

Hydrologic exchanges and baldcypress water use on deltaic hummocks, Louisiana, USA

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ABSTRACT

Coastal forested hummocks support clusters of trees in the saltwater–freshwater transition zone. To examine how hummocks support trees in mesohaline sites that are beyond physiological limits of the trees, we used salinity and stable isotopes (^2H and ^{18}O) of water as tracers to understand water fluxes in hummocks and uptake by baldcypress (*Taxodium distichum* (L.) Rich.), which is the most abundant tree species in coastal freshwater forests of the southeastern U.S. Hummocks were always partially submerged and were completely submerged 1 to 8% of the time during the two studied growing seasons, in association with high water in the estuary. Salinity, $\delta^{18}\text{O}$, and $\delta^2\text{H}$ varied more in the shallow open water than in groundwater. Surface water and shallow groundwater were similar to throughfall in isotopic composition, which suggested dominance by rainfall. Salinity of groundwater in hummocks increased with depth, was higher than in swales, and fluctuated little over time. Isotopic composition of xylem water in baldcypress was similar to the vadose zone and unlike other measured sources, indicating that trees preferentially use unsaturated hummock tops as refugia from higher salinity and saturated soil in swales and the lower portions of hummocks. Sustained upward gradients of salinity from groundwater to surface water and vadose water, and low variation in groundwater salinity and isotopic composition, suggested long residence time, limited exchange with surface water, and that the shallow subsurface of hummocks is characterized by episodic salinization and slow dilution. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS tidal wetland; coastal swamp; *Taxodium distichum*; saline flooding; water use; microtopography; sea-level rise

Received 28 July 2015; Revised 5 February 2016; Accepted 21 March 2016

INTRODUCTION

Forested deltaic swamps at the transition of forest–marsh mosaics are often characterized by microtopographic variation in the form of hummock-and-swale topography (HST). The tops of hummocks are less than 0.5 m above mean water level, formed mainly by organic accretion, and typically vegetated (Duberstein and Conner, 2009). In HST, trees are generally restricted to hummocks (Rheinhardt and Hershner, 1992), or at least preferentially established on hummocks (Huenneke and Sharitz, 1986; Light *et al.*, 2007), especially when inundation of swales is for more than half of the growing season (Day *et al.*, 2007; Duberstein and Conner, 2009).

The elevation of hummocks above mean water level generally promotes tree survival and regeneration by providing refuge from hypoxia and flood stress (Dommain *et al.*, 2010; Courtwright and Findlay, 2011). However,

flood stress does not limit tree growth in some forested HST (Duberstein *et al.*, 2013); other factors such as erosion in swales (Day *et al.*, 2007) or seedling recruitment (Huenneke and Sharitz, 1986; Peterson and Baldwin, 2004) appear to control plant distribution in some cases. Mechanisms that control plant growth and distribution vary depending on whether HST is formed in a relatively stable landform, such as peat bogs (Malmer and Wallén, 1999) or along stable coasts (Rheinhardt and Hershner, 1992), as opposed to their formation in submerging landforms such as rapidly subsiding deltas (DeLaune *et al.*, 1994).

In many coastal wetlands, salinity is important in structuring vegetation communities in general, but the interaction of salinity and flood stressors in controlling plant communities in HST is not well understood. Salinity has been found to favor formation of HST in at least one location (Stribling *et al.*, 2007), but that phenomenon has not been described in forested wetlands. Instead, HST is more often lost in strongly tidal freshwater forested wetlands as mean salinity increases and biogeochemical processes are altered, as has been observed along the Atlantic coast of the US (Noe *et al.*, 2013).

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In the lower delta of the Mississippi River, the forest–marsh boundary is controlled by flooding and salinity (Allen *et al.*, 1996; Krauss *et al.*, 2009; Day *et al.*, 2012), and recent rapid subsidence has caused widespread increased flooding and saltwater intrusion (Boesch *et al.*, 1994). In forest–marsh ecotones with HST, trees often exclusively occupy hummock tops. However, it is not clear whether hummocks provide refuge from flood stress, salinity stress, or both. For example, in one forested wetland in South Carolina, USA, the highest rate of baldcypress transpiration was when water level was sufficient to just submerge most hummocks, suggesting that hummock heights may be a consequence of trees being better adapted to specific flood regimes (Duberstein *et al.*, 2013). That study was conducted on a freshwater site, so salinity influences were not considered.

Hydrologic and salinity regimes of wetlands are well known to control distributions and growth of plants at small scales (Mitsch and Gosselink, 2007). Hummocks are more suitable for tree growth generally, but the reasons for this remain unclear in many places, in part because of uncertainty about hydrologic and salinity regimes. For example, two alternative regimes may dominate hummock hydrology and salinity: when evapotranspiration (ET) exceeds precipitation, net flux of swamp water likely increases salinity in hummocks because of evaporative concentration (e.g. Bauer-Gottwein *et al.*, 2008; Gardner, 2009), but when precipitation exceeds ET, subsurface salinity likely decreases because of flushing by net flux out of hummocks. In addition, temporal variability in hydrologic and salinity budgets may overwhelm mean conditions to define limiting conditions for plant growth. It is important, therefore, to hydrological functioning of HST to understand the role of hummocks in vegetative communities.

Baldcypress (*Taxodium distichum* (L.) Rich.) is the most prevalent tree species in coastal forested wetlands of the southeastern U.S. that receive both tidal and riverine input (Conner and Day, 1988; Allen *et al.*, 1996). Adaptations to flooding enable baldcypress to tolerate frequent or extended inundation (Allen *et al.*, 1996; Oren *et al.*, 1999; Krauss *et al.*, 2009, 2012), although long-term, stagnant flooding is a stressor (Pezeshki, 1991; Pezeshki *et al.*, 1996; Anderson and Pezeshki, 2001).

Aside from flooding, coastal baldcypress often experiences stress from salinity. While somewhat tolerant of low salinity, salinity reduces hydraulic efficiency (Stiller, 2009) and regeneration success of baldcypress (Pezeshki *et al.*, 1996; Krauss *et al.*, 1999, 2009). Baldcypress seedlings are known to tolerate only low salinity (up to 4 ppt in short-term experimental culture, and even less under field settings) (Pezeshki, 1990; Allen *et al.*, 1994, 1997; Conner, 1994; Krauss *et al.*, 1999), but studies of responses to salinity by mature trees are limited (but see Krauss and

Duberstein, 2010). Clusters of baldcypress and its associates may be adapted to tidal flooded wetlands even with occasional episodic saltwater intrusion events (Day *et al.*, 2007; Krauss and Duberstein, 2010). In coastal areas the spatial distribution of baldcypress generally follows variations in mean soil pore water salinity, with forests generally transitioning to marsh as soil salinity exceeds 2 ppt chronically (Krauss *et al.*, 2007), but these same forests are able to survive acute pulses of greater salinity (Conner and Inabinette, 2003).

Furthermore, tree root systems exploit resources depending on availability of advantageous conditions (e.g. White *et al.*, 1985). Baldcypress in coastal wetlands, where they experience multiple stressors and occupy a varying environment, may benefit from systematically occupying favorable soils. Non-halophytes, such as baldcypress, do not have a known mechanism to exclude salt, although exclusion of Na⁺ and Cl[−] from shoot tissue has been linked to intraspecific variation in salt tolerance (Allen *et al.*, 1997). Water source selection to avoid salinity may also occur by selective root occupation of favorable, fresher sites. It remains unclear whether baldcypress can persist in chronically mesohaline, flooded wetlands by enduring unfavorable conditions or through avoidance by using other water sources.

Stable isotopes of water are useful for identifying sources of water to soils (Gat, 1971; Barnes and Allison, 1988) and those used by plants (Roden *et al.*, 2000; Stratton *et al.*, 2000; Dawson *et al.*, 2002; Sekiya and Yano, 2002; Schoonmaker *et al.*, 2007). Isotopes allow identification of mixing, or lack of mixing, in the subsurface (Gazis and Feng, 2004; Brooks *et al.*, 2010), so they are an important tool to identify hydrologic effects of hummock-swale terrain on salinity and flooding variations. Furthermore, while both relative humidity and air temperature influence the fractionation of water in the leaves, fractionation does not occur with water uptake from root to shoot along xylem conduits. Hence, xylem sap is relatively consistent along the path of the tree and reflects the water sources to roots (Washburn and Smith, 1934; Dawson and Ehleringer, 1991, 1993; Walker and Richardson, 1991; Ehleringer and Dawson, 1992; Thorburn *et al.*, 1993). By measuring the isotopic composition of water in the xylem and multiple potential sources of water in the environment, the source of tree water use can be identified.

The first objective of this study was to determine how fluxes of precipitation, groundwater, and surface water affect salinity in hummocks and adjacent swales in the lower Mississippi River Delta. Specifically, we examined whether there is a difference in the salinity and flooding regimes of hummocks as compared to swales, using stable isotope tracers to distinguish water flow paths. Our second objective was to determine the sources of waters available to and used by baldcypress on coastal swamp hummock-

swale topography in an attempt to explain survival in areas where salinity is otherwise too high to explain survival based on known salt tolerances.

METHODS

Study site

This study took place over 18 months in Jean Lafitte National Historical Park and Preserve, between Lake Salvador and Bayou Segnette in the Barataria Basin of the Mississippi River Delta, Louisiana, USA (29.756° N, 90.146° W; Figure 1). Site elevation is less than 0.5 m amsl (above mean sea level; Jiang and Middleton, 2011) near the transition between forested, baldcypress (*T. distichum*) swamp and non-forested marsh and ~100 m from the site characterized previously by Krauss *et al.* (2009). The site is on young, deltaic sediments and subsiding at a rate of approximately 3–5 mm/y (Lane *et al.*, 2006) from compaction of shallow, deltaic deposits (Törnqvist *et al.*, 2008). The Mississippi River is no longer connected to these sites because of leveeing, so there is no active mineral accretion.

The site is characterized by occasional surface hydrologic connection to the Barataria estuary associated with rain events or high tides driven by wind (Krauss *et al.*, 2009). The Barataria Basin experiences a micro-tidal influence from the Gulf of Mexico, and water level and salinity vary in response to lunar and wind tides, lateral inflows from the estuary, and rainfall (Swarzenski, 2003; Habib *et al.*, 2007; Inoue *et al.*, 2008). Salinity increases seasonally during water deficit in the late spring (Sklar,

1983) and in the fall associated with accumulated ET and low discharge from the Mississippi River (Baumann, 1987). The disconnection of the Mississippi River from these sites because of leveeing creates the opportunity for us to identify survival mechanisms of these residual and transitioning forests related to flooding and salinity. Thus, high-salinity events are caused by occasional tropical cyclones (Conner *et al.*, 2007) and by droughts that allow saltwater intrusion (Swarzenski, 2003; Habib *et al.*, 2007; Day *et al.*, 2012) without concomitant flushing (Conner *et al.*, 2007).

The soil is fine-textured and semi-fluid, mapped by the USDA Soil Conservation Service as a very-fine, smectitic, nonacid, hyperthermic Typic Hydraquent of the Barbary series. Organic matter is ~60% at the surface but declining with depth to semi-fluid, mineral sediments, and bulk density $< 0.3 \text{ g/cm}^3$ in the top 20 cm and generally $< 1 \text{ g/cm}^3$ throughout (Conner *et al.*, 2007; Krauss *et al.*, 2009; Jiang and Middleton, 2011). Hummocks are organic accumulations of detritus and living roots that contain frequent large, internal voids above the muck and semi-fluid mineral sediment at their bases. The surface of swales is a poorly defined transition from floating and suspended organic matter to fluid, organic-rich sediments. Falling-head tests in two tubes inserted into the semi-fluid mineral sediments indicated saturated hydraulic conductivity (K) of $\sim 10^1 - 10^2 \text{ m/day}$, and slug additions into a pit dug in the organic material indicated $K \approx 10^3 \text{ m/day}$. These tests were informal but clearly indicated high conductivity of soils as expected from its semi-fluid state and low bulk density.

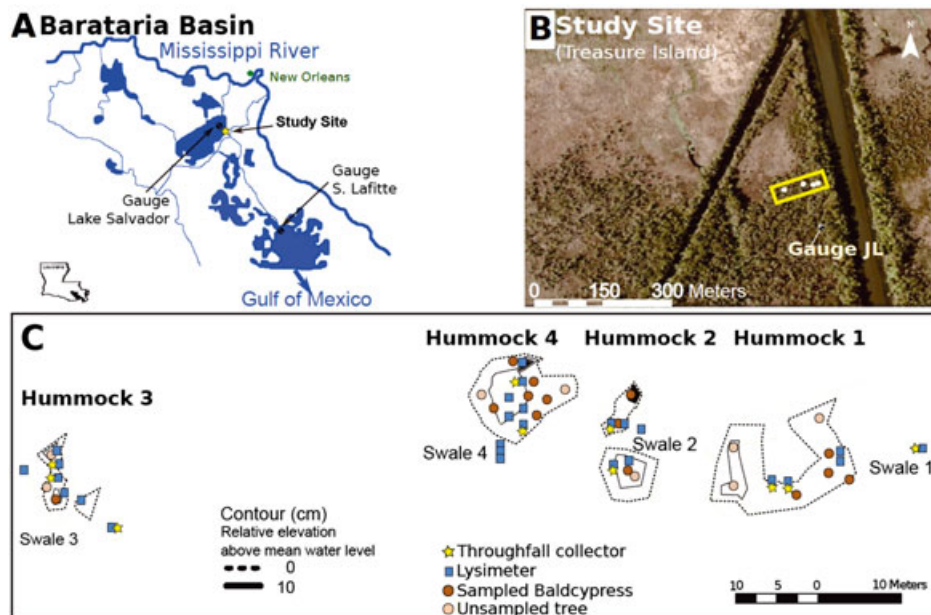


Figure 1. The study area. (A) Barataria Basin showing gauging stations; (B) site map showing water level gauge and study hummocks (dots) at the boundary between forested swamp and treeless marsh; and (C) map of study hummocks expanded from yellow box in (B).

Woody vegetation on hummocks comprised trees and shrubs, including baldcypress, *Morella cerifera*, *Triadica sebifera*, *Acer rubrum* var. *drummondii*, and *Sabal minor*. Floating and emergent herbaceous species occupy the swales, including *Sagittaria lancifolia*, *S. latifolia*, *Eleocharis fallax*, *Sphagnum* spp., *Schoenoplectus americanus*, *Decodon verticillatus*, *Alternanthera philoxeroides*, *Polygonum punctatum*, and *Typha* spp. (Nolfo-Clements, 2006); trees were virtually absent from swales.

Water levels were recorded about 100 m from the study site with a water level recorder inserted approximately 1 m into the soil (Infinites USA, Port Orange, FL, USA) and reporting at hourly intervals (Figure 2A). Salinity and water level data were obtained from USGS gauges in Lake Salvador (USGS 073802375) and Barataria Waterway (USGS 292859090004000) (Figures 1A and 2). Rainfall during the study was interpolated using the PRISM model to interpolate from nearby stations and terrain factors (Daly *et al.*, 1994; www.prism.oregonstate.edu).

Four hummocks were selected for measuring detailed site hydrological processes. Site topography was measured by topographic survey (TOPCON, Topcon Positioning Systems, Inc. Livermore, CA USA). Relative elevation was referenced to the mean water level at the nearby water level recorder, which was estimated to be ~30 cm above mean sea level based on assuming equal water surface elevation at the study site and in nearby Lake Salvador during high

water events (Figure 2A). Hummocks were from 15 to 59 cm above mean water level (~45–89 cm amsl) and 7.6–47.6 m² in area (Table I). The soil surface elevation of the swales was approximately 14 cm below the mean water level at 16 cm amsl. Jiang and Middleton (2011) measured swamp floor elevation nearby at ~10 cm amsl. Hummocks were completely inundated up to 8% of the time because of fluctuating water levels ranging from 25.6 cm below mean water level to 90.8 cm above (Figures 2A and 3). Inundation is from rainfall or by water with varying salinity (mean 0.7 ppt) from Lake Salvador (Figure 2B).

Field measurements

Water samples were collected in 13 sampling periods over a period of 18 months (Figure 2A) from surface water (SW) in swales by hand and in the saturated zone of soil beneath swales and hummocks (ground water, GW) using suction lysimeters. Lysimeters were 1.7 cm PEX[®] tubing, capped at the top, open at the sampling end, but plugged with plastic mesh to prevent ingress of sediment. Lysimeters were installed by pushing them into the soil using a steel rod. Using a hand pump, lysimeters were purged before acquiring water samples. Lysimeters were installed at nominal depths of 10, 30, 60, and 90 cm below the relative mean water level. Four to six lysimeters were within each hummock depending on our ability to install lysimeters

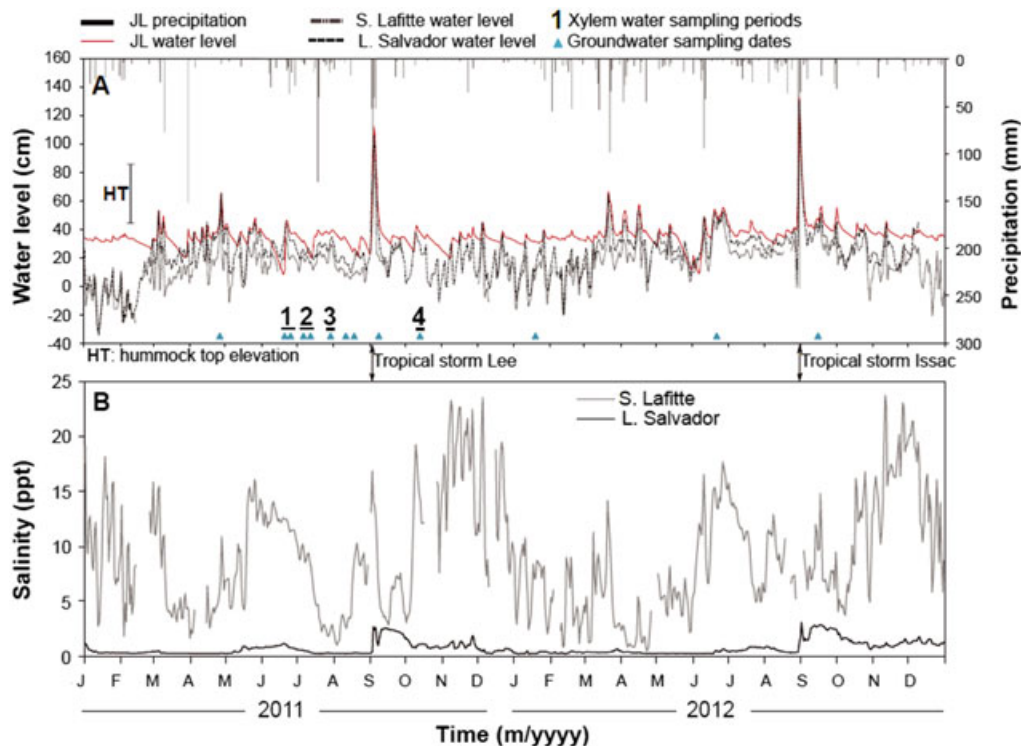


Figure 2. (A) Daily precipitation and water level at the study site (JL) and nearby water bodies (reference Figure 2); and (B) salinity fluctuations in the Barataria waterway and Lake Salvador near Lafitte, Louisiana, during the study period.

Table I. Characteristics of study hummocks.

Hummock ID	Relative elevation (cm) ^a		Area (m ²)	Time submerged (%)	
	Maximum	Mean		Completely	>50% area
1	15	4	32	8	42
2	59	6	8	<1	30
3	20	6	10	5	11
4	40	13	48	1	31

^a Above mean water level, which is ~30 cm above mean sea level.

through roots and undecomposed woody debris. At least one lysimeter was in each adjacent swale, depending on whether soil strength was sufficient to support installations (Figure 1C).

Within each hummock, we collected soil samples at 10-cm depth when the soil was not saturated in the vadose zone. Soil samples were stored in glass vials, kept on ice, brought back to the lab, and frozen for later cryogenic distillation and salinity analysis.

Throughfall (TF) water was collected in 11 collectors on both forested hummocks and above swales. Each collector funnel was 14 cm in diameter and contained 1 cm of mineral oil to avoid evaporation and isotopic fractionation of TF prior to analysis. All water samples were collected in 20-ml glass vials with zero headspace.

Isotopic composition of xylem water was used to assess the source of water use by baldcypress. Across the growing season, we sampled xylem water from 15 baldcypress trees four times (Figure 2). Baldcypress sample trees included all baldcypress trees on Hummocks 1–3, and the five largest baldcypress on Hummock 4. Sample cores 5-mm diameter were taken using an increment borer; bark, cambium, and phloem tissue were discarded. All samples were immedi-

ately sealed and transported to the lab for later cryogenic extraction of water. Samples included active and inactive xylem tissue (Ritchie and Hinckley, 1971; White *et al.*, 1985). A total of 41 samples were collected.

Analyses

Water in xylem and soil samples was extracted using cryogenic vacuum distillation (Ehleringer and Osmond, 1989; Ehleringer *et al.*, 2000; West *et al.*, 2006). Samples were heated above 100 °C in a 90-milliTorr vacuum using a hot saline water bath for 5 h. Vapor condensed by cooling with liquid nitrogen (−196 °C). After distillation, we added activated charcoal to water samples to reduce later analytical errors from volatile organic compounds (West *et al.*, 2006).

Isotopic composition of ¹⁸O and ²H (or deuterium, D) of water samples from all sources was analyzed using laser absorption spectroscopy (DLT-100, Los Gatos Research Inc., Mountain View, CA). The values were transformed with reference to a Vienna Standard Mean Oceanic Water, $\delta = R_{\text{sample}}/R_{\text{standard}} - 1$, where δ indicates deviation from the standard, R_{sample} is the ratio of ¹⁸O/¹⁶O or ²H/¹H in the sample, and R_{standard} is the same ratio in the standard. Deuterium excess (*d*) was calculated as $d = \delta D - 8 \times \delta^{18}O$ (Dansgaard, 1964). We calculated instrumental precision of the laser spectrometer as the standard deviation of the final three of six sequential standard injections, pooled over multiple months of analysis, and determined it to be ±0.7‰ for δ^2H and ±0.13‰ for $\delta^{18}O$.

We used several procedures to control and quantify error and precision in the isotope analysis. First, we used only the final three of six sequential injections for each sample or standard, which is expected to reduce memory effect in the laser spectrometer to 1% (Penna *et al.*, 2012). Second, laser spectroscopy is sensitive to contamination by organic

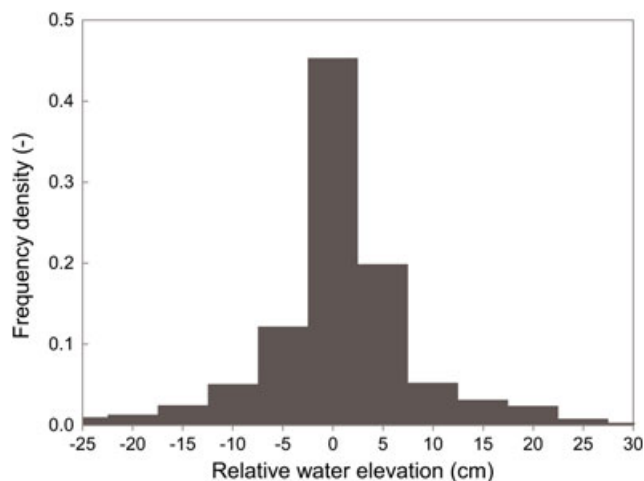


Figure 3. Frequency density of water level at the study area, from 2011 to 2012. Relative elevation zero is mean over the entire period and is near 30 cm msl.

compounds likely to exist in our samples (West *et al.*, 2010), so a spectral contaminant identifier (Leen *et al.*, 2012) was used to flag likely problem samples. When the absorption spectrum indicated contamination with methanol or ethanol (Brand, 2010; Schultz *et al.*, 2011), water samples were also analyzed using isotope ratio mass spectroscopy (Thermo Delta V Advantage), and the data obtained by laser spectroscopy were not used. In all cases, differences in isotopic composition between laser spectroscopy and mass spectroscopy were less than 1‰, including cases of suspected contamination and supplemental, uncontaminated samples analyzed as blind blanks. Third, we conducted controlled tests and determined bias caused by application of activated carbon was $-0.8‰$ for $\delta^2\text{H}$ and $-0.40‰$ for $\delta^{18}\text{O}$. Fourth, fractionation effects of distillation were minimized by ensuring high fractional mass extraction of water (0.98 ± 0.02 SE). Controlled tests found mean error in a typical 98% extraction was $-0.3‰$ for $\delta^2\text{H}$ and $+0.40‰$ for $\delta^{18}\text{O}$, which is similar to data reported by Araguás-Araguás *et al.* (1995) and smaller than expected from Rayleigh distillation theory. Finally, we interspersed standards and samples in the analysis sequence to reduce memory effects and account for drift (Wassenaar *et al.*, 2014).

We measured salinity of all water samples by proxy using electrical conductivity (EC300, YSI Inc. Yellow Spring, OH). For vadose zone salinity, dry soil samples remaining after cryogenic distillation were added to deionized water equal to 20 times the weight of soil, and the resulting slurry was measured for electrical conductivity (Rhoades *et al.*, 1989).

RESULTS

Hydrologic regime

Water level at the site fluctuated between -26 cm and 91 cm above mean water level (Figure 2A). Water levels in the study area rarely responded substantially to rainfall events; instead, high water events at the study site occurred in conjunction with high water in adjacent Lake Salvador in response to coastal wind and storms, including surges from two tropical cyclones (Figure 2A). This surface connectivity to Lake Salvador was apparent when the water level was more than ~ 5 cm above mean water level for the swamp (~ 35 cm amsl). Water level remained below mean water level for 22% of the time during the study period (Figure 3). Hummocks were completely submerged up to 8% of the growing season (Table I), and the majority of these events occurred when there was lateral connectivity with Lake Salvador. There was slow recession of water level between connectivity events, and low water in the study site occurred near the ends of long periods of low water in Lake Salvador.

Salinity variation

Salinity in the unsaturated portion of the hummocks (vadose zone) was 0.7 ± 0.4 ppt (Figure 4H), which was lower than any other water at the site except TF. Salinity of vadose zone water in hummocks and swales was higher than in TF and surface water throughout the experiment (Figure 4). There was a generally decreasing salinity gradient from vadose zone water to the water column above, with a trend of slightly greater salinity at depth in both hummocks and swales. Salinity in vadose zone water in swales was slightly lower (mean 2.0 ppt) than in hummocks (2.3 ppt).

Salinity of the soil and surface water (as opposed to vadose zone water) in the study site remained generally higher than in the neighboring open water of Lake Salvador (Figures 2 and 4). There was a salinity gradient out of the study site into Lake Salvador except during storm surge events and low water periods.

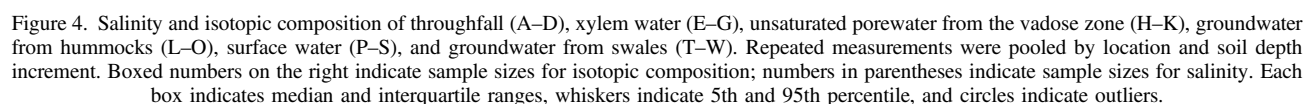
Isotope tracers of water sources to hummocks and trees

Isotopic composition of groundwater in hummocks was similar to that of swales, but with less temporal variation (Figures 4 and 5). Composition of groundwater in hummocks is the same with depth (Figure 4); vadose zone water was distinct from other water sources, generally offset below the local meteoric (TF) water line and with lower d (Figure 5). Isotopic composition of xylem water was more like vadose zone water than any other measured water sources at the site (Figure 5). The d was similar between vadose zone and xylem water, but generally lower than d of other sources (Figure 4).

DISCUSSION

Hydrology of hummock–swale terrain

Water in both hummocks and swales was most temporally variable in isotopic composition near the surface, and there was an upward gradient of decreasing salinity throughout the study. This, in addition to low variability in saturated-zone chemistry relative to free water and consistently low hydraulic gradients, supports the conclusion that vertical mixing in the shallow subsurface was slow, exchange between hummocks and swales was muted, and diffusion of salts toward the surface water dominated (Figure 6). Lower deuterium excess in the vadose zone suggests evaporation as expected because of high interaction with air, but does not appear to have resulted in high soil salinity because the vadose zone was low. This is in contrast to other studies in which ET increased salinity in marshes (Wang *et al.*, 2007; Tosatto *et al.*, 2009). Therefore, precipitation may be exceeding evaporation from hummock soils, with net flushing of salts from the vadose zone



vertical gradients in salinity than in floating marshes or swales. These patterns are consistent with our conclusion of minimal exchange between water in sediments and the water column.

Thus, baldcypress trees occupy nearly nonsaline hummock tops, but the soils are characterized by episodic salt influx followed by slow leaching, superimposed on a layer of salinity that lies apparently beneath the root zone for most of the growing season. The persistent gradient in salinity from groundwater to open water suggests salinity likely migrates mainly through diffusion, suggesting long residence times in both hummocks and the wetland as a whole. Solute transport is slow under low flow conditions (a chronically imposed state for the forested wetlands of this estuary), and the low flow gradients in the permanently

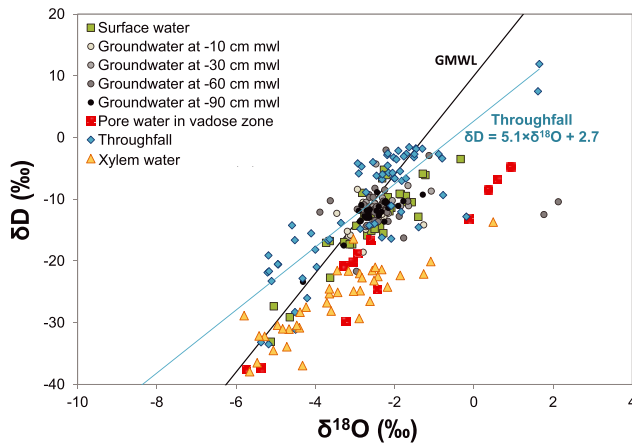


Figure 5. Isotopic composition of water samples. The local mean throughfall line was obtained by least squares from throughfall data and the Global Meteoric Water Line (GMWL) is $\delta D = 8 \times \delta^{18}O + 10$.

saturated groundwater zone persisted because of elevations near sea level and location in a microtidal deltaic estuary.

The dominant source of water to our study site appears to be the estuary, which is in turn dominated by rainfall in the estuarine basin. Salinity of Lake Salvador (the upper estuary near the study site) was generally lower and did not fluctuate as much as the estuary farther south, which is related to freshwater inputs from surrounding land (Inoue *et al.*, 2008) such as our study site. The fluctuation in water level at our study site was closely associated with that of adjacent Lake Salvador during episodic periods of connectivity; between periods of connection, the shallow water on the surface and near subsurface was sufficient to overwhelm precipitation and remain dominant as the water source to the study wetland. These periods of connection may be important for salinity as periods of elevated influx or efflux, depending on salinity in the lake.

The low slope of the local mean TF line compared to the GMWL (Figure 5) was unexpected, but there are two likely reasons for this. First, there are multiple examples of

humid, coastal sites having low LMWL slopes. For example, Dansgaard (1964) found LMWLs at Cape Hatteras, USA, of 4.5 and in Tokyo of 4.7; and Gat and Matsui (1991) found LMWLs in coastal French Guiana and Brazil with slopes of 5.3–6.2. Second, these are TF samples instead of rainfall, and some fractionation may have occurred in the canopy (Brodersen *et al.*, 2000; Hsueh *et al.*, 2016).

Xylem water and its water sources

Xylem water stable isotopes were more similar to water in the vadose zone (non-saturated zone of the hummock) than other measured water sources. Although there was some minor overlap in isotopic composition of xylem water with that of TF, surface water, and groundwater, most of the xylem water samples were outside the range of anything observed in those sources. Therefore baldcypress on hummocks appeared to use water primarily from the vadose zone during our study period. Similarly, hardwood hammocks overlying saline groundwater in south Florida Keys almost exclusively use soil water (Ish-Shalom-Gordon *et al.*, 1991). However, in contrast to the 40–70 cm vadose zone depth at those sites in the Florida Keys (Sternberg *et al.*, 1991), the hummocks in our study were 4–13 cm above mean water level, constituting a much smaller reservoir of plant available moisture during periods of high salinity and suggesting greater dependence on rainfall variability when salinity is high.

The isotopic composition of vadose zone water, and thus xylem water, is difficult to interpret. Simple evaporation and condensation of other measured water pools are not sufficient to explain deviations, mainly as lower δD but similar $\delta^{18}O$, from other samples. A similar deviation was observed by Brooks *et al.* (2010) and interpreted as derived from evaporation of isotopically light precipitation that was preferentially retained in soil because of its timing at the end of the dry season. It is possible that we observed a similar process, by which the soils retain some distinctly

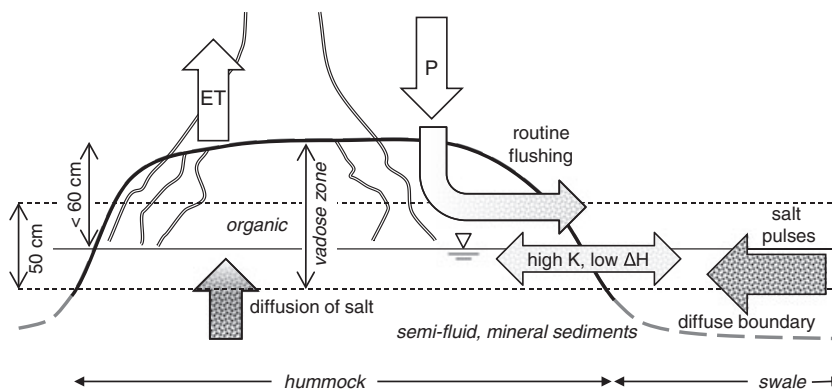


Figure 6. Conceptual diagram of water and salt fluxes in hummocks at the study site. Symbols are used for precipitation (P), evapotranspiration (ET), hydraulic conductivity (K), and hydraulic gradient (ΔH). Double lines indicate tree and active roots.

light precipitation that is subsequently modified by evaporation. However, we have no data to suggest this is likely, and can only conclude that the isotopic composition of vadose zone water is a complex result of some combination of selective retention in soil, evaporation, diffusion, condensation, and perhaps interaction with soil minerals (Oerter *et al.*, 2014) or organic matter.

Separation of isotopic domains for sources was clear despite samples coming from pools with different residence times associated with the greater temporal variability in xylem water, surface water, TF, and vadose water as compared to groundwater. There is greater variability in those water sources than we measured at both spatial (Zhao *et al.*, 2013) and temporal (Pangle *et al.*, 2013) scales, which broadens the domain and increases overlap of measured members. However, both the stable isotopic composition of groundwater and the highly variable isotopic composition of TF had substantial d offsets from xylem water and vadose water.

In our study we combined heartwood and sapwood samples to integrate over time and provide large enough xylem water samples without further damaging trees in the park. The most likely effect of combining sapwood and heartwood samples in our study is to mute measured temporal variation in isotopic composition in xylem water, and to measure the integrated isotopic regime of growing conditions. Ritchie and Hinckley (1971) suggested that during droughts and subsequent wetter periods, differences in contribution of exchange of water between the sapwood and heartwood can occur, and that trees integrate water sources depending on soil water availability over the season. Similarly, White *et al.* (1985) found no difference in δD in water extracted from both sapwood and heartwood of baldcypress from three swamp sites in Arkansas. The degree of exchange between sapwood and heartwood remains unclear for baldcypress especially under less flooded environments or saline flooding.

The use of vadose zone water by baldcypress in hummock–swale topography on our site appears to be the mechanism by which it avoids salinity and flooding stresses in the soil. Vadose zone salinity was low, and it remained unsaturated for the majority of the growing season, which appears to have created the most favorable conditions for roots. In general, roots of trees in forested wetlands occupy the shallow soil (e.g. Jones *et al.*, 2000; Baker *et al.*, 2001), and the same is apparently true in hummocks. For example, Colón-Rivera *et al.* (2014) suggested that roots of *Pterocarpus officinalis* were concentrated in the shallow soil on coastal hummocks and that water uptake was mostly from this zone. At our study site, hummocks were composed mainly of organic matter with high concentration of living roots. The results of this work suggest that roots within the vadose zone of the hummock provide the primary uptake of water for

baldcypress and that concentration of root growth in the hummocks is a feedback between the trees and their growing environment whereby the maintenance of hummocks by high root growth also provides a favorable environment for the trees.

The fact that baldcypress growing on hummocks did not use groundwater from the permanently saturated zone suggests it can avoid salinity and flood stresses at least for large portions of time. Reportedly, baldcypress is intolerant to chronic saline flooding at higher than 2 ppt (Pezeshki, 1990; Allen *et al.*, 1994, 1997; Conner, 1994; Krauss *et al.*, 1999), and this threshold is less than mean groundwater salinity of 2.5 ppt at the study site. Baldcypress may be restricted to the upper part of hummocks because higher salinity only involves short-term salinity pulses that are survivable by baldcypress.

While baldcypress trees on the hummocks in our study are currently able to access freshwater in the vadose zone, continued local subsidence and sea level rise will likely increase flooding and salinity in the long term and eventually reduce the sustainability of baldcypress cover. The subsidence rate at this site because of compaction of sediments is about 3 to 5 mm/yr (Lane *et al.*, 2006). Combined with eustatic sea level rise predicted to be 4 mm/yr (Church *et al.*, 2013), relative sea level rise is likely to be 7 to 9 mm/yr during the next century. Maintenance of hummocks in a subsiding environment depends on continued accretion, which Kirwan *et al.* (2010) estimated is likely insufficient to maintain marshes in a low-sediment, micro-tidal estuarine wetland experiencing such high relative sea level rise. We do not yet fully understand the process of hummock formation, how it compares to marsh accretion, and how changes in salinity and flooding alter the rates. Aside from hydrogeomorphic changes, changes in precipitation amount, timing, estuarine hydrological processes, and associated salinity will further affect this critical balance. Baldcypress in our study site may owe their existence to the hummocks, but hummock formation in a subsiding delta may not be rapid enough for long-term sustainability of forests.

CONCLUSIONS

Overall, salinity was slightly higher in groundwater in hummocks than in swales, but with substantial heterogeneity within hummocks. The shallow subsurface of hummocks is a zone characterized by slow dilution and episodic salinization rather than slow salinization and episodic flushing. Rainfall and frequent inundation by generally low-salinity water flushed salts and maintained lower salinity in upper layers. Groundwater below 60 cm in hummocks and 30 cm in swales was essentially decoupled from surface water because the water level rarely drops

below –15 cm. Thus, baldcypress trees occupy nearly nonsaline hummock tops, but the soils are characterized by episodic salt influx followed by slow leaching, superimposed on a layer of salinity that lies apparently beneath the root zone for most of the growing season.

Stable isotopic composition of xylem water in baldcypress was more similar to water in the vadose zone than in other measured water sources. Baldcypress on hummocks appear to use water from the vadose zone where the majority of roots were apparently located and thus avoid salinity and flooding stresses. Thus, hummocks may represent refugia for coastal swamp trees, as local subsidence and sea-level rise continue to increase exposure to both flooding and salinity.

ACKNOWLEDGEMENTS

The work was funded by George M. Wright Climate Change Fellowship, Lucius W. Gilbert Foundation, the USGS Climate and Land Use Change Research and Development Program, and the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award LAB94181. The authors are grateful to Jean Lafitte National Historical Park and Preserve for access to the site. Ryan Stewart provided valuable comments on an earlier version of this manuscript. The authors thank Brandon Edwards for his technical and field assistance; Julie Whitbeck for her help with the park; Holly Barnard for her assistance in distillation; Richard Day and Andrew From for maintaining the continuous site water level recorder; and Sairah Javed, Chieko Hunter, Sanjeev Joshi, Kuang-chi Hung, April Newman, Marcus Rutherford, Kaci Fisher, and Erin Johnson for field assistance. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author and do not necessarily reflect the view of the U.S. Department of Agriculture.

REFERENCES

- Allen JA, Chambers JL, McKinney D. 1994. Intraspecific variation in the response of *Taxodium distichum* seedlings to salinity. *Forest Ecology and Management* **70**: 203–214. DOI:10.1016/0378-1127(94)90087-6.
- Allen JA, Pezeshki SR, Chambers JL. 1996. Interaction of flooding and salinity stress on baldcypress (*Taxodium distichum*). *Tree Physiology* **16**: 307–313. DOI:10.1093/treephys/16.1-2.307.
- Allen JA, Chambers JL, Pezeshki SR. 1997. Effects of salinity on baldcypress seedlings: physiological responses and their relation to salinity tolerance. *Wetlands* **17**: 310–320. DOI:10.1007/BF03161419.
- Anderson PH, Pezeshki SR. 2001. Effects of flood pre-conditioning on responses of three bottomland tree species to soil waterlogging. *Journal of Plant Physiology* **158**: 227–233. DOI:10.1078/0176-1617-00267.
- Araguás-Araguás L, Rozanski K, Gonfiantini R, Louvat D. 1995. Isotope effects accompanying vacuum extraction of soil water for stable isotope analyses. *Journal of Hydrology* **168**: 159–171. DOI:10.1016/0022-1694(94)02636-p.
- Baker TT, Conner WH, Lockaby BG, Stanturf JA, Burke MK. 2001. Fine root productivity and dynamics on a forested floodplain in South Carolina. *Soil Science Society of America Journal* **65**: 545. DOI:10.2136/sssaj2001.652545x.
- Barnes CJ, Allison GB. 1988. Tracing of water movement in the unsaturated zone using stable isotopes of hydrogen and oxygen. *Journal of Hydrology* **100**: 143–176. DOI:10.1016/0022-1694(88)90184-9.
- Battaglia LL, Denslow JS, Inczauskis JR, Baer SG. 2009. Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. *Journal of Ecology* **97**: 239–246. DOI:10.1111/j.1365-2745.2008.01471.x.
- Bauer-Gottwein P, Rasmussen NF, Feifcová D, Trapp S. 2008. Phytotoxicity of salt and plant salt uptake: modeling ecohydrological feedback mechanisms. *Water Resources Research* **44**: . DOI:10.1029/2007WR006067.
- Baumann RH. 1987. Physical variables. In *The Ecology of Barataria Basin, Louisiana: An Estuarine Profile*, Conner WH, Day JW Jr (eds) U.S. Fish Wildlife Service Biological Report 85(7.13). US Fish & Wildlife Service: USA; 8–17.
- Boesch DF, Josselyn MN, Mehta AJ, Morris JT, Nuttle WK, Simenstad CA, Swift DJP. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research* **i**–103. DOI:10.2307/25735693.
- Brand WA. 2010. Comments on “Discrepancies between isotope ratio infrared spectroscopy and isotope ratio mass spectrometry for the stable isotope analysis of plant and soil waters.”. *Rapid Communications in Mass Spectrometry* **24**: 2687–2688. DOI:10.1002/rcm.4685.
- Brodersen C, Pohl S, Lindenlaub M, Leibundgut C, von Wilpert K. 2000. Influence of vegetation structure on isotope content of throughfall and soil water. *Hydrological Processes* **14**: 1439–1448. DOI:10.1002/1099-1085(20000615)14:8 < 1439:aid-hyp985 >3.0.co;2-3.
- Brooks JR, Barnard HR, Coulombe R, McDonnell JJ. 2010. Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience* **3**: 100–104. DOI:10.1038/ngeo722.
- Church MJ, Lomas MW, Muller-Karger F. 2013. Sea change: charting the course for biogeochemical ocean time-series research in a new millennium. *Deep Sea Research Part II: Topical Studies in Oceanography* **93**: 2–15. DOI:10.1016/j.dsr2.2013.01.035.
- Colón-Rivera RJ, Feagin RA, West JB, López NB, Benítez-Joubert RJ. 2014. Hydrological modification, saltwater intrusion, and tree water use of a *Pterocarpus officinalis* swamp in Puerto Rico. *Estuarine, Coastal and Shelf Science* **147**: 156–167. DOI:10.1016/j.eccs.2014.06.012.
- Conner WH. 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. *Journal of Coastal Research* **10**: 1045–1049.
- Conner WH, Day JW. 1988. Rising water levels in coastal Louisiana: implications for two coastal forested wetland areas in Louisiana. *Journal of Coastal Research* **4**: 589–596. DOI:10.2307/4297461.
- Conner WH, Inabinette LW. 2003. Tree growth in three South Carolina (USA) swamps after Hurricane Hugo: 1991–2001. *Forest Ecology and Management* **182**: 371–380. DOI:10.1016/s0378-1127(03)00087-2.
- Conner WH, Krauss KW, Doyle TW. 2007. Ecology of tidal freshwater forests in coastal deltaic Louisiana and Northeastern South Carolina. In *Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States*, Conner WH, Doyle TW, Krauss KW (eds). Springer: Netherlands; 223–253.
- Courtwright J, Findlay SEG. 2011. Effects of microtopography on hydrology, physicochemistry, and vegetation in a tidal swamp of the Hudson River. *Wetlands* **31**: 239–249. DOI:10.1007/s13157-011-0156-9.
- Daly C, Neilson RP, Phillips DL. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* **33**: 140–158. DOI:10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2.

- Dansgaard W. 1964. Stable isotopes in precipitation. *Tellus* **16**: 436–468.
- Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. *Nature* **350**: 335–337. DOI:10.1038/350335a0.
- Dawson TE, Ehleringer JR. 1993. Isotopic enrichment of water in the “woody” tissues of plants: implications for plant water source, water uptake, and other studies which use the stable isotopic composition of cellulose. *Geochimica et Cosmochimica Acta* **57**: 3487–3492. DOI:10.1016/0016-7037(93)90554-A.
- Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* **33**: 507–559. DOI:10.1146/annurev.ecolsys.33.020602.095451.
- Day RH, Williams TM, Swarzenski CM. 2007. Hydrology of tidal freshwater forested wetlands of the Southeastern United States. In *Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States*, Conner WH, Doyle TW, Krauss KW (eds). Springer: Dordrecht, The Netherlands; 29–63.
- Day JW Jr, Hunter R, Keim RF, DeLaune R, Shaffer G, Evers E, Reed D, Brantley C, Kemp P, Day J, Hunter M. 2012. Ecological response of forested wetlands with and without large-scale Mississippi River input: implications for management. *Ecological Engineering* **46**: 57–67. DOI:10.1016/j.ecoleng.2012.04.037.
- DeLaune RD, Patrick WH, Pezeshki SR. 1987. Foreseeable flooding and death of coastal wetland forests. *Environmental Conservation* **14**: 129–133. DOI:10.1017/S0376892900011486.
- DeLaune RD, Nyman JA, Patrick WH. 1994. Peat collapse, pending and wetland loss in a rapidly submerging coastal marsh. *Journal of Coastal Research* **10**: 1021–1030.
- Dommain R, Couwenberg J, Joosten H. 2010. Hydrological self-regulation of domed peatlands in south-east Asia and consequences for conservation and restoration. *Mires and Peat* **6**: 1–17.
- Duberstein JA, Conner WH. 2009. Use of hummocks and hollows by trees in tidal freshwater forested wetlands along the Savannah River. *Forest Ecology and Management* **258**: 1613–1618. DOI:10.1016/j.foreco.2009.07.018.
- Duberstein JA, Krauss KW, Conner WH, Bridges WC, Shelburne VB. 2013. Do hummocks provide a physiological advantage to even the most flood tolerant of tidal freshwater trees? *Wetlands* **33**: 399–408. DOI:10.1007/s13157-013-0397-x.
- Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell and Environment* **15**: 1073–1082. DOI:10.1111/j.1365-3040.1992.tb01657.x.
- Ehleringer JR, Osmond CB. 1989. Stable isotopes. In *Plant Physiological Ecology Field Methods and Instrumentation*, Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW (eds). Chapman and Hall Ltd.: London; 281–300.
- Ehleringer J, Roden J, Dawson T. 2000. Assessing ecosystem-level water relations through stable isotope ratio analyses. In *Methods in Ecosystem Science*, Sala O, Jackson R, Mooney H, Howarth R (eds). Springer: New York; 181–198.
- Gardner LR. 2009. Comment on “Spatial organization and ecohydrological interactions in oxygen-limited vegetation ecosystems” by Marco Marani et al. *Water Resources Research* **45**: W05603. DOI:10.1029/2007wr006165.
- Gat JR. 1971. Comments on the stable isotope method in regional groundwater investigations. *Water Resources Research* **7**: 980–993. DOI:10.1029/WR007i004p00980.
- Gat JR, Matsui E. 1991. Atmospheric water balance in the Amazon Basin: an isotopic evapotranspiration model. *Journal of Geophysical Research, [Atmospheres]* **96**: 13179–13188. DOI:10.1029/91JD00054.
- Gaziz C, Feng X. 2004. A stable isotope study of soil water: evidence for mixing and preferential flow paths. *Geoderma* **119**: 97–111. DOI:10.1016/S0016-7061(03)00243-X.
- Habib E, Nuttle WK, Rivera-Monroy VH, Gautam S, Wang J, Meselhe E, Twilley RR. 2007. Assessing effects of data limitations on salinity forecasting in Barataria basin, Louisiana, with a Bayesian analysis. *Journal of Coastal Research* **23**: 749–763. DOI:10.2112/06-0723.1.
- Hsueh Y-H, Allen ST, Keim RF. 2016. Fine-scale spatial variability of throughfall amount and isotopic composition under a hardwood forest canopy. *Hydrological Processes*. DOI:10.1002/hyp.10772.
- Huenneke LF, Sharitz RR. 1986. Microsite abundance and distribution of woody seedlings in a South-Carolina cypress-tupelo swamp. *American Midland Naturalist* **115**: 328–335. DOI:10.2307/2425869.
- Inoue M, Park D, Justic D, Wisemanjr W. 2008. A high-resolution integrated hydrology–hydrodynamic model of the Barataria Basin system. *Environmental Modelling & Software* **23**: 1122–1132. DOI:10.1016/j.envsoft.2008.02.011.
- Ish-Shalom-Gordon N, Sternberg LSL, Ross M, O’Brien J, Flynn L. 1991. Water utilization of tropical hardwood hammocks of the Lower Florida Keys. *Oecologia* **92**: 108–112. DOI:10.1007/BF00317270.
- Jiang M, Middleton BA. 2011. Soil characteristics of sediment-amended baldcypress (*Taxodium distichum*) swamps of coastal Louisiana. *Wetlands* **31**: . DOI:10.1007/s13157-011-0189-0.
- Jones RH, Henson KO, Somers GL. 2000. Spatial, seasonal, and annual variation of fine root mass in a forested wetland. *Journal of the Torrey Botanical Society* **127**: 107–114. DOI:10.2307/3088688.
- Kirwan ML, Guntenspergen GR, D’Alpaos A, Morris JT, Mudd SM, Temmerman S. 2010. Limits on the adaptability of coastal marshes to rising sea level: ecogeomorphic limits to wetland survival. *Geophysical Research Letters* **37**: L23401. DOI:10.1029/2010GL045489.
- Krauss KW, Duberstein JA. 2010. Sapflow and water use of freshwater wetland trees exposed to saltwater incursion in a tidally influenced South Carolina watershed. *Canadian Journal of Forest Research* **40**: 525–535. DOI:10.1139/x09-204.
- Krauss KW, Chambers JL, Allen JA, Luse BP, DeBosier AS. 1999. Root and shoot responses of *Taxodium distichum* seedlings subjected to saline flooding. *Environmental and Experimental Botany* **41**: 15–23. DOI:10.1016/S0098-8472(98)00051-3.
- Krauss K, Chambers J, Creech D. 2007. Selection for salt tolerance in tidal freshwater swamp species: advances using baldcypress as a model for restoration. In *Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States*, Conner WH, Doyle TW, Krauss KW (eds). Springer: Dordrecht, The Netherlands; 385–410.
- Krauss KW, Duberstein JA, Doyle TW, Conner WH, Day RH, Inabinette LW, Whitbeck JL. 2009. Site condition, structure, and growth of baldcypress along tidal/non-tidal salinity gradients. *Wetlands* **29**: 505–519. DOI:10.1672/08-77.1.
- Krauss KW, Whitbeck JL, Howard RJ. 2012. On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). *Plant and Soil* **358**: 265–274. DOI:10.1007/s11104-012-1182-y.
- Lane RR, Day JW, Day JN. 2006. Wetland surface elevation, vertical accretion, and subsidence at three Louisiana Estuaries receiving diverted Mississippi River water. *Wetlands* **26**: 1130–1142. DOI:10.1672/0277-5212(2006)26[1130:WSEVAA]2.0.CO;2.
- Leen JB, Berman ESF, Liebson L, Gupta M. 2012. Spectral contaminant identifier for off-axis integrated cavity output spectroscopy measurements of liquid water isotopes. *Review of Scientific Instruments* **83**: 044305. DOI:10.1063/1.4704843.
- Light HM, Melanie RD, Mattson RA. 2007. Ecological characteristics of tidal freshwater forests along the Lower Suwannee River, Florida. In *Ecology of Tidal Freshwater Forested Wetlands of the Southeastern United States*, Conner WH, Doyle TW, Krauss KW (eds). Springer: Dordrecht, The Netherlands; 291–320.
- Malmer N, Wallén B. 1999. The dynamics of peat accumulation on bogs: mass balance of hummocks and hollows and its variation throughout a millennium. *Ecography* **22**: 736–750. DOI:10.2307/3683328.
- Mitsch WJ, Gosselink JG. 2007. *Wetlands*. John Wiley & Sons: New Jersey; 582.
- Noe GB, Krauss KW, Lockaby GB, Conner WH, Hupp CR. 2013. The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. *Biogeochemistry* **114**: 225–244. DOI:10.1007/s10533-012-9805-1.
- Nolfo-Clements LE. 2006. Vegetative survey of wetland habitats at Jean Lafitte National Historical Park and preserve in southeastern Louisiana. *Southeastern Naturalist* **5**: 499–514. DOI:10.1656/1528-7092(2006)5[499:vsowha]2.0.co;2.
- Oerter E, Finstad K, Schaefer J, Goldsmith GG, Dawson T, Amundson R. 2014. Oxygen isotope fractionation effects in soil water via interaction with cations (Mg, Ca, K, Na) adsorbed to phyllosilicate clay minerals. *Journal of Hydrology* **515**: 1–9. DOI:10.1016/j.jhydrol.2014.04.029.

- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schafer KVR. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment* **22**: 1515–1526. DOI:10.1046/j.1365-3040.1999.00513.x.
- Pangle LA, Klaus J, Berman ES, Gupta M, McDonnell JJ. 2013. A new multisource and high-frequency approach to measuring $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in hydrological field studies. *Water Resources Research* **49**: 7797–7803. DOI:10.1002/2013WR013743.
- Penna D, Stenni B, Šandra M, Wrede S, Bogaard TA, Michelini M, Fischer BMC, Gobbi A, Mantese N, Zuecco G, Borga M, Bonazza M, Sobotková B, Wassenaar LI. 2012. Technical note: Evaluation of between-sample memory effects in the analysis of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water samples measured by laser spectrometers. *Hydrology and Earth System Sciences* **16**: 3925–3933. DOI:10.5194/hess-16-3925-2012.
- Peterson JE, Baldwin AH. 2004. Variation in wetland seed banks across a tidal freshwater landscape. *American Journal of Botany* **91**: 1251–1259. DOI:10.3732/ajb.91.8.1251.
- Pezeshki SR. 1990. A comparative study of the response of *Taxodium distichum* and *Nyssa aquatica* seedlings to soil anaerobiosis and salinity. *Forest Ecology and Management* **33–34**: 531–541. DOI:10.1016/0378-1127(90)90216-X.
- Pezeshki SR. 1991. Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. *Trees-Structure and Function* **5**: 180–186. DOI:10.1007/BF00204341.
- Pezeshki SR, Pardue JH, DeLaune RD. 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. *Tree Physiology* **16**: 453–458. DOI:10.1093/treephys/16.4.453.
- Rheinhardt RD, Hershner C. 1992. The relationship of belowground hydrology to canopy composition in 5 tidal fresh-water swamps. *Wetlands* **12**: 208–216. DOI:10.1007/BF03160611.
- Rhoades JD, Manteghi NA, Shouse PJ, Alves WJ. 1989. Estimating soil salinity from saturated soil-paste electrical conductivity. *Soil Science Society of America Journal* **53**: 428. DOI:10.2136/sssaj1989.03615995005300020019x.
- Ritchie GA, Hinckley TM. 1971. Evidence for error in pressure-bomb estimates of stem xylem potentials. *Ecology* **52**: 534. DOI:10.2307/1937640.
- Roden JS, Lin GG, Ehleringer JR. 2000. A mechanistic model for interpretation of hydrogen and oxygen isotope ratios in tree-ring cellulose. *Geochimica et Cosmochimica Acta* **64**: 21–35. DOI:10.1016/S0016-7037(99)00195-7.
- Schoonmaker AL, Teste FP, Simard SW, Guy RD. 2007. Tree proximity, soil pathways and common mycorrhizal networks: their influence on the utilization of redistributed water by understory seedlings. *Oecologia* **154**: 455–466. DOI:10.1007/s00442-007-0852-6.
- Schultz NM, Griffis TJ, Lee X, Baker JM. 2011. Identification and correction of spectral contamination in $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ measured in leaf, stem, and soil water: Correction of $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ in plant and soil water using IRIS. *Rapid Communications in Mass Spectrometry* **25**: 3360–3368. DOI:10.1002/rcm.5236.
- Sekiya N, Yano K. 2002. Water acquisition from rainfall and groundwater by legume crops developing deep rooting systems determined with stable hydrogen isotope compositions of xylem waters. *Field Crops Research* **78**: 133–139. DOI:10.1016/S0378-4290(02)00120-X.
- Sklar F. 1983. Water budget, benthological characterization, and simulation of aquatic material flows in a Louisiana freshwater swamps. PhD Dissertation, Louisiana State University, Baton Rouge, Louisiana.
- Sternberg LSL, Ish-Shalon-Gordon N, Ross M, O'Brien J. 1991. Water relations of coastal plant communities near the ocean/freshwater boundary. *Oecologia* **88**: 305–310. DOI:10.1007/BF00317571.
- Stiller V. 2009. Soil salinity and drought alter wood density and vulnerability to xylem cavitation of baldcypress (*Taxodium distichum* (L.) Rich.) seedlings. *Environmental and Experimental Botany* **67**: 164–171. DOI:10.1016/j.envexpbot.2009.03.012.
- Stratton LC, Goldstein G, Meinzer FC. 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia* **124**: 309–317. DOI:10.1007/s004420000384.
- Stribling JM, Cornwell JC, Glahn OA. 2007. Microtopography in tidal marshes: ecosystem engineering by vegetation? *Estuaries and Coasts* **30**: 1007–1015. DOI:10.1007/BF02841391.
- Swarzenski CM. 2003. Surface-water hydrology of the Gulf Intracoastal Waterway in south-central Louisiana, 1996–99, U.S. Geological Survey Professional Paper 1672.
- Swarzenski CM, Swenson EM. 1994. Effect of mat movement on soil salinity fluctuations in some coastal Louisiana marshes. *Estuarine, Coastal and Shelf Science* **39**: 143–156. DOI:10.1006/ecss.1994.1054.
- Thorburn PJ, Walker GR, Brunel J-P. 1993. Extraction of water from Eucalyptus trees for analysis of deuterium and oxygen-18: laboratory and field techniques. *Plant, Cell and Environment* **16**: 269–277. DOI:10.1111/j.1365-3040.1993.tb00869.x.
- Törnqvist TE, Wallace DJ, Storms JEA, Wallinga J, Van Dam RL, Blaauw M, Derksen MS, Klerks CJW, Meijneken C, Snijders EMA. 2008. Mississippi Delta subsidence primarily caused by compaction of Holocene strata. *Nature Geoscience* **1**: 173–176. DOI:10.1038/ngeo129.
- Tosatto O, Belluco E, Silvestri S, Ursino N, Comerlati A, Putti M, Marani M. 2009. Reply to comment by L. R. Gardner on “Spatial organization and ecohydrological interactions in oxygen-limited vegetation ecosystems”. *Water Resources Research* **45**: W05604. DOI:10.1029/2007WR006345.
- Walker CD, Richardson SB. 1991. The use of stable isotopes of water in characterizing the source of water in vegetation. *Chemical Geology: Isotope Geoscience* **94**: 145–158. DOI:10.1016/S0009-2541(10)80026-9.
- Wang H, Hsieh YP, Harwell MA, Huang W. 2007. Modeling soil salinity distribution along topographic gradients in tidal salt marshes in Atlantic and Gulf coastal regions. *Ecological Modelling* **201**: 429–439. DOI:10.1016/j.ecolmodel.2006.10.013.
- Washburn EW, Smith ER. 1934. The isotopic fractionation of water by physiological processes. *Science* **79**: 188–189. DOI:10.2307/1659858.
- Wassenaar LI, Coplen TB, Aggerwal PK. 2014. Approaches for achieving long-term accuracy and precision of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ for waters analyzed using laser absorption spectrometers. *Environmental Science & Technology* **48**: 1123–1131. DOI:10.1021/es403354n.
- West AG, Patrickson SJ, Ehleringer JR. 2006. Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry* **20**: 1317–1321. DOI:10.1002/rcm.2456.
- West AG, Goldsmith GR, Brooks PD, Dawson TE. 2010. Discrepancies between isotope ratio infrared spectroscopy and isotope ratio mass spectrometry for the stable isotope analysis of plant and soil waters. *Rapid Communications in Mass Spectrometry* **24**: 1948–1954. DOI:10.1002/rcm.4597.
- White JWC, Cook ER, Lawrence JR, Broecker WS. 1985. The D/H ratios of sap in trees—implications for water sources and tree-ring D/H ratios. *Geochimica et Cosmochimica Acta* **49**: 237–246. DOI:10.1016/0016-7037(85)90207-8.
- Zhao P, Tang X, Zhao P, Wang C, Tang J. 2013. Identifying the water source for subsurface flow with deuterium and oxygen-18 isotopes of soil water collected from tension lysimeters and cores. *Journal of Hydrology* **503**: 1–10. DOI:10.1016/j.jhydrol.2013.08.033.