983	0.001***
Type	1	0.2484	1.9332	0.002**
Residual	74	9.5077		

Note: *** denotes a test-statistic significant at a $p < 0.001$ and ** denotes a test-statistic significant at $p < 0.01$. * denotes a test-statistic significant at $p < 0.05$

of species composition. Generally, vegetation assemblages have a single prominent important species with good fidelity. The most important species typically occurred in all plots of a duster and were absent or infrequent in other clusters suggesting the nine optimum clusters are floristically appropriate (Table 2). Clusters are generally discrete with sharp boundaries (Fig. 2).

Electric conductivity, total carbon, soil value, soil type, elevation, and canopy closure are important environmental variables contributing to the distribution of species across the site (Table 2). The CCA model permutation test suggests the null hypothesis (that there is no relationship between environmental variables and species distribution) can be rejected. Electric conductivity is an important environmental variable of inland saline wetlands globally contributing to the distribution of species (Pan 1998; Ungar 1998; Eallonardo & Leopold 2014). Onsite soils are predominantly saline with three plots having non saline soils (ECe < 2ds/m). The distribution and abundance of most species in this study are limited by high electric conductivity and tend to occur in areas that are not strongly saline (i.e., less than 21 ds/m ECe) and only the most salt tolerant species tend to occur beyond an ECe of 21 ds/m.

Elevation was a significant environmental gradient onsite influencing the distribution of species (Table 2). The importance of elevation was consistent with previous research (Burchill & Kenkel 1991; Pan et al. 1998). However, there was no linear relationship between elevation and ECe. Relationships between elevation and ECe have been observed elsewhere. Burchilll and Kenkell (1991) found that the lowest relative elevations had the highest salinity and Grunsta and Van Auken (2007) found the highest areas were the most saline.

Canopy closure was an important explanatory variable of ground cover composition and species distribution (Table 2). Increased shrub and canopy cover can be an indicator of a shade tolerant groundcover or the result of altered ecosystem process. Anthropogenic disruption of the fire and hydrologic regime can change community structure and composition of natural communities resulting in increased shrub and canopy cover (Noss 2018). For example, increases in *Salix caroliniana* Michx. in the USJRB are attributed to altered hydrology and fire regimes (Quintana-Ascencio et al. 2013). Some areas of the inland saline wetland landscape have a moderate canopy closure which may indicate a shift in hydrologic and fire regimes across the site.

Total soil carbon, soil value, and soil type were all significant environmental variables in the CCA permutation tests (Table 2). The importance of these variables may suggest the importance of soil organic material and prolonged inundation on the distribution of species. However, total carbon includes both organic and inorganic fractions and Florida soils can contain influential amounts of inorganic carbon from soil parent material, either marine or from the formation of marl. Mineral soils neither contained shell fragments nor marl material (fine texture), were textured as sand, and visibly determined to be quartz based on transparency of sand grains with high soil value. Furthermore, quartz marine parent material is typical of the peninsula (Watts & Collins 2008). Other research found that soil organic matter was important in inland saline wetlands, with the highest saline areas having the least amount of soil organic matter (Burchill & Kenkel 1991) but not every study measured soil organic matter (Pan 1998; Piernik 2003; Eallonardo & Leopold 2014).

Soil pH is a master soil variable influencing many soil properties (Weil & Brady 2017). However, results indicate it was not a significant environmental variable (Table 2). Early work indicated that pH was not important (Ungar 1968; Ungar 1970), however, others found that pH was important and significantly different across community types (Burchill & Kenkel 1990; Pan et al. 1998; Piernick 2003; Eallonardo & Leopold 2014). Given the high pH and ECe of the salt pans further work could focus on cation concentration and measurements of sodium adsorption ratio. Previous work indicated sodium chloride as the primary salt influencing the salinity of groundwater in the upper SJRB but the relative proportions of salts in the soils is not known (Belaineh et al. 2011). Furthermore, others found that the ratio of calcium to sodium was an important factor in plant distribution (Piernick 2003).

Only two of the 7 plots with 100% bare ground had ECe higher (88.1 ds/m) than ECe observed in plots where halophytes including *Distichlis spicata, Sesuvium portulacastrum*, *Salicornia ambigua*, *Sporobolus virginicus*, and *Salicornia bigelovii* were present. Moreover, total carbon, total nitrogen, pH, and elevation of the 100% bare ground plots overlapped with plots containing halophytes, suggesting that an unmeasured environmental variable, interaction of variables, seasonal changes of ECe, species biology, or disturbance, limits species distribution in the barrens. A limitation of this study was a lack of quantitative hydrology or soil moisture at plots. Other research found that soil moisture was an important factor in determining species distribution of inland saline wetlands (Ungar 1973; Pan 1998; Ungar 1998). Eallonardo and Leopold (2014) found that flood duration and water table elevation were significantly different across inland saline wetland communities and the higher saline environments were related to increased flood duration or a shallow water table depth. Similarly Pan et al. (1998) found that concave basins had higher soil moisture and higher salinity. Unauthorized off road vehicle use was observed throughout the salt pans and halophyte mortality observed following the prolonged deep inundation of Hurricane Ian in 2022. Further work could be carried out to understand the impact of flooding and disturbance events on floristic composition and community structure. Moreover, increased salinity inhibits germination and reduces growth rates of halophytes (Martinez et al. 1992; Lokhande et al. 2011). Further work could evaluate how seasonal fluctuation of ECe impacts germination and growth rates of dominate halophytes onsite.

The CCA tri-plot (Fig. 6) displays many plots and species in the top center that are not positively associated with an environmental variable, however, these species do have a negative association with increasing elevation. Many of the species have adaptations to anerobic environments and perhaps some component of hydrologic regime (soil moisture, depth to water table, flooding frequency or duration) could explain the variation. *Juncus roemerianus* is a typical high marsh species in coastal environments and was also at high elevations onsite and further research could be conducted to see if similar competitive exclusion occurs between high marsh and low marsh species in the inland saline wetlands (Bertness & Ellison 1987; Pennings et al. 2005).

Inland saline wetlands of the upper SJRB are dominated by halophytic and heliophytic forbs, grasses, sedges, and rushes with most soils ranging from moderately to very strongly saline. The distribution of vegetation and plant species was related to environmental gradients of ECe, soil value, elevation, total carbon and canopy closure. However, unexplained variation remains, and further work should be conducted to determine the influence of additional environmental variables, soil moisture, biological interactions, and the mechanistic relationship between elevation, salinity, and hydrology.

ACKNOWLEDGMENTS

I thank my graduate chair Mark Clark and committee members Laura Reynolds, and Matt Cohen for edits, comments, and guidance. Chelsea Piner, James Weber, Jake Lyons, Ginger Soumar, Penny Cople, Dale Dowling, and Mike Dennis assisted with field work and provided initial support, thank you. Thank you, Graham Willimas at the St. Johns River Water Management District for providing access to the site. Thank you, Alan Franck, at the University of Florida Herbarium for assistance with identification and accepting voucher specimens. Additionally, I thank George Rogers and an anonymous reviewer for their reviews of the manuscript.

REFERENCES

Adams, D. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44:445–456.

Alvarez-Rogel, J., J. Martinez-Sanchez, L. Blazquez, & M. Semitiel. 2006. A conceptual model of salt marsh plant distribution in coastal dunes of southeastern Spain. Wetlands 26:703–717.

Austin, M. 2013. Vegetation and environment: discontinuities and continuities. In: E. van der Maarel & J. Franklin, eds. Vegetation ecology second edition. Wiley-Blackwell, UK. Pp. 271–107.

Belaineh, G., J. Stewart, P. Sucsy, L. Motz, K. Park, S. Rouhani, & M. Cullum. 2011. Groundwater hydrology. In: E. Lowe, L. Battoe, H. Wilkening, M. Cullum, & T. Bartol, eds. St. Johns. River water supply impact study technical publication SJ2012-1. St. Johns River Water Management District, Florida. Pp. 4-1 – 2-100.

Berntess, M. & A. Ellison. 1987. Determinants of patterns in a New England salt marsh plant community. Ecol. Monogr. 57:129–147.

Burchill, C. & N. Kenkel. 1991. Vegetation-environmental relationships of an inland boreal salt pan. Canad. J. Bot. 69:722–732.

Bui, E. 2013. Soil salinity: a neglected factor in plant ecology and biogeography. J. Arid Environm. 92:14–25. doi.org/10.1016/j.jaridenv.2012.12.014.

Eallonardo, A. & D. Leopold. 2014. Inland salt marshes of the northeastern United States: Stress, disturbance and compositional stability. Wetlands 34:155–166. https://doi.org/10.1007/s13157-013-0493-y.

Florida Natural Areas Inventory. 2006. Natural community descriptions to accompany a vegetation map of Salt Lake Wildlife Management Area, unpublished report to the Florida Fish and Wildlife Conservation Commission. Florida Natural Areas Inventory, Tallahassee, Florida, U.S.A.

Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida. Florida Natural Areas Inventory, Tallahassee, Florida, U.S.A.

Flowers, T. & T. Colmer. 2008. Salinity tolerance in halophytes. New Phytol. 179:945-963. https://doi.org/10.1111/j.1469-8137.2008.02531.x.

Grunstra, M. & O. Van Auken. 2007. Using GIS to display complex soil salinity patterns in an inland salt marsh. In: D. Sarkar, R. Datta & R. Hannigan, eds. Developments in Environmental Science Volume 5 Elsevier, https://doi.org/10.1016/S1474-8177(07)05019-X.

Hanlon, E. 2015. Soil pH and electrical conductivity: A county extension soil laboratory manual, UF IFAS extension circular 1081. UF IFAS, Gainesville, Florida, U.S.A.

Kinser, P., S. Fox, & A. Ceric. 2012. Description of river segments used in the WSIS study. In: E. Lowe, L. Battoe, H. Wilkening, M. Cullum, & T. Bartol, eds. St. Johns. River Water Supply Impact Study Technical Publication SJ2012-1. Florida. Pp.2-1 – 2-35.

Legendre, P., J. Oksanen, & C. ter Braak. 2011. Testing the significance of canonical axes in redundancy analysis. Meth. Ecol. & Evol. 2:269–277. https://doi.org/10.1111/j.2041-210X.2010.00078.x.

Ljevnaic-Masic, B., D. Dzigurski, L. Nikolic, M. Brdar-Jorkanovic, R. Cabilovski, V. Ciric, & A. Petrovic. 2020. Assessment of the habitat conditions of a rare and endangered inland saline wetland community with *Bolboschoenus maritimus* (L.) Palla dominance in southeastern Europe: The effects of physical-chemical water and soil properties. Wetlands Ecol. Managem. https://doi.org/10.1007/s11273-020-09721-4.

Lokhande, V., T. Nikam, V. Patade, M. Ahire, & P. Suprasanna. 2011. Effects of optimal and supra-optimal salinity stress on antioxidative defense, osmolytes and in vitro growth responses in *Sesuvium portulacastrum* L. J. Pl. Biotechnol. 104:41–49. https://doi.org/10.1007/s11240-010-9802-9.

Lowe, E. 1983. Distribution and structure of floodplain plant communities in the upper basin of the St. Johns. River Florida. St. Johns River Water Management District technical publication SJ83-8. Florida, Pp. 1–74.

Lowe, E. 1986. The relationship between hydrology and vegetational pattern within the floodplain marsh of a subtropical Florida lake. Florida Sci. 49:213–233.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, & K. Hornik. 2021. Cluster: Cluster analysis basics and extensions. R package version 2.1.2.

Martinez, M., T. Valverde, & P. Moreno-Casasola. 1992. Germination response to temperature, salinity, light and depth of sowing of ten tropical dune species. Oecologia 92:343–353.

Mitsch, W. & J. Gosselink. 2007. Wetlands. John Wiley & Sons, New Jersey, U.S.A.

Montague, C. & R. Wiegert. 1990. Salt marshes. In: R. Myers & J. Ewel, eds. Ecosystems of Florida. University of Central Florida Press, Orlando Florida, U.S.A. Pp. 481–516.

Noss, R. 2018. Fire ecology of Florida and the southeastern coastal plain. University Press of Florida, Gainesville, U.S.A.

Odum, W. 1988. Comparative ecology of tidal freshwater and salt marshes. Ann. Rev. Ecol. Syst. 19:147–176.

Oksanen, J., F. Guillaume, F. Blanchet, M. Friendly, R. Kindt, R. Legendre, D. McGlinn, P. Minchin, R. O'Hara, G. Lmpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, & H. Wagner. 2020. Vegan: Community ecology package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan.

Palmer, M. n.d. Environmental variables in constrained ordination (e.g. CCA, RDA, DCCA). Oklahoma State University. https://ordination.okstate.edu/envvar.htm. Accessed March 2024.

Pan, D., A. Bouchard, P. Legendre, & G. Domon. 1998. Influence of edaphic factors on the spatial structure of inland halophytic communities: A case study in China. J. Veg. Sci. 9:797–804.

Peet, R. & D. Roberts. 2013. Classification of natural and semi-natural vegetation. In: E. van der Maarel & J. Franklin, eds. Vegetation Ecology Second Edition. Wiley-Blackwell, UK. Pp. 28–60.

Pennings, S., M. Grant, & M. Bertness. 2005. Plant zonation in low-latitude salt marshes: Disentangling the roles of flooding, salinity and competition. J. Ecol. 93:159–167. https://doi.org/10.1111/j.1365-2745.2004.00959.x.

Piernik, A. 2003. Inland halophilous vegetation as indicators of soil salinity. Basic Appl. Ecol. 4:525–536. https://doi.org/10.1078/1439-1791-00154.

Quintana-Ascencio, P., J. Fauth, C. Morales, K. Ponzio, D. Hall, & K. Snyder. 2013. Taming the Beast: Managing hydrology to control willow (*Salix caroliniana*) seedlings and cutting. Restorat. Ecol. 21:636–647 https://doi.org/10.1111/j.1526-100X.2012.00940.x.

Sieben, E., N. Collins, H. Mtchali, & C. Venter. 2016. The vegetation of inland wetlands with salt-tolerant vegetation in South Africa: Description, classification, and explanatory environmental factors. S. African J. Bot. 104:199–207.

Toth, D. 1988. Saltwater intrusion in coastal areas of Volusia, Brevard and Indian River counties St. Johns River Water Management District Technical Publication SJ88-1. St. Johns River Water Management District, Florida, U.S.A. Pp. 1–191.

Tug, G., O. Ketenoglu, & A. Bilgin. 2012. The relationships between plant zonation and edaphic factors in halophytic vegetation around Lake Tuz, central Anatolia Turkey. Rendiconti Lince Scienze Fisiche e Naturali 23:355–363. https://doi.org/10.1007/s12210-012-0197-x.

Ungar, I. 1967. Vegetation-soil relationships on saline soils in northern Kansas. Amer. Midl. Naturalist 78:98–120.

Ungar, I. 1968. Species-soil relationships on the great salt plains of northern Oklahoma. Amer. Midl. Naturalist 80: 392–406.

Ungar, I. 1970. Species-soil relationships on sulfate dominated soils of South Dakota. Amer. Midl. Naturalist 83: 343–357.

Ungar, I. 1973. Salinity tolerance of inland halophytic vegetation of North America. Bull. Soc. Bot. France 120:217–222. https://doi.org/10.1080/00378941.1973.10839158.

Ungar, I., D. Benner, & D. McGraw. 1979. The distribution and growth of *Salicornia europaea* on an inland salt pan. Ecology 60:329–336.

Ungar, I. 1998. Are biotic factors significantly influencing the distribution of halophytes in saline habitats? Bot. Rev. 64:179–199.

United States Salinity Laboratory Staff. 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook No. 60. United States Department of Agriculture, Washington, DC, U.S.A.

Vasilas, L., W. Hurt, & J.F. Berkowitz, eds. 2018. Field indicators of hydric soils in the United States, Version 8.2. United States Department of Agriculture, Natural Resources Conservation Service, in cooperation with the National Technical Committee for Hydric Soils.

Watts, F. & M. Collins. 2008. Soils of Florida. Soil Science Society of America, Wisconsin, U.S.A.

Weil, R. & N. Brady. 2017. The nature and properties of soils. Peason, London, UK.

Whittaker, R. 1967. Gradient analysis of vegetation. Bio. Rev. 28:1–239.

Wu, M., Y. Hu, P. Wu, P. He, N. He, B. Zhang, & S. Zhang. 2020. Does soil pore water salinity or elevation influence vegetation spatial patterns along coasts? A case study of restored coastal wetlands in Nanhui, Shanghai. Wetlands 40:2691–2700. https://doi.org/10.1007/s13157-020-01366-6.