ECOHYDROLOGY
Ecohydrol. **8**, 838–850 (2015)
Published online 30 March 2015 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/eco.1625

Hydrologic remediation for the Deepwater Horizon incident drove ancillary primary production increase in coastal swamps

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ABSTRACT

As coastal wetlands subside worldwide, there is an urgency to understand the hydrologic drivers and dynamics of plant production and peat accretion. One incidental test of the effects of high rates of discharge on forested wetland production occurred in response to the 2010 Deepwater Horizon incident, in which all diversions in Louisiana were operated at or near their maximum discharge level for an extended period to keep offshore oil from threatened coastal wetlands. Davis Pond Diversion was operated at six times the normal discharge levels for almost 4 months, so that *Taxodium distichum* swamps downstream of the diversion experienced greater inundation and lower salinity. After this remediation event in 2010, above-ground litter production increased by 2.7 times of production levels in 2007–2011. Biomass of the leaf and reproductive tissues of several species increased; wood litter was minimal and did not change during this period. Root production decreased in 2010 but subsequently returned to pre-remediation values in 2011. Both litter and root production remained high in the second growing season after hydrologic remediation. Annual tree growth (circumference increment) was not significantly altered by the remediation. The potential of freshwater pulses for regulating tidal swamp production is further supported by observations of higher *T. distichum* growth in lower salinity and/or pulsed environments across the U.S. Gulf Coast. Usage of freshwater pulses to manage altered estuaries deserves further consideration, particularly because the timing and duration of such pulses could influence both primary production and peat accretion. © 2015 The Authors. *Ecohydrology* published by John Wiley & Sons Ltd.

KEY WORDS saltwater intrusion; *Taxodium distichum*; tidal freshwater swamp; oil spill

Received 17 October 2014; Revised 7 February 2015; Accepted 15 February 2015

INTRODUCTION

Coastal subsidence and sea level rise are inundating freshwater wetlands of the world's coasts with saline water, leading to vegetation shifts and wetland loss (Poff *et al.*, 2002). Freshwater tree species have specific adaptations to cope with flooding, but saltwater can limit production (Kozlowski, 1997). Therefore, freshwater remediation might help to rejuvenate these forests by restoring the biogeochemistry of pulsed systems (i.e. decreased salinity or anoxia; Junk *et al.*, 1989; Middleton, 1999). The Comprehensive Master Plan for the coast of Louisiana (CPRA, 2012) recommends the usage of freshwater diversions to deliver sediment and water from the Mississippi River, and such approaches could be applied elsewhere. A diversion is a restoration structure, which redirects water to a wetland, usually from a river or other water source. Louisiana diversions were mostly constructed to deliver sediment and water to rebuild coastal wetlands, barrier islands, and ridges, although the purpose of Davis Pond Diversion was mostly to reduce salinity in the lower estuary for fisheries (CPRA, 2012). Importantly, increases in freshwater flow have the potential to reduce salinity or change other biogeochemical processes in receiving wetlands, so that these diversions have the potential to change plant production levels. Unexpectedly, the Deepwater Horizon oil spill of 2010 provided a field test of the idea that the input of river water might improve growing conditions for freshwater species in hydrologically altered estuaries.

On 20 April 2010, an explosion on the Deepwater Horizon drilling rig resulted in a massive oil spill about 84 km from Venice, LA (Lubchenco *et al.*, 2012). This spill threatened coastal and offshore ecosystems of the entire Gulf Coast of the United States. As a preventative measure to keep oil away from wetlands, all of Louisiana's coastal diversions began operating at or near full capacity as early as 30 April 2010 with many being kept open for an extended period. Davis Pond Freshwater Diversion, located directly upstream of our long-term research sites in the

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Barataria Basin, was operated at or near full capacity (six times higher than normal) for a period of almost 4 months (May–August; Bianchi *et al*., 2011). At the beginning of the remediation event on 30 April, flow from the Davis Pond Freshwater Diversion was $113\,m^3\,s^{-1}$. By 10 May, the flow was at full capacity at ~$300\,m^3\,s^{-1}$, and remained above $200\,m^3\,s^{-1}$ on most days through August 2010 with rates after September less than ~$25\,m^3\,s^{-1}$ (Bianchi *et al*., 2011). Much consideration was given to the effects of oil and its remediation on biota (Lubchenco *et al*., 2012), but the potential effects of freshwater release on estuaries received little attention (Bianchi *et al*., 2011).

Operation of the Davis Pond Diversion during this remediation event caused a reduction of salinity in the centre of Barataria Bay of ~5 ppt (Bianchi *et al*., 2011). This diversion delivered freshwater to Jean Lafitte National Historical Park & Preserve (JLNHP & P; Figure 1a), which is part of our long-term study network [North American Baldcypress Swamp Network (NABCSN); Figure 1a–b]. *Taxodium distichum* swamps mostly occur in freshwater tidal environments of the Southeastern United States with mean salinity below 0.5 ppt, although the boundary of tidal freshwater and oligohaline systems oscillates with drought and flood periods (Kaplan *et al*., 2010). *T. distichum* occurs where flood waters do not exceed 2 ppt salinity more than 50% of the time, but the highest density of trees is found in salinity nearest 0 ppt (Wicker *et al*., 1981). Trees exposed to salinity levels of ~1–4.5 ppt experience 10–80% mortality in 5 years (Hoeppner *et al*., 2008).

This oil spill remediation may have been damaging from some perspectives (Martínez *et al*., 2012) because of the potential of freshwater release to lower salinity in oyster beds (GNO Inc., 2010). At the same time, the historical

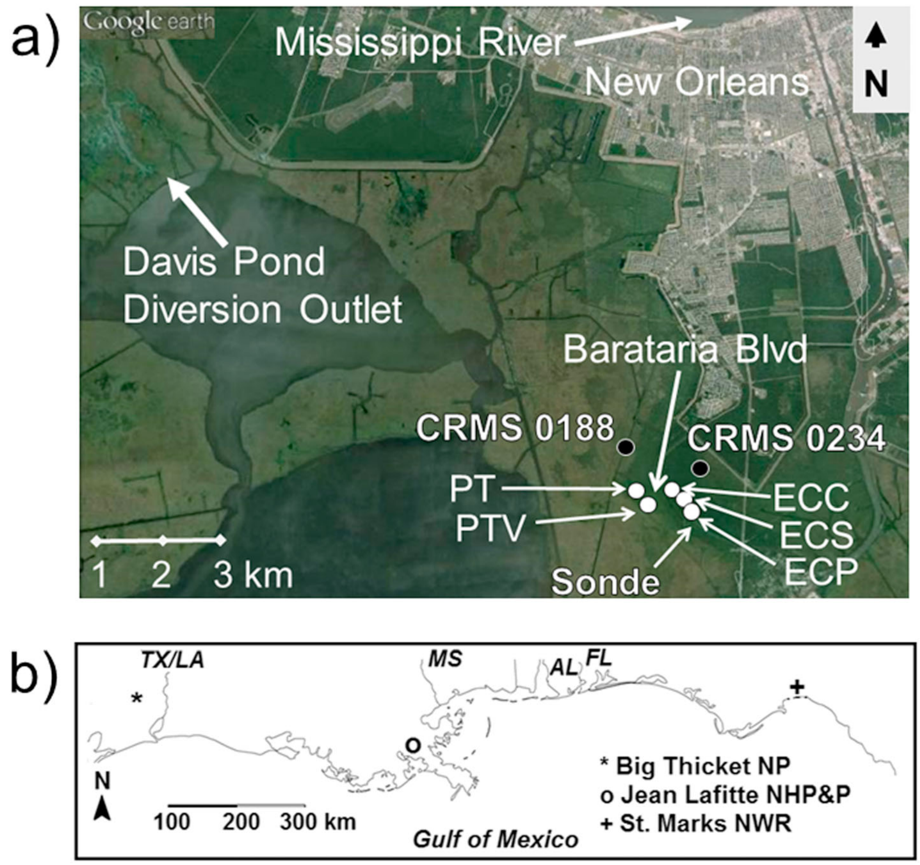

Figure 1. (a) Location of structures and water releases in 2010 – Barataria Bay, LA. Davis Pond Diversion was operated to discharge more freshwater from May to August 2010. Arrow points away from the diversion outlet towards long-term research sites (North American Baldcypress Swamp Network) in Jean Lafitte National Historical Park & Preserve (NHP & P). Water and surface water salinity level data are from publically available long-term data from water gauges [Louisiana Department of Natural Resources; Coastwide Reference Monitoring System (CRMS) 0234 and CRMS 0188; Education Center (EC) and Palmetto Trail (PC) units on either side of Barataria Blvd] including five long-term production sites [Education Center Parking (ECP)/ Education Center Spur (ECS)/Education Center Canal (ECC) vs PT/Palmetto Trail Visitors (PTV), respectively]. The PC unit is open to the Kenta Canal, which is connected to the Barataria Estuary. A water gauge was deployed to examine short-term pulses of water during Hurricane Isaac from 28 August to 4 September 2012 (USGS Sonde #0004264; USGS, 2012) and was located less than 100 m from the ECP logger. Based on a freshwater pulse recorded by this Sonde recorder during Hurricane Isaac, it was apparent that the EC unit can be connected hydrologically to other parts of the region at times (Figure 1 in the Supporting Information). (b) Gulf Coast portion of a long-term research network (NABCSN) in which tree growth was studied including Jean Lafitte NHP & P, Big Thicket National Preserve (NP), and St. Marks National Wildlife Refuge (NWR).

setting of these estuaries is important to recognize. Salinity has increased during recent decades, particularly during droughts (Visser *et al.*, 2001), and because of extensive human modification, these wetlands became disconnected from the river (Wissel and Fry, 2005). In response, diversion structures have been built along the lower Mississippi to reconnect coastal wetlands to their river source. Davis Pond Diversion began operation in 2003 to mimic spring floods and release freshwater into estuaries to improve fisheries, reduce land loss (CPRA, 2013), and increase primary production by altering sediment, water, and nutrient levels (i.e. subsidy–stress model; Mitsch *et al.*, 2001). After the construction of the diversion, increases in secondary production have been documented along the flow path (Wissel and Fry, 2005).

Tidal forests south of the Davis Pond Diversion in JLNHP & P (Figure 1a) have been undergoing increased subsidence, flooding, and salinity (Day, 2000) because of shifting faults, sediment, and water loading (Dokka, 2006), oil and gas exploration, canal and levee construction, and reduction in sediment input (Day, 2000). Subsidence might be slowed by projects such as Davis Pond Diversion (U.S. A.C.O.E., 2000), particularly if hydrologic manipulation can increase primary production. Freshwater remediation might reinvigorate plant growth because salinity causes injury to cells, metabolic dysfunction, and leaf shedding in freshwater tree species (Kozlowski, 1997). Few studies to date have evaluated threshold salinity levels for *T. distichum* maintenance and growth with the data available suggesting these values to be about 2.0 and 0.7 ppt (Krauss *et al.*, 2009, and Kaplan *et al.*, 2010, respectively), noting that photosynthesis can be reduced at even lower levels of salinity (Pezeshki *et al.*, 1987).

The objectives of this project were to determine if hydrologic remediation efforts during the 2010 Deepwater Horizon incident could have led to reduced salinity and consequently increased production in coastal freshwater forests. We tested the hypothesis that production of Gulf Coastal *T. distichum* swamps was higher during hydrologic remediation than at other times, following predictions of the subsidy–stress model (Mitsch *et al.*, 2001).

STUDY SITE

Hydrologic remediation event and study site details

Davis Pond Diversion is located at the northern end of Lake Cataouatche, upstream of New Orleans, and north of the head of the Mississippi River passes (~25 and 199 km, respectively). Davis Pond Diversion from the Mississippi River was operated to discharge a large amount of freshwater from May to August 2010 (Bianchi *et al.*, 2011). Water and salinity levels were monitored with two permanent water gauges [Coastwide Reference Monitoring System (CRMS) 0234 and CRMS 0188] operated by the Louisiana Department of Natural Resources (LA DNR) in separate hydrologic units on either side of Barataria Blvd in JLNHP & P [Education Center (EC) unit and Palmetto Trail (PT) unit, respectively; Figure 1a; Table I].

Five research sites within coastal *T. distichum* swamp were selected in JLNHP & P (Figure 1a) to evaluate inter-annual variability in production within the EC and PT units [sites: Education Center Parking (ECP)/Education Center Spur (ECS)/Education Center Canal vs Palmetto Trail (PT)/Palmetto Trail Visitors (PTV), respectively; Table I]. Two of these sites were selected for *T. distichum* tree growth studies in addition to two sites each in Big Thicket National Preserve (Texas) and St. Marks National Wildlife Refuge/Big Bend Wildlife Management Area (Florida), which comprise a portion of the NABSCN (Figure 1b and Table I). Most swamps in this network are deeply flooded for many months of the year, so that methodology is optimized for access during consistently unflooded seasons (August–December).

METHODS

Tree production and growth

Annual peak litterfall production was measured using floating litterfall collectors (diameter = 0.3 m^2; Middleton, 1995; Middleton and McKee, 2005) in plots within five sites in JLNHP & P (Table I). Five production plots were selected along one 125-m-long linear transect within each of these sites at stratified random positions at 25-m intervals to the right of the transect and marked with a wooden stake. Traps were set in August and litter removed after peak litterfall (main season) each December in 2007–2011, with off-season quarterly samples collected in 2007 and 2011. Means of the total biomass captured in the 2007/2011 quarterly samples were used to create a correction factor for the main season of capture, noting that most dominant species were deciduous. Litterfall was sorted by species into leaf, stem (wood), and reproductive components, dried at 70 °C, and weighed. Note that any large woody material falling on the litter trap (stem >0.5-cm diameter) was not likely to have been produced during that growing season, and was removed from the sample. To measure annual root production, a soil core (7 cm diameter × 30 cm depth) was filled with an implanted root bag (root ingrowth core; Lund *et al.*, 1970) adjacent to each of the five plot markers after the previous year's core had been removed during seasonal drawdown (August 2007–2011). After removal, cores were divided into three depths (0–10, 10–20, and 20–30 cm) and washed through a sieve to separate soil from roots. Collected roots were dried to a constant mass at 70 °C and

Table I. Locations of study sites, hydrological units, CRMS water recorders (water level and salinity: LA DNR, 2013), Solinst water recorders, production sites in JLNHP & P, and tree growth sites in JLNHP & P, BTNP, and SMNWR/BBWMA.

Site and years	Location	Site type	Hydrological unit	CRMS # and dates	Solinst and dates	Sonde #0004264 and dates	Site coordinates
Education Center Parking (ECP) 2007–2011	JLNHP & P, LA	Production and tree growth	EC unit	CRMS 0234-H01: 1 January 2002–31 December 2011	Education Center 13 August 2012–27 September 2012	28 August 2012–4 September 2012	29.785N;−90.113W
Education Center Spur (ECS) 2007–2011	JLNHP & P, LA	Production and tree growth	EC unit	CRMS 0234-H01: 1 January 2002–31 December 2011	Education Center 13 August 2012–27 September 2012	na	29.786N;−90.114W
Education Center Canal (ECC) 2007–2011	JLNHP & P, LA	Production	EC unit	CRMS 0234-H01: 1 January 2002–31 December 2011	Education Center 13 August 2012–27 September 2012	na	29.787N;−90.115W
Palmetto Trail (PT) 2007–2011	JLNHP & P, LA	Production	PT unit	CRMS 0188-H01: 1 January 2002–31 December 2011	Education Center 13 August 2012–27 September 2012	na	29.791N;−90.122W
Palmetto Trail Visitors (PTV) 2007–2011	JLNHP & P, LA	Production	PT unit	CRMS 0188-H01: 1 January 2002–31 December 2011	Education Center 13 August 2012–27 September 2012	na	29.789N;−90.121W
Lake Bayou (LB) 2011–2012	BTNP, TX	Tree growth	na	na	na	na	30.150N;−94.096W
Lower Cypress Tract (LCT) 2011–2012	BTNP, TX	Tree growth	na	na	na	na	30.134N;−94.081W
Buckhorn Creek (BUC) 2012	SMNWR, FL	Tree growth	na	na	na	na	30.030N;−84.470W
Mandalay Road (MR) 2012	BBWMA, FL	Tree growth	na	na	na	na	30.129N;−83.962W

CRMS 0234 and CRMS 0188 were on the EC versus PT sides of Barataria Blvd (EC vs PT units, respectively). Sediment elevation tables were inserted into ECP and ECS in 2007 and PT and PTV in 2011. Day-of-visit salinity pore water salinity samples were measured throughout the study, and more intensively in 2011–2012. Surface water salinity at the CRMS recorders were measured from the same height below the soil or water column as the water sensor. Davis Pond Diversion discharge and salinity data were available from 1 January 2008–31 December 2011 (USGS #295501090190400). Also see Figure 1.

CRMS, Coastwide Reference Monitoring System; JLNHP & P, Jean Lafitte National Historical Park & Preserve; BTNP, Big Thicket National Preserve; LA DNR, Louisiana Department of Natural Resources ; BBWMA, Big Bend Wildlife Management Area; SMNWR, St. Marks National Wildlife Refuge.

weighed. Annual sampling allowed many months for the regrowth of roots into the core (Vogt *et al.*, 1998; Hertel and Leuschner, 2002). Other root production approaches could not be used because of flooded seasons in network swamps (water depth >75 cm).

Annual growth (incremental circumference increase) of *T. distichum* trees and knees was measured using dendrometer bands (Anemaet and Middleton, 2013), which were placed on the nearest tree and knee (one each) to mark production plots (plot #1, 3, and 5) along each transect in two sites (ECP and ECS) in JLNHP & P in 2006 ($n=3$ per site). *T. distichum* trees more than 20 m from a large tree and emerged into the canopy were selected for banding. We used a similar procedure to examine tree growth and salinity across the U.S. Gulf Coast, except that we used five trees adjacent to all five production plots in each site in Texas and Florida (Lake Bayou and Lower Cypress Tract vs Buckhorn Creek and Mandalay Road, respectively) (Table I and Figure 1b) in 2011 and 2012, respectively. Note that the bands placed on trees in JLNHP & P in 2006 were of an older style, and could not be measured until 2008 (Anemaet and Middleton, 2013). Tree bands were placed at ~1.5 m height on the tree above any fluting or buttressing. Knee bands were placed ~6 cm from the tip of the knee.

Water dynamics and salinity

Day-of-site visit measurements. Within 1 m of each plot, a sipper was used to extract soil pore water during each site visit (five samples per site). Water was transported in a portable freezer to the lab and the salinity measured with a YSI EC 300® probe. Water depth was measured adjacent to each plot marker with a metre stick.

Water gauge analyses. To study water dynamics over time, we analyzed patterns in daily mean and maximum values of discharge ($m^3 s^{-1}$) and surface water salinity (ppt) from three recording gauges including the Davis Pond Diversion (U.S. Geological Survey #DCPBA03 2013) and CRMS recorders (Table I; CRMS 0234 and CRMS 0188; LA DNR, 2013). Water level and salinity patterns in 2010 (year of hydrologic remediation) were compared with the average of various groups of years in the available data set (2003–2011; long-term), the average of comparably wet years (2008–2011; wet), and each individual year during 2006–2011. All comparisons were conducted for three periods within each year and/or period: pre- (days 1–119; 1 January–30 April), during (days 120–244; 1 May–1 September), and post- (days 245–365; 2 September–31 December).

Water patterns were compared during the year of hydrologic remediation (2010) with sets of long-term, wet, and individual years. We used maximum daily values of both water level and surface salinity for these analyses because maximum values are more likely than mean values to capture short-term changes in photosynthesis. Note that mean versus maximum daily values varied little from each other [mean vs maximum % difference ± standard error (SE) = 1.05 ± 0.0018%].

To determine if short-term water level fluctuation within plots generally followed those of CRMS gauges, we inserted Solinst water level recorders (Levelogger Gold) within the ECP and PT sites in JLNHP & P on 13 August 2012 (~0.5–1.0 km apart within EC unit and PT unit, respectively; Figure 1a and Table I). Daily mean and maximum adjusted water levels and surface salinity levels from CRMS gauges (publically available data) were compared with those from Solinst water recorders and day-of-site visit measurements during periods of overlap (13 August–27 September 4 December 2012; Table I). Mean day-of-visit pore water salinity from sites were compared with those from CRMS gauges during 2011–2012.

Flood water was assumed to be connected by a contiguous water sheet across units and consistent within elevations corresponding to CRMS gauges, Solinst water recorders, sediment elevation table (SET) monuments, plots, and the Sonde. Following this idea, hydrographs were constructed for each Solinst water logger, SET monument, and plot stake by offsetting elevation of the water sheet and matching water level fluctuations with the continuous CRMS gauges within the hydrological unit (i.e. EC unit and PT unit gauge to SET offset: +10 and −50 cm, respectively). Water levels were not adjusted to a common datum. Water depths were measured on days of visits at each plot stake and SET, which here were used as a surface water-recording benchmark (Cahoon *et al.*, 2002); two SETs were placed within both ECP and ECS in 2006, and PT and PTV in 2011 (eight total SETs). Absolute elevations at SETs near ECP/ECS in 2007 were about 0.093 m above sea level (Middleton and Jiang, 2013).

A water gauge was deployed less than 100 m from ECP to examine short-term pulses of water during Hurricane Isaac from 28 August–4 September 2012 (Sonde #0004264; USGS, 2012; Figure 1b and Table I). All water measurement devices in units on both the EC side and PT side of Barataria Blvd detected the pulse signal from Hurricane Isaac (Table I). By comparing water records from these various sources, it was determined that water levels measured with CRMS recorders within EC unit vs PT unit were relevant to those of production plots (Figure 1 in the Supporting Information).

Climate analysis. Monthly total precipitation (mm) and mean temperature (°C) were acquired from a weather station about 1 km away from the JLNHP&P study plots [Marrero 9 SSW Station, LA; 29.7853°N, 90.1158°W] and data from 2002 to 2012 were compared with those of 2010 during pre-remediation, during remediation, and post-remediation periods (NOAA, 2013)].

DATA ANALYSIS

Vegetation production

Annual total litterfall (leaf and wood) was calculated from peak litterfall estimates by determining the percentage of annual litterfall collected during the main season (mean of 2007/2011 correction factor = 0.718 ± 0.176 SE), so that biomass captured during the main season of each year was divided by 0.7180 to express yearly production. This correction factor better portrayed annual total litterfall based on peak litterfall while fully recognizing that certain swamp species do not lose their leaves during this period (e.g. *Myrica cerifera*). Most deciduous trees shed all of their leaves within 30–60 days (Dixon, 1976) from September through mid-November (*T. distichum* swamp; North Carolina; Brinson *et al.*, 1980) or into December farther southward (e.g. South Carolina mixed bottomland forest; Shure and Gottschalk, 1985).

Litterfall totals by year, species, and tissue type (leaf, reproductive, and wood) from 2007 to 2011 were analyzed using repeated measures analysis nesting plot within year in analysis of variance (ANOVA) (one-way or two-way ANOVA; JMP SAS, 2012). For annual log root production, ANOVA was used by nesting plot (depth, year). Root production by year did not interact with depth (year × depth interaction; $p > 0.05$), so that total root production was analyzed by year. The lower two root depths (10–20 and 20–30 cm) did not differ ($t = 0.97$; $p = 0.33$), so that a mean of these two depths was calculated (10–30 cm) and compared with the upper depth (0–10 cm). In all ANOVA analyses, the highest-order significant interaction or main effect was tested using one degree-of-freedom contrasts in JMP SAS (2012). Data were appropriately transformed to meet assumptions of ANOVA and multiple comparisons adjusted using Bonferroni corrections (two one-degree-of-freedom contrasts or three one degree-of-freedom contrasts: $p = 0.025$ or 0.0167, respectively).

Tree and knee growth were analyzed by comparing means of growth (circumference ratios, i.e. year's circumference divided by previous year's circumference) for 2008–2011. For the Gulf Coast-wide assessment of tree growth and salinity, regression analysis compared means of tree growth (circumference ratios) in LA, TX, and FL (2011–2012) versus annual mean salinity. Annual mean salinity was based on the mean of day-of-visit measurements from 2011 to 2012 (7 to 14 measurements with all seasons represented).

Climate

We used ANOVA to compare monthly total precipitation and mean temperature by year and remediation period using the main effects and interactions of year and remediation period.

Water environment and remediation

Water and salinity level shifts and remediation. To determine if the water dynamics differed from expected conditions, we compared mean and maximum values of daily levels of water and surface salinity during times of interest. Because short periods of high salinity or anoxia were likely to affect tree production and growth, we focused on daily maximum water level for these analyses. Water comparisons were made of three time periods in 2010 (pre-remediation, during, and post-remediation) with the same periods in other years in three ways: wet years (mean of 2008–2011), long-term (mean of 2003–2011), and individual years (2006–2011). These comparisons were made using autoregressive integrated moving average (ARIMA) models (detailed description provided in Table 1 in the Supporting Information) generated in SAS Institute Inc. (2002), which are appropriate for comparing water and salinity levels shifts over time because these models can predict the shape of the function and account for the autocorrelation of the samples over time better than other statistical approaches (SAS Institute Inc., 2002). A nonparametric sign test compared number of times the 2010 series had more water or salinity than the average of the comparison series and vice versa.

Predicted daily threshold values of salinity in production plots. To determine the number of days that production sites exceeded threshold values of various salinity levels, the following procedure was followed. Using linear regression, mean daily surface water salinity from CRMS gauges in the EC and PT units on specific days were plotted against mean pore water salinity on day-of-visit in production plots and SET monuments in 2011–2012 (Table I). Equations generated from this process were used to predict daily mean salinity levels in sites from 2008 to 2011 (for equations, see Figure 2 caption in the Supporting Information), as well as the percentage of growing season days (1 April–31 October) each year above certain salinity levels (i.e. 0.1, 0.3, 0.7, 1.0, 1.5, and 2.0 ppt).

RESULTS

Production and vegetation responses to hydrologic remediation

Total litter biomass was 2.7 times higher after hydrologic remediation in 2010 and 2011 than before remediation in 2007–2009 (Figure 2a; Table IIa; one degree-of-freedom contrast: $t = 83.8$, $p < 0.0001$). In litterfall, *T. distichum* leaf biomass was 3.1 and 2.5 times higher in 2010 and/or 2011, respectively, than in 2007–2009 (Table IIa), while reproductive biomass was 7.7 times in 2011, but not different in 2010 (Table IIa and Table III). In addition, leaf and reproductive tissue biomass in litterfall was higher in 2010

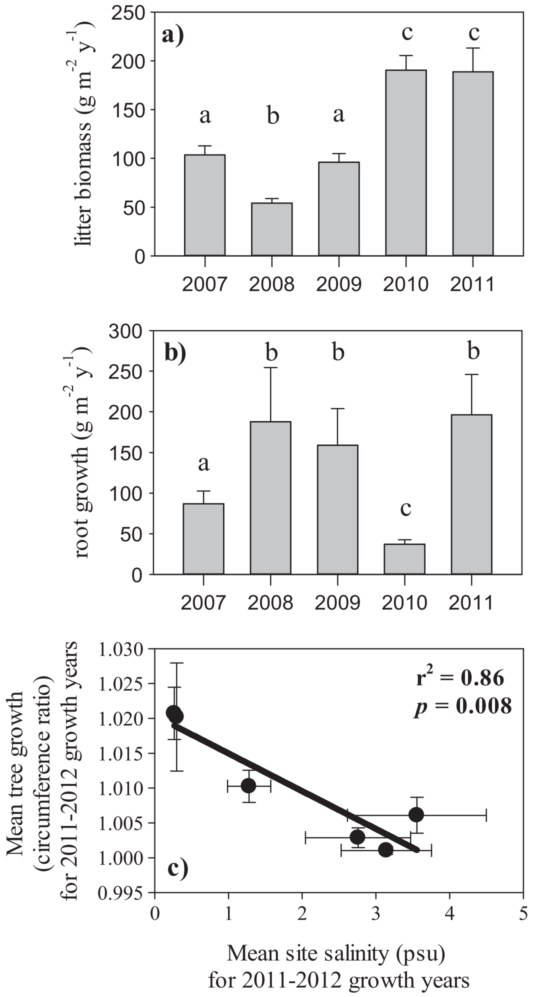

Figure 2. Total annual mean production from 2007 to 2011 including (a) total litter biomass (leaf, reproductive, and wood) [$g\,m^{-2}\,y^{-1} \pm$ standard error (SE)], and (b) total annual root biomass (total of all depths, 0–30 cm; $g\,m^{-2}\,y^{-1} \pm$ SE) in Jean Lafitte National Historical Park & Preserve ($n = 25$). Different letters indicated that means of years differed statistically (one degree-of-freedom contrasts: $p < 0.05$). (c) Regression analysis of stem growth expressed as mean salinity (ppt) versus *Taxodium distichum* circumference ratio ± SE along the Gulf Coast ($R^2 = 0.86$). Salinity is based on means of pore water salinity during day-of-visit measurements.

and/or 2011 than in 2007–2009 for *Acer rubrum* (not in 2007), *Liquidambar styraciflua*, and *M. cerifera* (Table IIa and Table III). Annual litterfall biomass of wood tissue did not change from 2007 to 2011, although the mean was substantially higher in 2010 (Table IIb; $p < 0.05$). Annual log root biomass was higher in shallower than deeper soil depths (Figure 2b and Table IIb; 0–10 vs 10–30 cm; $t = -2.79$, $p = 0.0058$, $N = 5$), and total root biomass varied by year and was 2.3–5.3 times lower in 2010 than in 2007–2011 (Figure 2b; $t = 4.89$, $p < 0.0001$, $N = 5$).

Neither tree nor knee growth varied with circumference increasing by 1.8 ± 0.1% and 2.9 ± 1.0%, respectively, per year during 2008–2011 in JLNHP & P ($p > 0.05$; Table IIc–d). In JLNHP & P, we found no relationship between tree growth and the percentage days per year a site exceeded published thresholds of salinity (e.g. 0.7 or 2.0 ppt; $p > 0.05$; Table IV). In 2010, both EC and PT units had fewer days with salinity >0.3 ppt, and in 2008, more days with salinity >2.0 ppt (Table IV; Figure 1 in the Supporting Information). Across the Gulf Coast, *T. distichum* growth varied from 0.11% to 2.1% increase in circumference per year with average annual salinity explaining 86% of the variance in growth with the highest growth observed in the lowest mean pore water salinity (e.g. JLNHP & P; Figure 2c).

Climate and environment

Regionally, mean annual precipitation was 1320.9 ± 106.5 mm per year from 2002 to 2012 (National Oceanic and Atmospheric Administration (NOAA), 2013) but did not vary by year or remediation period ($p > 0.130$; Table V). Mean monthly air temperature did not vary by year but did vary by remediation period (mean monthly temperatures during pre-remediation, remediation, and post-remediation: 15.7 ± 0.6 °C, 26.9 ± 0.3 °C, and 18.7 ± 0.8 °C, respectively; $F = 81.7$, $p < 0.001$; Table V) (NOAA, 2013).

Water and salinity responses to hydrologic remediation

Short-term water and salinity comparisons – 2010 versus wet years (2008–2011). Davis Pond, CRMS 0188, and CRMS 0234 had higher discharge/water level and lower salinity during the remediation period in 2010 than during wet years. As based on ARIMA time series comparisons, water discharged from Davis Pond in 2010 exceeded mean and maximum daily discharge of wet years (mean daily discharge of 2010 vs wet years: 113 out of 119 days, respectively; maximum daily discharge of 2010 vs wet years: 102 out of 119 days, respectively; sign tests: $p < 0.0001$; Figure 3a and Table 2 in the Supporting Information). Discharge rates from the Davis Pond Freshwater Diversion and water levels at gauges were lower in 2010 during the post-remediation period than in wet years (Figure 3a and Table 2 in the Supporting Information). Maximum daily gauge levels were higher during hydrologic remediation in 2010 than in wet years (CRMS 0234: 0.26 vs 0.11 m, respectively; Figure 3b; CRMS 0188: 1.15 vs 1.06 m, respectively; Figure 3c and Table 2 in the Supporting Information).

Long-term gauging stations can be used to indicate conditions at sites even though salinity relationships were somewhat different (i.e. EC sites had significantly higher salinity than CRMS 0234, and PT sites had significantly lower salinity than CRMS 0188 as based on day-of-visit measurements). Salinity environments in the EC and PT sites were relatively similar (Figure 2 in the Supporting Information). Nevertheless, maximum daily water levels at CRMS 0234 were linearly related to day-of-visit water

Table II. Analysis of variances of production variables in JLNHP & P from 2007 to 2011.

	DF	F	p		Mean ± SE
(a) Total annual production					
Litterfall ($g\,m^{-2}\,y^{-1}$)					
Year	4	23.6	<0.0001	***	
Root biomass ($g\,m^{-2}\,y^{-1}$)					
Year	4	8.4	<0.0001	***	
Depth	1	7.8	0.0225	*	
Year × depth	4	1.0	0.4142	n.s.	
(b) Tissue type					
Leaf					
Species	15	15.5	<0.0001	***	
Year	4	156.6	<0.0001	***	
Species × year	60	4.1	<0.0001	***	
Reproductive					
Species	5	40.0	<0.0001	***	
Year	4	6.9	<0.0001	***	
Species × year	20	4.4	<0.0001	***	
Wood					
Year	4	2.1	0.0794	n.s.	
(c) Tree growth (annual circumference ratio)					
Initial tree circumference (covariate)	1	3.8	0.0668	n.s.	
Year	3	0.1	0.9718	n.s.	
2008					1.019210 ± 0.0055
2009					1.018628 ± 0.0071
2010					1.018855 ± 0.0038
2011					1.015170 ± 0.0022
(d) Knee growth (annual circumference ratio)					
Initial knee circumference (covariate)	1	0.5	0.4945	n.s.	
Year	4	0.9	0.4628	n.s.	

Mean total annual production of (a) litterfall ($g\,m^{-2}\,y^{-1}$; including leaves, reproductive material, and wood), and log root biomass ($g\,m^{-3}\,y^{-1}$). (b) Mean biomass of tissue types of dominant species including leaf, reproductive, and wood. Dendrometer bands were used to measure incremental increase in circumference; growth was estimated as a year-to-year ratio of circumference change of *Taxodium distichum* from 2008 to 2011 for (c) trees and (d) knees. Mean comparisons that differed based on contrasts indicated by '***', '*', or n.s. ($p < 0.0001$, $p < 0.05$, $p > 0.05$, respectively; Figure 2). See Table III for tissue type × species interactions.
JLNHP & P, Jean Lafitte National Historical Park & Preserve; SE, standard error; DF, degrees of freedom; n.s, not significant.

depths at SETs in the EC unit (i.e. SETs at ECP and ECS; Figure 2 in the Supporting Information; $r = 0.6043$, $p = 0.0015$). As indicated in the Section on Methods to justify the selection of salinity variables and analyses, overall maximum daily values were within 1.05 ± 0.0018% of mean values. Mean daily salinity levels at CRMS 0234 and CRMS 0188 were linearly related to day-of-visit salinity at SETs and plots within the same hydrological units (EC unit: $r = 0.600$, $p = 0.0004$, Figure 2b in the Supporting Information; PT unit: $r = 0.702$, $p = 0.0005$, Figure 2c in the Supporting Information).

Long-term water level comparisons – 2010 versus long-term (2003–2011). Water discharge from Davis Pond in 2010 during hydrologic remediation was higher than in the long-term set of years (2003–2011; mean discharge per day = 198.3 ± 4.9 vs 33.1 ± 1.6 $m^3\,s^{-1}$, respectively), and maximum daily water levels at CRMS 0234 and CRMS 0188 also were higher (sign tests: $p < 0.0001$; Figure 4 in the Supporting Information).

Individual year water and salinity level comparisons – 2010 vs 2006–2011. Comparisons of maximum daily water level and salinity levels during 2010 to individual years were similar to the comparisons of 2010 to sets of wet and long-term years (i.e. 2008–2011 and 2003–2011, respectively). As expected, discharge levels for Davis Pond and water levels at CRMS 0234 and CRMS 0188 were significantly higher during hydrologic remediation in 2010 compared with those in any individual year from 2006 to 2011 ($p < 0.0001$). One exception was that maximum salinity was higher in 2010 than in 2009 at CRMS 0234 ($p < 0.0001$).

DISCUSSION

Freshwater flow variability controls ecological processes in estuaries so that alteration of water delivery is a key conservation challenge (Lester *et al*., 2013). Unfortunately, information on how to manage salinity flux in freshwater wetlands in altered estuaries is lacking (Kaplan *et al*., 2010;

Table III. Means ± SE listed by species dominance of dry litterfall biomass ($g\,m^{-2}$) based on species × year interactions for leaf, reproductive, and wood tissue from 2007 to 2011 in JLNHP & P.

	Year				
Species	2007	2008	2009	2010	2011
Leaf tissue					
Taxodium distichum	26.4 ± 4.8 ^{b}	15.0 ± 2.5 ^{c}	29.1 ± 4.8 ^{b}	**72.3 ± 9.1** ^{a}	**59.0 ± 11.2** ^{a}
Acer rubrum	23.9 ± 5.3 ^{ab}	12.3 ± 2.6 ^{b}	18.4 ± 435 ^{b}	**24.9 ± 4.5** ^{a}	**25.8 ± 4.7** ^{a}
Fraxinus pennsylvanica	6.5 ± 2.1 ^{b}	2.8 ± 0.9 ^{c}	11.7 ± 2.9 ^{a}	13.6 ± 3.8 ^{a}	3.4 ± 2.2 ^{c}
Liquidambar styraciflua	4.7 ± 1.4 ^{b}	2.3 ± 0.6 ^{b}	4.5 ± 1.7 ^{b}	**6.9 ± 1.4** ^{a}	4.9 ± 1.6 ^{b}
Nyssa aquatica	8.0 ± 2.6 ^{a}	0.9 ± 0.8 ^{b}	1.4 ± 1.2 ^{b}	1.9 ± 1.1 ^{b}	0.0 ± 0.0 ^{b}
Myrica cerifera	0.0 ± 0.0 ^{c}	1.8 ± 0.7 ^{b}	2.3 ± 0.7 ^{b}	**4.1 ± 1.2** ^{a}	2.1 ± 0.7 ^{b}
Salix nigra	2.2 ± 1.1 ^{a}	1.3 ± 0.9 ^{a}	0.2 ± 0.1 ^{a}	3.9 ± 3.5 ^{a}	1.7 ± 1.6 ^{a}
Ulmus americana	1.0 ± 0.6 ^{a}	0.1 ± 0.1 ^{b}	0.4 ± 0.2 ^{b}	1.4 ± 0.8 ^{a}	2.1 ± 0.9 ^{a}
Quercus nigra	0.7 ± 0.2 ^{a}	0.1 ± <0.1 ^{a}	0.8 ± 0.3 ^{a}	1.6 ± 0.6 ^{a}	0.9 ± 0.5 ^{a}
Other leaf	1.2 ± 0.4 ^{c}	1.8 ± 0.7 ^{c}	2.6 ± 0.7 ^{b}	4.5 ± 1.5 ^{b}	14.4 ± 3.2 ^{a}
Cephalanthus occidentalis	2.3 ± 0.9 ^{a}	0.0 ± 0.0 ^{b}	0.1 ± 0.1 ^{b}	<0.1 ± <0.1 ^{b}	0.0 ± 0.0 ^{b}
Acer spp.	2.2 ± 1.8 ^{a}	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}
Carya aquatica	0.0 ± 0.0 ^{a}	1.8 ± 0.9 ^{a}	0.2 ± 0.2 ^{a}	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}
Quercus spp. (red)	0.5 ± 0.4 ^{a}	0.3 ± 0.2 ^{a}	0.2 ± 0.1 ^{a}	0.4 ± 0.2 ^{a}	0.0 ± 0.0 ^{a}
Triadica sebifera	0.0 ± 0.0 ^{a}	0.2 ± 0.1 ^{a}	0.1 ± <0.1 ^{a}	0.9 ± 0.6 ^{a}	0.6 ± 0.3 ^{a}
Gleditsia aquatica	1.4 ± 0.6 ^{a}	0.0 ± 0.0 ^{b}	0.0 ± 0.0 ^{b}	0.0 ± 0.0 ^{b}	0.0 ± 0.0 ^{b}
Reproductive tissue					
Taxodium distichum	6.5 ± 3.0 ^{b}	0.6 ± 0.4 ^{c}	5.5 ± 3.1 ^{b}	5.7 ± 1.8 ^{b}	**32.5 ± 13.9** ^{a}
Other reproductive	<0.1 ± <0.1 ^{b}	<0.1 ± <0.1 ^{b}	0.2 ± 0.1 ^{b}	0.2 ± 0.1 ^{b}	**4.4 ± 2.4** ^{a}
Fraxinus pennsylvanica	0.5 ± 0.1 ^{b}	0.4 ± 0.1 ^{b}	0.3 ± 0.1 ^{b}	**2.5 ± 0.7** ^{a}	0.1 ± 0.1 ^{b}
Liquidambar styraciflua	0.9 ± 0.9 ^{a}	0.0 ± 0.0 ^{a}	<0.1 ± <0.1 ^{a}	0.5 ± 0.5 ^{a}	0.0 ± 0.0 ^{a}
Nyssa aquatica	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}	0.0 ± 0.0 ^{a}	0.4 ± 0.4 ^{a}	0.0 ± 0.0 ^{a}
Wood tissue					
Wood total, all species	2.2 ± 0.5 ^{a}	2.8 ± 1.2 ^{a}	5.0 ± 2.1 ^{a}	12.9 ± 5.4 ^{a}	9.2 ± 4.3 ^{a}

Different letters indicate significant differences of litterfall biomass of species based on one-degree-of-freedom contrasts. Dominant species are listed with biomass >$0.2\,g\,m^{-2}$, with the biomass of non-dominant species summed in an ‘other’ group. Species with significantly higher litterfall in 2010 and/or 2011 after Bonferroni correction are listed in bold letters.
SE, standard error.

Kingsford, 2011). Out of necessity, programmes to manage flood flow are emerging in the United States, Australia, South Africa, and to a lesser extent Europe (Hughes and Rood, 2003). As an example, the Comprehensive Master Plan for Louisiana has proposed to use diversions to release river water and sediment to rebuild coastal wetlands (CPRA, 2012). While managed flood releases are used increasingly in restoration (Middleton, 1999; Schmidt *et al*., 2001; Souter *et al*., 2014), these approaches may become even more important as salinity increases with changes in climate, sea level, subsidence, and surface/groundwater levels (Poff *et al*., 2002; Kaplan *et al*., 2010; Souter *et al*., 2014). Studies such as ours can inform management procedures to explore the utility of freshwater release for coastal conservation.

Various studies demonstrate the potential benefits of short periods of increased freshwater flow to hydrologically altered coastal forests. While hydrologic remediation lasted only 2 to 4 months in this study and the Souter *et al*. 2014 study, tree responses were impressive. After freshwater remediation in JLNHP & P, high levels of above-ground litter production persisted for several species for one or more growing season (this study). Similarly, healthy trees of *Eucalyptus camaldulensis* Dehnh. in the Murray River drainage (Australia) vigorously grew more foliage, while highly stressed or defoliated trees responded positively but less vigorously for two growing seasons following ~2 months of freshwater release (Souter *et al*., 2014). In the Lake Pontchartrain Basin of Louisiana, coastal *T. distichum* trees grew two times faster with periodic flow of river water (Day *et al*., 2012). In addition, reproductive output was higher in 2010 and especially in 2011 for certain tree species, suggesting that resource matching may have occurred, i.e. species varied reproductive output to match available resources (Kelly, 1994). In the context of this study, the hydrologic remediation may have allowed these trees to build up their physiological resources via higher levels of photosynthetic activity prior to mass flowering.

Environmental flow prescriptions might revive moribund coastal swamps, yet no definitive range of flow amount or timing has been identified to improve environments related to salinity, anoxia, nutrients, or other factors. We linked sharply higher production of litter (leaf and reproductive) in 2010 to hydrologic remediation in salinity levels well below 2.0 ppt with maximum measured values at plots of EC vs PT sites: 0.4

Table IV. Percentage of days exceeding predicted values for maximum and mean daily salinity levels (ppt) in the EC and PT units in JLNHP & P (sites: ECS/ECP/ECC vs PT/PTV, respectively).

Year	Unit	Total days	% Days per year exceeding maximum						% Days per year exceeding mean					
			>0.1	>0.3	**> 0.7**	>1.0	>1.5	**>2.0**	>0.1	>0.3	**> 0.7**	>1.0	>1.5	**>2.0**
2008	**EC-**	**214**	100.0	22.9	19.6	0.0	0.0	0.0	100.0	21.5	19.2	0.0	0.0	0.0
2009	**EC-**	**214**	100.0	88.3	0.0	0.0	0.0	0.0	100.0	82.7	0.0	0.0	0.0	0.0
2010	**EC-**	**214**	100.0	37.8	0.0	0.0	0.0	0.0	100.0	19.6	0.0	0.0	0.0	0.0
2011	**EC-**	**125**	100.0	63.2	0.0	0.0	0.0	0.0	100.0	49.6	0.0	0.0	0.0	0.0
2008	**PT-**	**214**	76.1	35.9	28.0	28.0	19.2	6.5	72.4	28.0	28.0	28.0	18.2	3.2
2009	**PT-**	**214**	73.5	47.0	1.9	0.0	0.0	0.0	70.1	36.9	1.4	0.0	0.0	0.0
2010	**PT-**	**214**	93.0	13.6	0.0	0.0	0.0	0.0	85.5	0.0	0.0	0.0	0.0	0.0
2011	**PT-**	**214**	86.9	75.7	8.4	1.4	0.0	0.0	81.8	75.2	2.8	1.4	0.0	0.0

Percent (%) days per year exceeding the specified maximum or minimum values of salinity (e.g. >0.1 to 2.0 ppt) were predicted from linear regression analysis of surface salinity levels at CRMS 0234 and CRMS 0188 gauges (EC and PT units, respectively) versus day-of-visit pore water salinity at production sites including ECS/ECP/ECC and PT/PTV (Figure 4). Total days are the number of days per year during the growing season (1 April–31 October 2008–2011). Published threshold salinity levels for forest tree maintenance/flooded seedling photosynthesis and basal area growth (size) are thought to be 2.0 and 0.7 ppt (in bold letters; Kaplan *et al.*, 2010/Pezeshki *et al.*, 1987, and Krauss *et al.*, 2009, respectively). Dark to light grey highlights indicate percent (%) days per year exceeding maximum values as 70–100%, 30–70%, 1–30%, and 0%, respectively.
ECS, Education Center Spur ; ECP, Education Center Parking ; ECC, Education Center Canal ; PT, Palmetto Trail; PTV, Palmetto Trail Visitors ; EC, Education Center; JLNHP & P, Jean Lafitte National Historical Park & Preserve.

Table V. Analysis of variances of climate variables for JLNHP & P from Marrero 9 SSW weather station data (NOAA, 2013) for years 2002–2012, remediation periods relative to the hydrologic remediation period in 2010 (pre-remediation, remediation, and post-remediation) including mean monthly (a) total precipitation and (b) temperature.

Variable	DF	*F*	*p*	
(a) Precipitation				
Year	10	1.2	0.3339	
Remediation period	2	2.1	0.1297	
Year × remediation period	20	1.1	0.4077	
(b) Temperature				
Year	10	0.1	0.9989	
Remediation period	2	81.7	<0.0001	***
Year × remediation period	20	0.2	0.9999	

DF, degrees of freedom.

and 0.5 ppt, respectively (also see Figure 2a and Table IV). In contrast to 2008, predicted levels of salinity were high in both the EC and PT units (Table IV), and total annual leaf litter biomass by individual species was low (*A. rubrum*, *T. distichum*, *Fraxinus pennsylvanicum*, *M. cerifera*, and *Salix nigra*; Figure 2a and Table III). Nevertheless, rendering a simple statement of an ideal threshold of salinity for these swamps is impractical. Among other problems, field environments are difficult to characterize simply (e.g. salinity levels vary by depth in the vadose zone).

Trees in JLNHP & P responded positively to remediation, but we recognize that this unplanned study did not permit us to determine whether changes in salinity or some other unmeasured biogeochemical factors were ultimately responsible for the observed responses. Tidal flow reconnection in previously restricted salt marshes decreases soil anoxia and sulphides, and changes pH, nutrient availability, and decomposition rates (Anisfeld and Benoit, 1997). The fact that we detected increased water levels and decreased salinity with freshwater remediation indicated that other important site characteristics and biogeochemical shifts likely were occurring at JLNHP & P. Unfortunately, we do not have any other supportive data especially as related to any possible causal linkages.

Photosynthetic stressors such as salinity and anoxia may be more harmful during the growing season. Flooding reduces regeneration; seedlings and saplings of *T. distichum* survive overtopping by flooding while dormant but not during the growing season, and most tree species will not germinate underwater (Middleton, 2000). A better understanding of any seasonal component of remediation response is critical to hydrologic remediation planning for management.

The immediate mechanisms of increased tree production with improved environment are not well studied, but may be related to the photosynthetic regulation of trees to changes in environment. As salinity (at some level) enters the transpiration stream, stomata close and photosynthesis decreases (Stiller, 2009). Any short-term increase in

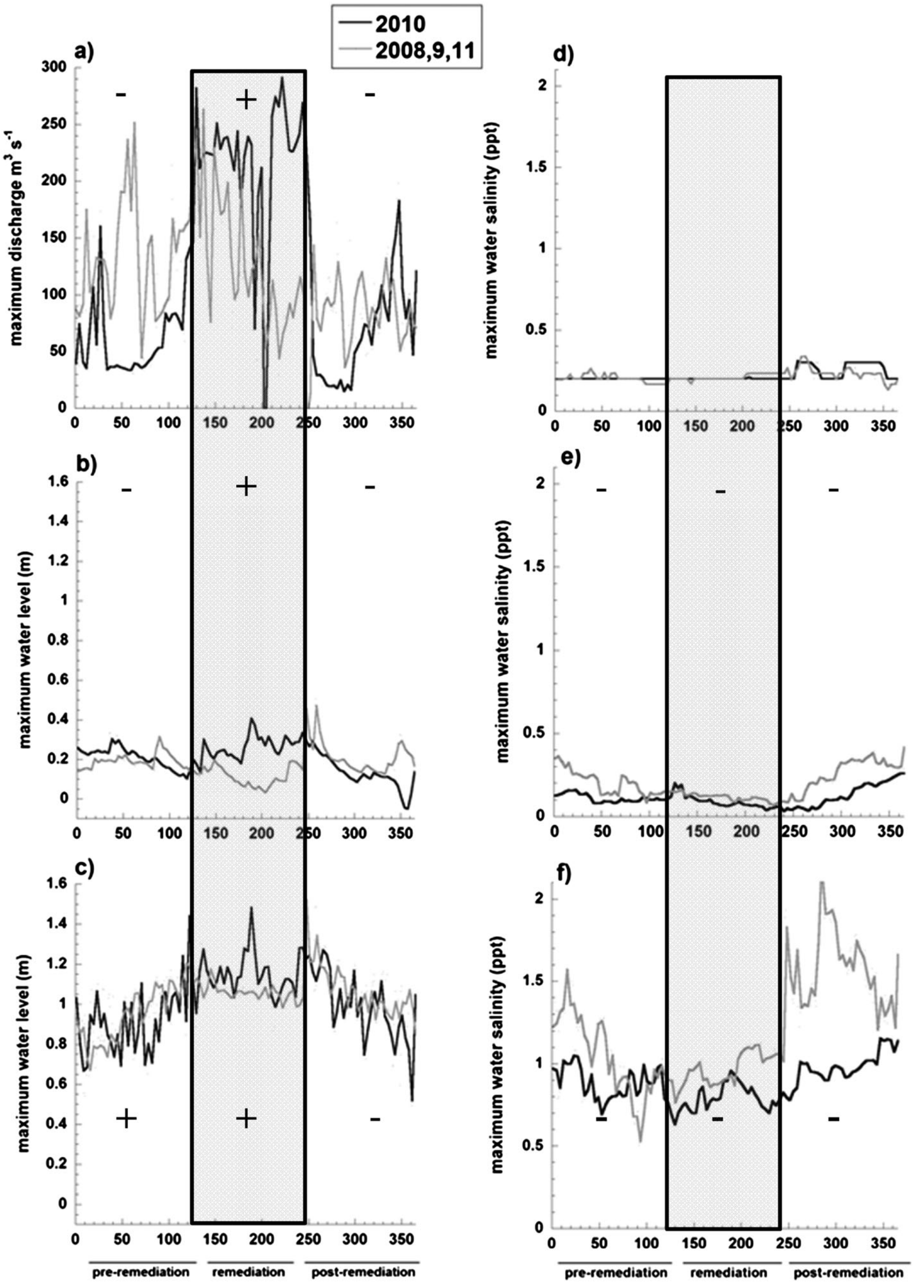

Figure 3. State of Louisiana water recorder information for maximum (a) daily discharge ($m^3 s^{-1}$) from Davis Pond Diversion and adjusted water levels (m) at (b) Coastwide Reference Monitoring System (CRMS) 0234 and (c) CRMS 0188; and salinity (ppt) of (d) discharge of diversion and surface water at (e) CRMS 00234 and (f) CRMS 0188 during hydrologically remediated (2010) versus 'wet' years (mean of 2008, 2009, and 2011). CRMS 0234 and CRMS 0188 are in the same hydrological units as the Education Center and Palmetto Trail plots, respectively, in JLNHP & P. Pre-remediation, remediation, and post-remediation days of the year included days 1–119, 120–244, and 245–365, respectively. Sign tests indicated that 2010 was higher, lower, or not different from wet years as '+', '-', or 'n.s.', respectively ($p < 0.0001$). Only significant variables of time were kept. p values for the sign test comparisons were based on normally distributed error with constant variance. All tests of fit were performed at $p = 0.05$, except that one test was performed at $p = 0.01$ to obtain a model fit. Equations were based on the difference of the two year groups (2010 vs set of years compared). Mean daily discharge values are not shown, but these comparisons were also significant using similarly constructed ARIMA models and sign tests ($p < 0.0001$). Note that short periods of missing data were interpolated linearly. Longer periods of missing data were omitted, e.g. Davis Pond Diversion had no discharge data available for 1–28 January 2010. Note that the measured water and salinity levels at plots in the EC and PT units were intermediate and similar to each other (see Supplementary Figure 2).

photosynthetic output and leaf production after freshwater remediation is most likely to occur in healthy trees with relatively intact leaf architecture such as *T. distichum* in JLNHP & P or *E. camaldulensis* trees along the Murray River in Australia (Souter *et al.*, 2014). The positive effects of remediation may have broad application in freshwater forests, particularly because several species responded positively to freshwater remediation in JLNHP & P.

In our study, litter but not root production increased during the year of hydrologic remediation. If environment conditions improved in 2010, trees may have been experiencing a fast spurt of leaf litter production at the expense of roots (Figure 2b). Falling root:shoot ratios are an indicator of fast shoot growth in response to favourable environments (Harris, 1992; Litton *et al*., 2007), and *T. distichum* root and shoot allocation patterns shift in response to changing resources (Megonigal and Day, 1992). Note that we did not distinguish between species of roots in our study. Alterations in root and shoot allocations following hydrologic remediation may have important implications for the elevation of subsiding swamps by influencing peat accumulation. The decrease in root growth during remediation is important because root tissues often contribute more to the accumulation of peat than leaf or woody tissue (Middleton and McKee, 2002). While reinvigorating the production of freshwater coastal vegetation overall, hydrologic remediation may reduce root growth for some tree species at least temporarily (this study). Therefore, a better understanding of the relationship of remediation and root growth is critical (Langley *et al*., 2010, Wigand *et al*., 2014) to the development of management techniques related to remediation.

CONCLUSION

Concerns are growing because of losses of coastal wetlands along the Gulf Coast (Kaplan *et al*., 2010; CPRA, 2012). Special attention should be given to our findings that freshwater release might reinvigorate the production of freshwater coastal vegetation. Our study has worldwide implications in that it demonstrates that sustained releases of freshwater can affect the primary production of many species. Freshwater coastal species are increasingly affected by saltwater intrusion, so this idea deserves further exploration for the management of coastal freshwater wetlands.

ACKNOWLEDGEMENTS

This work is funded by the U.S. Geological Survey and National Science Foundation (DEB-1049838). Special thanks are given to Evelyn Anemaet, Mel McCullough, Samantha Primer, Justin Stelly, Lei Ting, and Guodong Wang for their 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.

CONFLICT OF INTEREST

The authors declare no conflict of interest with this research.

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