



Stand density and carbon storage in cypress-tupelo wetland forests of the Mississippi River delta



Brandon L. Edwards^{a,*}, Scott T. Allen^b, DeWitt H. Braud^c, Richard F. Keim^d

^a USDA-ARS-Jornada Experimental Range, P.O. Box 30003, MSC 3JER, NMSU, Las Cruces, NM 88003, USA

^b Dept. of Environmental Systems Science, ETH Zurich, Zurich 8092, Switzerland

^c Coastal Studies Institute, Louisiana State University, Baton Rouge, LA 70803, USA

^d School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA

ARTICLE INFO

Keywords:

Forested wetlands
Mississippi River delta
Baldcypress
Water tupelo
Carbon cycle
Coastal change

ABSTRACT

Forested wetlands play a vital role in the coastal zone, but their vulnerability to coastal change—and the impact to high-value ecosystem services—is not as well established as that of more seaward systems such as saltmarsh and mangroves. To address this need, we develop field-based stand density classes, then classify baldcypress-water tupelo (*Taxodium distichum* (L.) Rich var. *distichum*; *Nyssa aquatica* L.) stand density on the Mississippi River delta using a multitemporal ordination of reflectance from Landsat Thematic Mapper imagery. Approximately 29, 50, and 21% of forest was classified as full canopy, intermediate, and open canopy, respectively. We estimate stand-level live-stem carbon stocks and annual accumulation rates of 96, 67, and 39 t-C ha⁻¹ and 1.9, 1.4 and 0.8 t-C ha⁻¹ yr⁻¹ for full-canopy, intermediate, and open-canopy forest, respectively. Regional live-stem carbon stocks are ~ 69 t-C ha⁻¹, and total carbon and annual increment for all forest analyzed are ~17 Mt-C and ~0.34 Mt-C yr⁻¹. Much of the cypress-tupelo forest on the delta stores carbon at rates significantly below the potential of fully stocked stands, yet overall rates of accumulation are comparable to other forest types and coastal systems. Delta-wide, there is a well-defined coastward gradient of stand density, which has important implications for the future of deltaic forests and their ecosystem services. The similarities between forest density gradients and well-documented marsh loss patterns in the region suggest that the same processes driving coastal marsh loss—relative sea level rise exacerbated by human activity—are likely responsible for a second, more gradual interface of land loss at the marsh-forest boundary. Results highlight the potential response of coastal forests to continued environmental change—and associated impacts to the carbon cycle—and provide a baseline for detecting future change to forests on the Mississippi River delta.

1. Introduction

Given current and projected relative sea level rise coupled with human pressure and intensive hydrological management, many of the world's deltas and coastal wetlands are vulnerable to land loss and ecosystem conversions (Coleman et al., 2008; Giosan et al., 2014; Syvitski et al., 2009; Tessler et al., 2015). Much of the global discussion and efforts to mitigate loss and restore coastal systems has focused on marsh and nearshore environments (e.g., CPRA, 2017), but wetland forests also play an important role in the coastal zone. For example, they store and release carbon, provide critical habitat, and stabilize soils—among other high-value ecosystem services (e.g., Day et al., 2004; Dybala et al., 2018; Krauss et al., 2018).

Deltaic freshwater forests can extend far inland from the coastline yet remain vulnerable to broad-scale coastal change processes,

especially on the Mississippi River delta (e.g., Craig et al., 1979; Day et al., 2007; Pezeshki et al., 1990). Forested wetlands occupy a unique niche in the flooding continuum; flooding creates long periods of inhospitable conditions punctuated by periodic episodes of pro-regenerative conditions sufficient to sustain forest (Mattoon, 1915). Baldcypress (*Taxodium distichum* (L.) Rich var. *distichum*) and water tupelo (*Nyssa aquatica* L.) compete well under these conditions and form the nucleus of the cypress-tupelo swamp ecosystem that occupies many deepwater swamp regions of the delta and riparian corridors across the southeastern USA (Conner and Buford, 1998). Both are long-lived canopy species that can grow vigorously in flooded conditions, but, because of physiological responses to drivers operating over multiple spatial and temporal scales, they often form stands of varying structure and density (Allen et al., 2015; Keim et al., 2013). Cypress-tupelo swamps are resilient, but salinity severely limits growth and can

* Corresponding author.

E-mail address: bedwar4@nmsu.edu (B.L. Edwards).

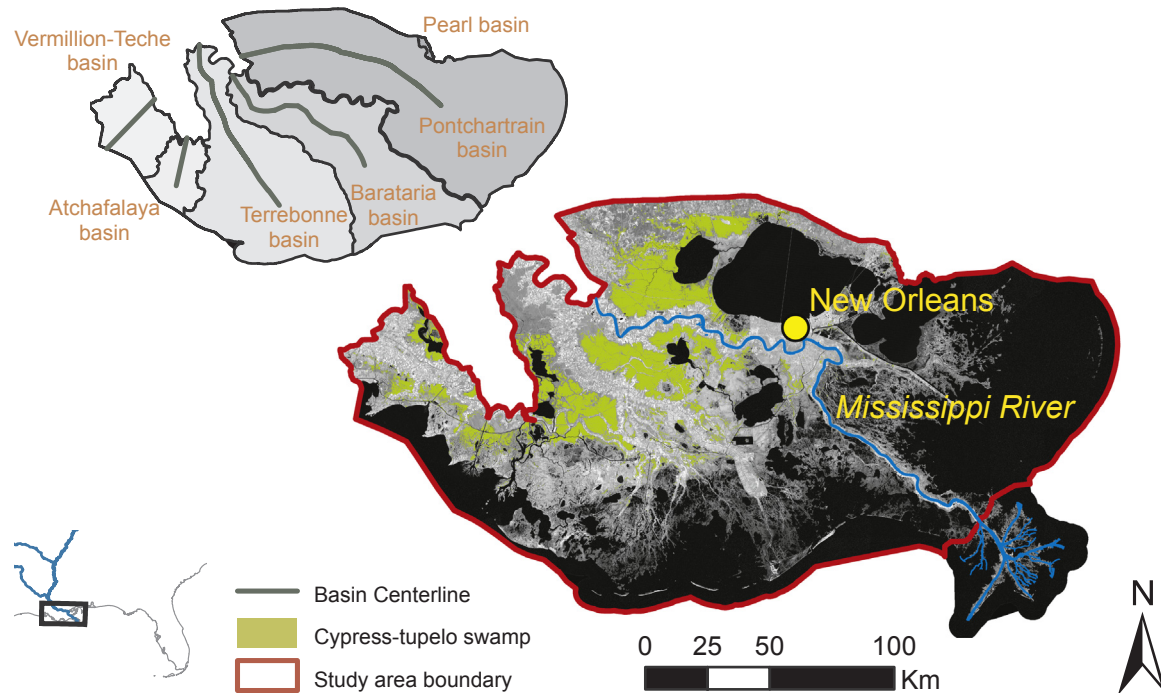


Fig. 1. Study area, coastal basins and digitized centerlines, and cypress-tupelo forested wetland pixels classified. Basin centerlines extend from the upper margin (normalized distance = 0) to the seaward of extent (normalized distance = 1) of forest in each basin. Background image: 2005 Landsat TM mosaic of Louisiana (LOSCO, 2007).

lead to mortality while increasing water levels or prolonged inundation prevent regeneration (Allen et al., 1996; Egler and Moore, 1961; Krauss et al., 2009). Large areas of forest on the delta have already converted to treeless marsh or open water because of these stressors (Craig et al., 1979; Shaffer et al., 2016), which has led stakeholders, researchers and policy makers to ask: *what is the future of cypress-tupelo forest in the delta?* This is a globally significant question because of the extent of the delta and its impact on global carbon and nutrient cycling but is difficult to answer because mechanistic understanding of the relationships between tree vigor, stand density, and flooding are lacking (Allen et al., 2019; Keim et al., 2006) and time scales of response in forests are often long relative to more seaward systems.

Because we lack mechanistic understanding to predict the fate of deltaic forests in the face of rapid change, robust data are needed to link patterns in forest structure and ecological services with broad-scale coastal change. Nowhere is this need greater than in the delta of the Mississippi River, where cumulative effects of hydrologic modifications to the river and its distributaries have resulted in tipping the balance between deltaic and marine processes, causing widespread land loss and ecosystem conversions (e.g., Day et al., 2000; Shaffer et al., 2009, 2016). To understand the trajectory of deltaic cypress-tupelo forest, we analyze gradients in stand density to infer driving mechanisms. We then use field-based measurements of stand structure and growth to produce estimates of stand- and landscape-level live-stem carbon stocks and accumulation rates. Results highlight the contribution of deltaic wetland forests (compared to e.g., marsh and mangroves) to the global carbon cycle, and indicate that broad-scale coastal change processes (i.e., sea level rise and increasing salinity) largely drive gradients in deltaic wetland forest density, which have significant implications for carbon storage potential. The data presented here also provide a baseline for detecting future change to forests on the delta in addition to highlighting the need for further research on how coastal change processes are impacting forested wetlands globally.

2. Study site

The Mississippi River deltaic plain comprises a series of delta lobes (Roberts, 1997). The location of active delta building changes at a frequency of ~1–2 kyr and includes three stages of development: rapid growth, stability, and abandonment (Roberts, 1997). Following abandonment, marine processes dominate progressively further landward as subsidence occurs over the relict lobe (Penland et al., 1988). The areas between former alluvial, distributary ridges form coastal basins which support ecosystems that transition from forested wetlands to fresh, brackish, and salt marsh, to open estuary (Coleman et al., 1998; Roberts, 1997). Cypress-tupelo swamp is the dominant forest type in the major inter-distributary basins of the delta.

Forested wetlands are a vital component of the delta and contribute high-value ecosystem services such as water quality, biodiversity, primary production, and carbon sequestration, and act as a dampening barrier to storm damage (e.g., Conner and Day, 1976; Engle, 2011; Gresham et al., 1991). Many coastal systems trap sediments and produce organic material to maintain elevation despite ongoing subsidence, but reductions in sediment load from the river over the past two centuries have largely negated this mechanism (Paola et al., 2011). Declining freshwater influxes because of flood control structures have also led to changes in salinity, altering ecosystems, biogeochemical pathways, and decomposition rates (Delaune and Pezeshki, 2003). Increasing salinity coupled with deeper flooding from sea level rise can result in episodic mortality (Day et al., 2012), stress to individual trees (Krauss et al., 2009; Shaffer et al., 2009), and recruitment limitation (Effler and Goyer, 2006; Jones et al., 1994). Further, flood control, navigation systems, and other hydrologic modifications have fragmented wetlands, creating local, stagnant impoundments (e.g., Conner et al., 1981; Ko and Day, 2004). Together, these factors have accelerated ecological transitions from forest to marsh and open water associated with progressive subsidence of relict delta complexes (Penland et al., 1988; Roberts, 1997).

Forest condition data presented here are from a series of efforts to classify discrete reaches of cypress-tupelo forest separated by major

relict distributary ridges of the Mississippi River (Fig. 1). The classified area includes portions of the Pontchartrain (with a small portion of the Pearl basin included), Barataria, Terrebonne, Atchafalaya, and Vermillion-Teche inter-distributary basins. Cypress-tupelo forest inside the Atchafalaya Basin Floodway levees and most of the floodplain of the Pearl River were excluded because of different geological and ecological settings. There is also a portion of cypress-tupelo forest in the upper Terrebonne basin that was not classified because of limitations of the landcover mask.

3. Methods

3.1. Classification methods

The classification scheme we used to classify forest density was developed in Keim et al. (2013), and then extended to other areas of the delta during subsequent efforts. Forest reaches in the study area were classified piecemeal largely because independent field data were collected for each study area, except the Barataria basin. First, Keim et al. (2013) classified forest in part of the Terrebonne basin. Then, we classified cypress-tupelo forest density for the remaining forest in the Terrebonne basin combined with forest from the adjacent Vermillion-Teche and Atchafalaya basins (those portions outside the Atchafalaya Basin Floodway System levees). Finally, we classified cypress-tupelo forest in the Pontchartrain basin. Finally, we classified cypress-tupelo forest in the Barataria basin.

3.1.1. Field data collection

Overall, 83 field training sites were used in the classification. Twenty-nine sites were established for the initial classification scheme development (Keim et al., 2013). Subsequently, these sites were used to extend classification to the remaining forest in the Terrebonne, Vermillion-Teche, and Atchafalaya basins. An additional 54 sites were used for classification of forest in the Pontchartrain basin.

Field measurements of stand parameters (Keim et al., 2013) were conducted in 30×30 m (900 m^2) field plots (\approx Landsat TM pixel size). For each field plot, tree diameter at 3 m height and the heights of the five tallest trees were measured. All trees ≥ 5 cm diameter at 3 m height were counted, and the crown score method of Meadows et al. (2001) was used to assess crown size and balance for 12–15 overstory trees. These data capture important characteristics of forest condition that are detectable in satellite imagery (Keim et al., 2013). Seedlings and saplings (< 5 cm diameter) in randomly selected 2 m radius subplots within each main plot were counted, identified by species, and their heights measured. Herbaceous and woody vegetation was identified to the most precise taxonomic level possible, and percent cover was recorded. These data were used to classify each training site as full canopy, intermediate, or open canopy (Fig. 2).

For the Barataria basin, we used 2010, 0.15-m resolution orthophotography (Louisiana Governor's Office of Homeland Security and Emergency Preparedness, <https://atlas.ga.lsu.edu/datasets/gohsep>) rather than field plots to identify training sites. Given our experience with the 3 prior classification efforts, we deemed using high resolution imagery was sufficient for training site selection.

3.1.2. Image processing and classification

Classifications were produced from Landsat Thematic Mapper (TM) imagery collected between October 2005 and February 2012 (Table S1). Images from mid-winter or summer/fall were used to avoid periods characterized by leaf-fall and leaf-out. Thus, all imagery used was from January-February and June-October. Few cloud-free summer images ($\approx 10\%$) are available for Louisiana, so most of the leaf-on information for this study was from October

All images were projected to the NAD83 UTM (zone N15) coordinate system. Data for each image was then converted to reflectance to provide a common radiometric scale. Edge distortion was removed,

and images were mosaiced where needed. Reflectance data from bands 3, 4, and 5 for each image were stacked to create multitemporal data sets for each study area. A cypress-tupelo forest mask created from the U.S. Fish and Wildlife Service National Wetland Inventory (NWI) data (Cowardin et al., 1979) modified for coastal Louisiana (Barras et al., 1994) was used in the initial study (Keim et al., 2013). Landcover data later developed by the USGS National Wetlands Research Center was used to restrict subsequent analyses to cypress-tupelo swamp within the study areas (Couvillion et al., 2011).

We used Principal Component Analysis (PCA) to identify the most statistically significant variance in multitemporal reflectance for field site pixels. To avoid GPS and image registration errors, we used a 3×3 -pixel window (8100 m^2 field area) to represent the field locations in image space, and the ordination was restricted to these locations. Spectral signatures of the field training site pixels were created. We then defined each forest pixel for the study areas within the continuum of an ordination of multitemporal reflectance from field site pixels. We multiplied the multitemporal reflectance of each forest pixel by the eigenvectors from the ordination of field site pixels to place all cypress-tupelo pixels into the PC space of field condition class. Spectral signatures of the training site pixels were created, and nonparametric class boundaries were created within the PC space based on signature ellipses representing the three condition classes. Supervised classifications were performed for each study area. Non-contiguous areas of less than 2 ha were eliminated to remove spurious data and restrict the classification to forested wetlands sufficiently large to warrant management.

3.2. Coastward gradients

To examine gradients in forest structure, basin centerlines were calculated for each basin (Fig. 1). All forest pixels in each basin were then mapped to the centerline to calculate their position relative to the coastward forest margin. Along-basin distances were normalized by centerline length to allow a delta-wide assessment of gradients in forest density and above ground carbon storage.

3.3. Forest productivity estimation

Effects of stand openness on forest production were assessed in 25 plots (0.025 – 0.07 ha) in the Mississippi River delta (Atchafalaya basin and Pontchartrain basin). Diameters of all trees were measured, and increment cores were taken from three or four trees per plot to calculate tree-level basal area growth as a function of sapwood, which was then upscaled to the stand level using measured diameters and a diameter-sapwood area allometric relationship; this process is described by Allen et al. (2019). Plot level basal area increment was calculated as an average of 10-years growth. Stand-level basal area and basal area increments were converted to biomass stock and increments by allometric relationships (Muzika et al., 1987; Scott et al., 1985), and then multiplied by 0.50 to estimate carbon stock and increments (Swift et al., 1979). Above ground forest carbon change accounts for components of net primary productivity that are in long-term biomass storage. Using these data, we also quantified Reineke's (1933) stand density index (SDI), which was used to relate the productivity and stock measurements in these 25 plots to the canopy class values and their respective SDI values in the remote-sensing validation plots. Carbon stored in live-stem biomass was modeled as 0.12 t-C ha^{-1} per unit SDI ($R^2 = 0.86$, $p < 0.001$); Annual carbon increment in live stems was modeled as $2.47 \times 10^{-3} \text{ t-C ha}^{-1} \text{ yr}^{-1}$ per unit SDI ($R^2 = 0.75$, $p < 0.001$).

4. Results

4.1. Stand characteristics defining forest density classes

There were 26, 40, and 17 field sites defined as full-canopy, intermediate, and open-canopy forest, respectively. Trees in full-canopy sites

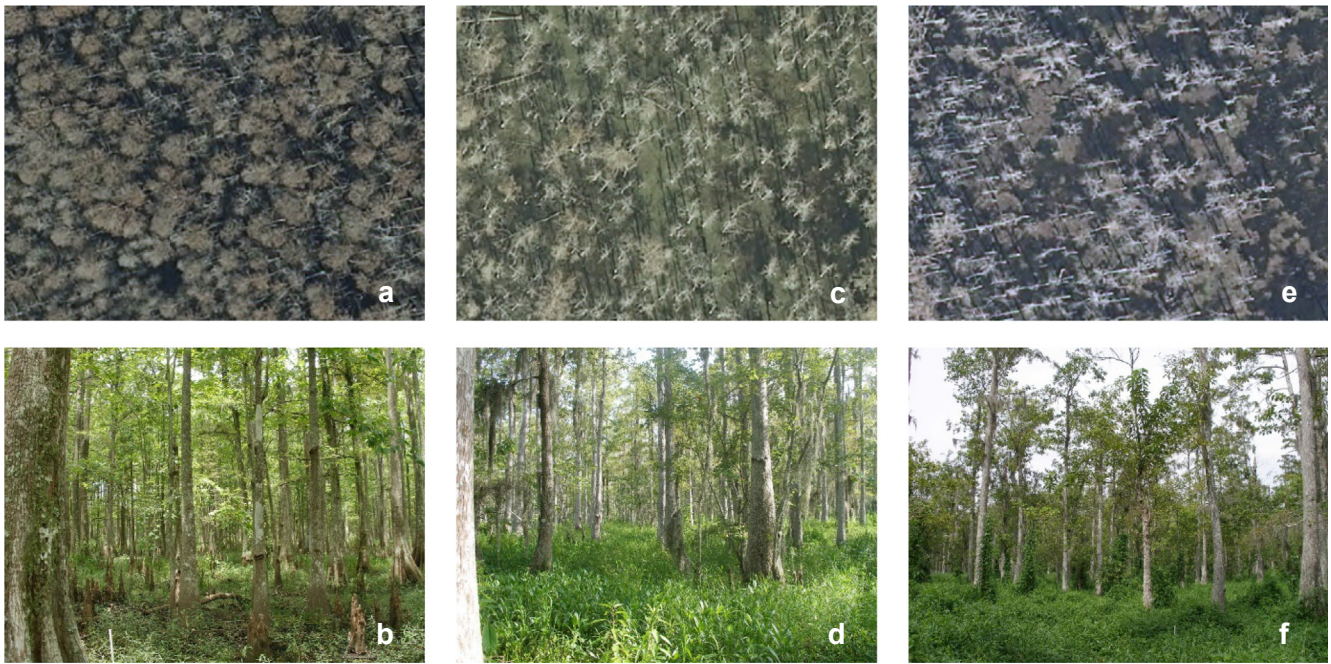


Fig. 2. Co-located ground-based and aerial photographs of example cypress-tupelo forested wetlands on the Mississippi River deltaic plain, illustrating (a and b) full-canopy; (c and d) intermediate; and (e and f) open-canopy conditions. Extent of aerial photos is 100 × 75 m (0.75 ha). Ground-based photos by J.A. Zoller (2006); aerial photos (2010, 0.15 m resolution) from the Louisiana Governor’s Office of Homeland Security and Emergency Preparedness (<https://atlas.ga.lsu.edu/datasets/gohsep>).

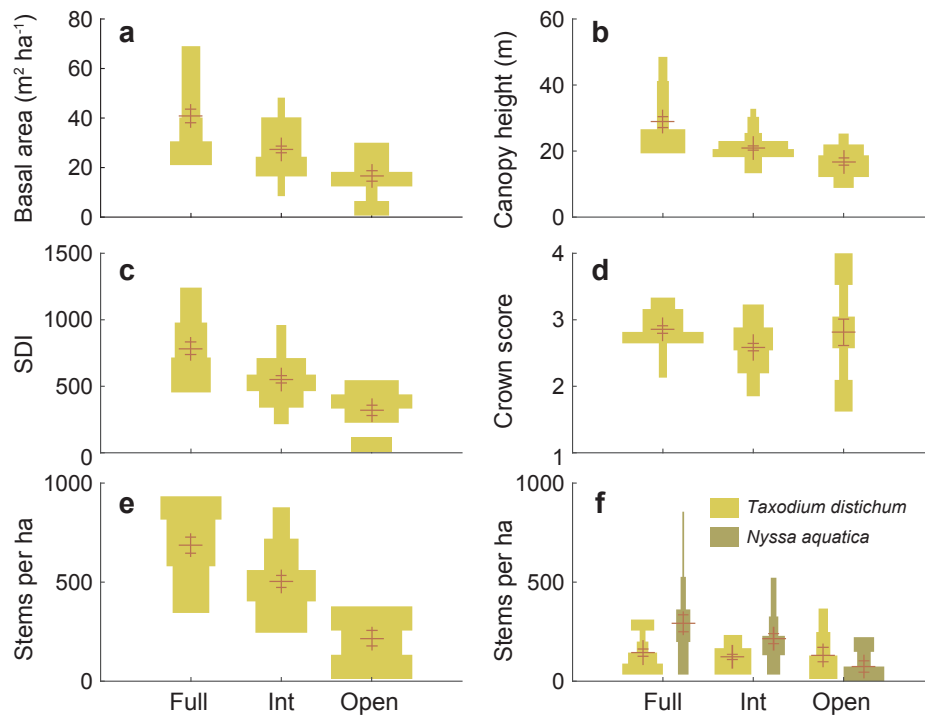


Fig. 3. Distribution of forest condition indicators from 900 m² field plots used to establish condition classes and train ordination of reflectance in the remote sensing classification (n = 83). Width represents relative density within each bin. Mean and standard error of the mean are indicated by crosses.

were approximately twice the height of trees in open sites (Fig. 3b). Further, there was clear separation among classes for stem density and basal area (Fig. 3a and e). Interestingly, tree counts decreased across class for tupelo trees but not cypress (Fig. 3f). While there were generally more cypress trees per plot in full-canopy sites, there was substantially more variability in open plots, with many having a high number of smaller stems (Fig. 3a and f).

Stand density index, a proxy for crown competition, can be used to analyze the competitive status of cypress-tupelo forests. Keim et al. (2010) suggested that trees in stands with SDI > ~660 compete for resources strongly, causing mortality by self-thinning, and SDI < ~360 indicates strong limitations on regeneration and mortality of trees by stressors not related to inter-tree competition. Most full-canopy sites were above the self-thinning threshold of SDI = 660 (Fig. 3c),

Table 1Area and percent of cypress-tupelo forested wetlands (contiguous area ≥ 2 ha) classified as full canopy, intermediate, and open canopy.

Study Area	Classified cypress-tupelo forest	Full-canopy forest (ha)	Intermediate forest (ha)	Open-canopy forest (ha)	Full-canopy forest (%)	Intermediate forest (%)	Open-canopy forest (%)
Terrebonne/Vermillion-Teche basin	94,680	19,860	47,164	27,656	21	50	29
Pontchartrain basin	94,118	38,636	46,432	9,050	41	49	10
Barataria basin	51,613	10,791	27,785	13,037	21	54	25
Total	240,411	69,287	121,381	49,743	29	50	21

meaning that they are mostly fully stocked stands that have high production potential. In intermediate plots, where SDI was lower and thus competition less, trees had lower crown scores than in full-canopy sites (Fig. 3c and d). This pattern contradicts expected density-driven tree morphology, suggesting there may be allogenic growth limitations such as from flooding or salinity. Both full-canopy and intermediate sites often had trees with lower crown scores than open-canopy sites, which had SDI below the site-occupancy threshold, implying trees in open stands experience minimal competition. Open stands were highly variable in composition: some were composed of trees with full, healthy crowns while others were composed of trees with lower crown scores (Fig. 3d).

4.2. Cypress-tupelo forested wetland condition on the Mississippi River delta

Overall, approximately 29, 50, and 21% of cypress-tupelo forest was classified as full canopy, intermediate, and open canopy, respectively (Table 1 and Fig. 4). In the Pontchartrain basin, 41, 49, and 10% of forest was classified as full canopy, intermediate, and open, respectively. The proportion of forest classified as full canopy is much higher in the Pontchartrain basin than the Barataria, Terrebonne, or Vermillion-Teche basins. It should be noted, however, that much of the former

extent of forest in the basin has already converted to marsh (Shaffer et al., 2016), and that some forested areas were previously farmland (Shirley and Battaglia, 2006). Open-canopy forests are mostly near Lake Maurepas or the margins of Lake Pontchartrain, whereas full-canopy forests are largely concentrated farthest from lake margins.

In the Terrebonne, Atchafalaya, and Vermillion-Teche basins, collectively, 21, 50, and 29% of cypress-tupelo forest was classified as full canopy, intermediate, and open, respectively. This area contains the highest proportion of open forest, likely because it lies within the extent of relatively older delta lobes (Roberts, 1997) and has been exposed longer to marine influences (Penland et al., 1988). In the western half of the area, there is a clear coastward gradient from full-canopy and intermediate forest to open forest, though there is also significant area of open forest in the eastern portion of the study area.

In the Barataria basin, 21, 54, and 25% cypress-tupelo forest was classified as full canopy, intermediate, and open, respectively. This basin contains a more consistent transition from upland to coast, likely because of its relative youth (Coleman et al., 1998; Roberts, 1997). Most of the full-canopy forest is in landward portions of the basin near the Mississippi River ridge or in the central basin adjacent to minor ridges. Open forest also transitions to marsh and relict forest near the margins of large lakes. There are also significant areas of bottomland

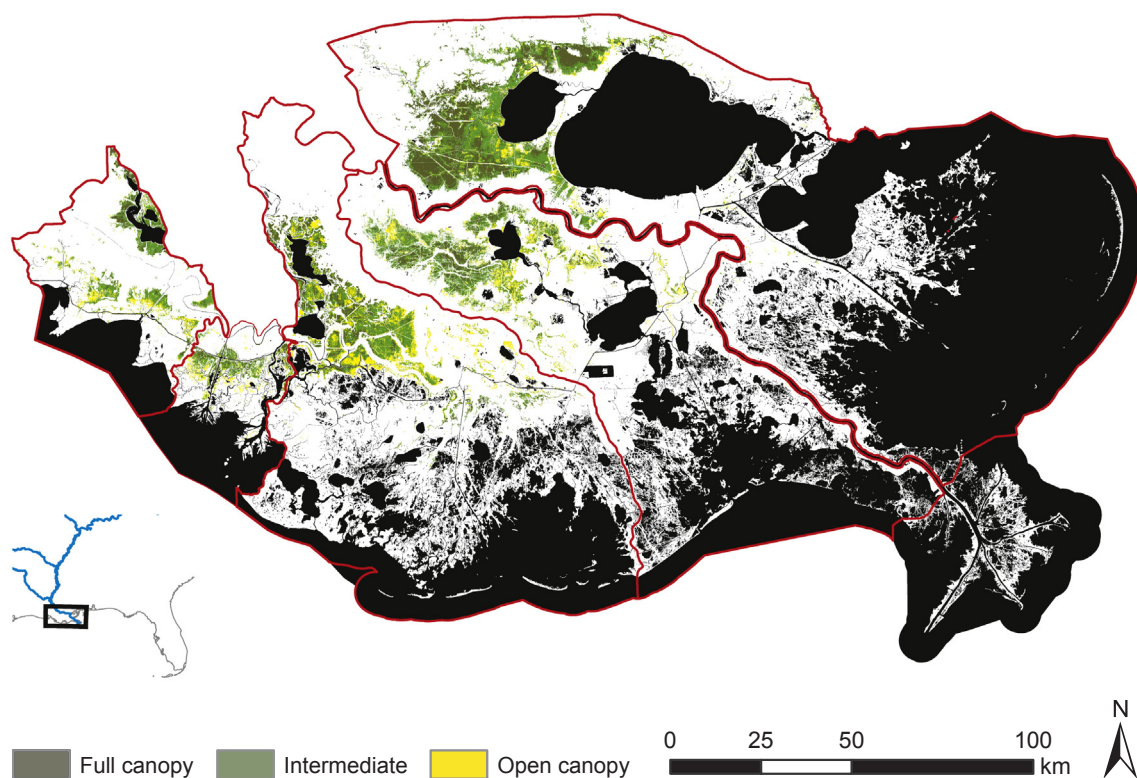


Fig. 4. Cypress-tupelo forested wetland classification results. Approximately 29, 50, and 21% of cypress-tupelo forest was classified as full canopy, intermediate, and open canopy, respectively. In general, cypress-tupelo forest on the delta transitions from full-canopy and intermediate forest in upper basins to open-canopy forest toward the coast.

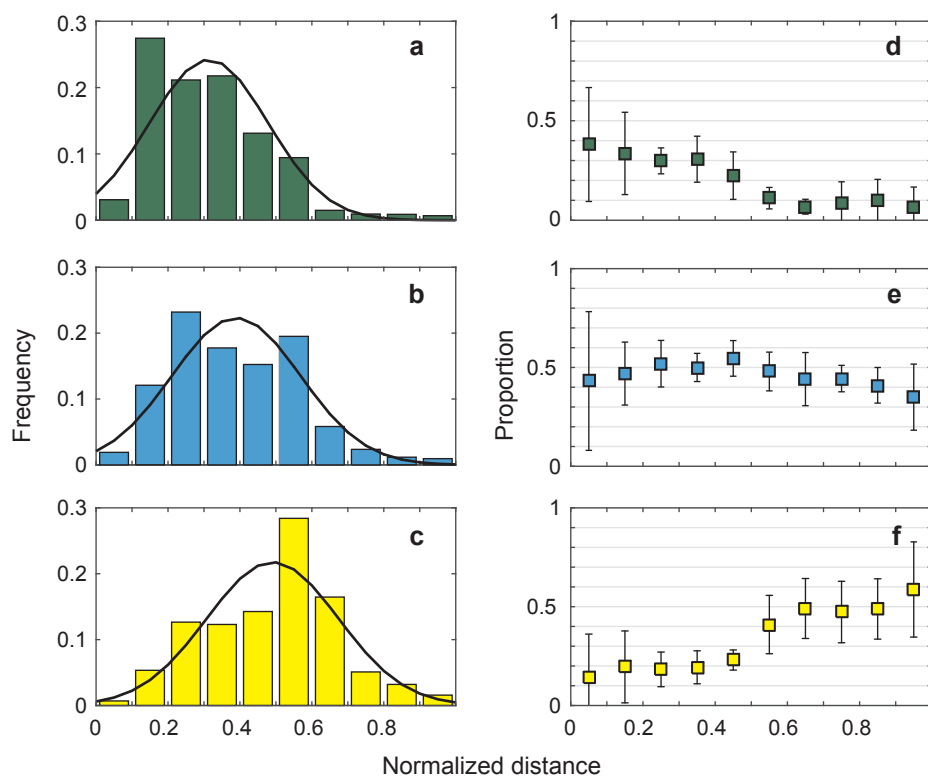


Fig. 5. Class-specific probability distributions of (a) full-canopy, (b) intermediate, and (c) open-canopy forest in the coastward direction, normalized for basin centerline length (upper basin margin = 0, seaward extent of forest = 1), and mean proportion of total forest consisting of (d) full-canopy, (e) intermediate, and (f) open-canopy forest. Error bars in panels d–f are ± 1 standard deviation of inter-basin forest values.

hardwoods and mixed forest adjacent to and on active and former natural levees. The mixed forest is mainly transitional from bottomland hardwoods to cypress-tupelo forest as flood stress increases due to subsidence (as described by Conner et al., 1981; Keim et al., 2012). In general, forested wetlands in the basin transitions from bottomland hardwoods to mixed forest to cypress-tupelo forest in the coastward direction.

4.3. Delta-wide patterns in forest density

Overall, the majority cypress-tupelo forest near the coast is open canopy, and full-canopy cypress-tupelo forest is much more common in the upper portions of inter-distributary basins (Fig. 5). Less than 10% of cypress-tupelo forest below the midpoints of basins is full canopy (Fig. 5d), and less than 25% of forest above midpoints is open canopy. The proportion of intermediate forest is relatively constant throughout and constitutes a majority of forest in the central portions of basins (Fig. 5e). The data suggest that in the upper basins, full-canopy forest decreases coincident with increases in both intermediate and open forest, but in the lower basins increases in open-canopy forest are coincident with decreases in intermediate forest only.

4.4. Carbon stocks and growth increments

Regression of carbon on mean SDI from each class results in estimated live-stem carbon stocks of 96, 67, and 39 t-C ha⁻¹ and production rates of 1.9, 1.4, and 0.8 t-C ha⁻¹ yr⁻¹ for full-canopy, intermediate, and open-canopy sites, respectively (Fig. 6). These values may underestimate carbon stocks and increments for the densest full-canopy sites because remote sensing validation plots did not have as high densities as can occur in baldcypress; maximum SDI in baldcypress is approximately 1200 (Keim et al., 2010), which would correspond with stem carbon stocks of 146 t-C ha⁻¹ and production rates of 3.0 t-C ha⁻¹ yr⁻¹. Thus, we estimate that C is 66, 46, and 27% of potential maximum stocks in full-canopy, intermediate, and open stands, respectively. Compared to estimates of C at the self-thinning threshold SDI of

~660 (80 t-C ha⁻¹), we estimate that C in intermediate and open stands is 84 and 59% of the minimum C stocks expected for stands without regenerative and physiological limitations. Therefore, across these basins, the deficit in live-stem C stock from a full-canopy forest is 6.3 Mt. A conversion of all forests characterized as full and intermediate to open would be a loss of ~7.3 Mt-C. A complete loss of cypress-tupelo forests in these basins would be ~17 Mt-C.

5. Discussion

5.1. A coastal gradient of sparseness

We observed that ~50% of cypress-tupelo forests on the Mississippi River delta have intermediate densities, and full-canopy and open stands occur over a similar extent, except for in the more inland Pontchartrain basin (Table 1). The spatial distribution of forest density varies by basin, but delta-wide, sparseness increases substantially toward the coast (Fig. 5). Overall, full-canopy and intermediate stands in landward reaches and near higher elevation ridges transition to intermediate and open stands in mid- to coastward reaches, where lower elevation, interior basins experience deeper, often near-permanent flooding. There is a shared inflection where intermediate stands compose over 50% of total forest. Landward of this point, full-canopy forest decreases as both intermediate and open-canopy forest increase; below it, open forest progressively replaces intermediate forest. In the coastward margins of forest, open-canopy stands compose nearly 60% of total forest, with less than 10% full canopy (Fig. 5).

Here, the consistent, coastward trend of decreasing density likely indicates the impacts of rising sea levels and salinity on deltaic cypress-tupelo forests, in which case sparseness would be symptomatic of ecosystem degradation from previous, denser conditions. The Mississippi River delta is intensively engineered, resulting in modified local hydrology that affects salinity, chemistry, and water level variability, and these factors have known detrimental effects on forests (Allen et al., 1996; Krauss et al., 2009). Discrete patches of open forest that are in regions of otherwise dense forest (Fig. 3) are likely

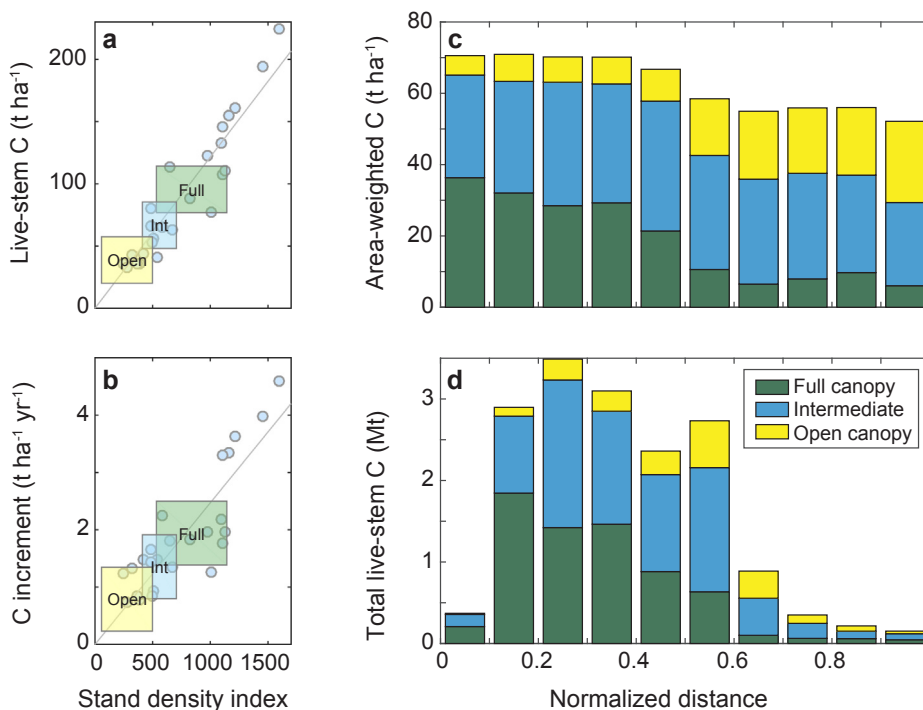


Fig. 6. Predicted (a) carbon stocks and (b) annual carbon-gain increments for cypress-tupelo forests in different stand conditions. Observations (circle markers in panels a and b) were used to establish relationships between SDI and stocks (0.12 t-C ha^{-1} per unit SDI, $R^2 = 0.86$) and between SDI and increments ($2.47 \times 10^{-3} \text{ t-C ha}^{-1} \text{ yr}^{-1}$ per unit SDI, $R^2 = 0.75$); data are from Allen et al. (2019). Linear-regression models were developed and used to predict stocks and increments for each stand condition (shaded boxes). The shaded boxes' horizontal bounds are 5th-percentile and 95th-percentile SDI values of the field validation sites in each class, and the vertical bounds mark ± 1 RMSE from the regression-predicted stocks and increments, where mean SDI values of the training sites in each class were used as input data. Panels c and d are delta-wide c) area-weighted live-stem carbon stocks and b) total live-stem carbon stocks versus normalized along-basin distance.

attributable to local human impacts. However, these effects are likely secondary and increased flooding and salinity effects (because of sea-level rise) are the primary driver of observed patterns. For example, the upper Pontchartrain basin contains an extensive network of navigation channels, but also contains the highest percentage of full-canopy forest of any region of the delta (Fig. 3). Conversely, the absence of tupelo trees from many open stands (Fig. 3f) indicates some level of saltwater stress because of their lower tolerance for salinity (Shaffer et al., 2009). At the coastward forest margin, chronic stress and disturbance from marine influences result from loss or erosion of protective seaward systems such as barrier islands and marshes. Additionally, levees and channelization prevent fresh water and sediment from dispersing across the delta, starving basins of sediment and nutrients that would otherwise contribute to maintaining elevation.

Attributing structural variations to human activity is challenging because cypress-tupelo stands naturally exist in a wide range of forest structures. For example, within a single wetland, cypress-tupelo forest leaf area index ranged from 2 to 10 across hydrologically different plots (Allen et al., 2015). Denser cypress-tupelo forests, which have LAI similar to the densest forest biomes (Asner et al., 2003), reflect a combination of ideal growing and sufficient regeneration conditions. Baldcypress and water tupelo can both thrive in deeply flooded conditions, but they might only regenerate when stands are not flooded for adequate duration (Middleton, 2009). Indeed, deep flooding resulting in open stands may actually improve individual tree growing conditions in many instances because it reduces competition (e.g., Egger and Moore, 1961) and alleviates water deficits (e.g., Allen and Keim, 2017). Open sites had the greatest variability in crown score (Fig. 3d), suggesting that open stands contain both stressed and vigorous trees, manifesting in a bimodal distribution. However, sparseness is often associated with stressful conditions when it is driven by salinity (Allen et al., 1996, 2019; Krauss et al., 2009). Regardless of the effects of flooding on tree vigor, periodic mortality events may result in long periods of sparseness if conditions suitable for regeneration infrequently return; given rising sea levels, such conditions are likely to become rarer at any given point on the delta.

5.2. Carbon stocks and production in cypress-tupelo wetlands

Stand density is a predictor of carbon stocks and production in cypress-tupelo forests, regardless of whether density variations are natural or anthropogenic, or whether trees are stressed or not (Allen et al., 2019). Regional areal averages across the delta are 69 t-C ha^{-1} for live-stem stocks, and $1.4 \text{ t-C ha}^{-1} \text{ yr}^{-1}$ for annual stem increments. Both values decrease in the coastward direction (Fig. 6) as forest composition transitions from full-intermediate canopy in upper reaches to predominantly open canopy in lower reaches (Fig. 5). The regional average is similar to values reported for forested swamp elsewhere, e.g. in the Amazon River basin (see Fig. 3, Asner et al., 2010). However, if all stands were fully stocked ($\sim 146 \text{ t-C ha}^{-1}$), carbon storage would be on par with recently modeled values for equilibrium “warm and wet” riparian forest in the USA (Dybala et al., 2018), which highlights the significant impact of declining stand density on carbon potential of deltaic cypress-tupelo forests. Delta-wide, total carbon stocks for the forest analyzed are $\sim 17 \text{ Mt-C}$, of which ~ 7 , 8 , and 2 Mt-C were in full-canopy, intermediate and open-canopy forest, respectively. The total annual increment is $\sim 0.34 \text{ Mt-C yr}^{-1}$, with 0.13 , 0.16 , and $0.04 \text{ Mt-C yr}^{-1}$ for full, intermediate, and open canopy, respectively.

Much of the work to quantify carbon budgets of deltas and other coastal regions has focused on down-gradient marshes and mangroves (e.g., Baustian et al., 2017; Doughty et al., 2016; Duarte et al., 2013), but carbon accumulation in swamps is an important contribution. Here, we report delta-wide annual accumulation in aboveground live-stem biomass for cypress-tupelo forests ($1.4 \text{ t-C ha}^{-1} \text{ yr}^{-1}$) that is only slightly lower than more landward or higher elevation southern Louisiana bottomland hardwood (BLH) forests ($1.9\text{--}3.4 \text{ t-C ha}^{-1} \text{ yr}^{-1}$; Moerschbaecher et al., 2016). If all cypress-tupelo forests on the delta were fully stocked, annual rates of carbon sequestration ($3.0 \text{ t-C ha}^{-1} \text{ yr}^{-1}$) would be analogous to those of nearby BLH. In turn, our area-weighted stock estimates (69 t-C ha^{-1}) are higher than recently reported values from outside the delta for mangrove and marsh systems, generally positioned more seaward than forests (55 and 8 t-C ha^{-2} , respectively; Doughty et al., 2016). Further, aboveground annual increments for deltaic cypress-tupelo wetlands are on par with recently estimated short-term annual soil accumulation rates—average of 1.9 t-C

ha⁻¹ yr⁻¹—for Louisiana marshes (Baustian et al., 2017), and for mangrove forests world-wide (1.6 t-C ha⁻¹ yr⁻¹; Duarte et al. 2013). For Louisiana, accumulation rates for deltaic marsh were lower than those of adjacent marshes (see Fig. 7, Baustian et al., 2017), so live-stem accumulation rates in trees likely parallel or exceed those of marsh soils on the delta. There is a much greater extent of marsh compared to forest on the delta, but the contributions of deltaic cypress-tupelo swamps to overall carbon dynamics should not be ignored. For example, annual aboveground live-stem carbon accumulation in the ~ 240,400 ha deltaic forest analyzed in this study is > 10% of soil carbon accumulation in marsh (~ 1,433,700 ha) for all of Louisiana (Baustian et al., 2017), much of which is outside the delta; soil carbon accumulation in Louisiana marshes is estimated to be from 5 to 60% of total global marsh soil accumulation, depending on source (Baustian et al., 2017). It should be noted that this includes only stem carbon, not accumulation in the canopy, soil, or litter, which is not discussed here and remains poorly constrained.

Carbon production potential is important for ecosystem maintenance in coastal regions, beyond its effects on atmospheric greenhouse gasses. Carbon accretion allows for soil elevation gains that are necessary for wetlands to remain above rising sea levels (Morris et al., 2002). Although such processes have been mostly studied with respect to salt marshes (Kirwan et al., 2009), organic matter in forests can also contribute to elevation capital (Stagg et al., 2016). For example, larger woody debris can degrade to form hummocks, which facilitate persistence of forest in regions that are otherwise too saline or flooded (Hsueh et al., 2016). If carbon stocks and increments (and thereby organic accretion) decrease, there is risk of these forests degrading to open water bodies, inland from the marsh fringe. This would preclude the typical up-gradient migration of salt marsh that is occurring elsewhere with sea level rise (Donnelly and Bertness, 2001).

5.3. History and future of the forested wetlands of the Mississippi River delta

The pattern of forest density observed here prompts us to hypothesize that degradation of these forests may further exacerbate the already rapid land loss on the Mississippi River delta (Kolker et al., 2011), even though we cannot conclusively distinguish whether the more coastward forests are degrading or if they are stable in their open state. Allen et al. (2019) suggest that open forests affected by freshwater flooding may be in a relatively stable condition, whereas mortality and conversion to other ecosystems are likely in stands affected by salinity. Future research to distinguish the extent of saline versus freshwater flooding is needed to predict future conditions and develop appropriate management strategies.

When interpreting spatial data presented here, it is important to understand that these classifications are restricted to areas that are currently delineated as cypress-tupelo forest. That is, we used a forest type filter that aggressively removed bottomland hardwoods or any areas that were once forest but are now so open as to have lost that character. Much of the former extent of cypress-tupelo forest has already transitioned to marsh, shrub-scrub, or open water, although the historical extent of forest cover is not known. While broad ecosystem conversions have been reported elsewhere (Craig et al., 1979; Shaffer et al., 2016), this is a first characterization of condition within zones persisting as forest.

6. Conclusion

Approximately 29, 50, and 21% of cypress-tupelo forest analyzed on the Mississippi River deltaic plain is full-canopy, intermediate, and open-canopy forest, respectively. Across the delta, stand density decreases toward the coast, which is likely explained by both natural and anthropogenic factors. We estimate there to be 17 Mt of carbon in live-stem standing stock, however, the prevalence of open-canopy and

intermediate conditions constitute a 38% loss in potential stem carbon storage relative to expected values of full-canopy forests. Conversion of all forests characterized as either full or intermediate canopy to open canopy would be a loss of 7.3 Mt-C.

Although there is some evidence of local hydrological modification causing loss of stand density, delta-wide gradients indicate broad-scale processes, i.e., saltwater intrusion and subsidence, are driving the stand density and carbon gradients. Field observations suggest that open canopy sites do not always have stressed trees, but this is generally untrue of sites undergoing saltwater intrusion. Thus, the most important processes are those controlling forest loss at the coastal margin. The data produced in this work can be used as a baseline to assess coastal forest trajectory related to change on the delta.

Acknowledgments

Funding for remote sensing classifications was provided by the Louisiana Department of Environmental Quality to RFK and DHB and the Louisiana Coastal Protection and Restoration Authority to RFK, BLE and DHB. We would like to thank Jason Zoller and Xukai Zhang for their assistance developing forest classifications for the Terrebonne and Barataria basins.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.03.046>.

References

- Allen, J.A., Pezeshki, S.R., Chambers, J.L., 1996. Interaction of flooding and salinity stress on baldcypress (*Taxodium distichum*). *Tree Physiol.* 16 (1–2), 307–313.
- Allen, S.T., Keim, R.F., 2017. Wetland-tree growth responses to hydrologic variability derived from development and optimization of a non-linear radial growth model. *Ecol. Model.* 354, 49–61.
- Allen, S.T., Whitsell, M.L., Keim, R.F., 2015. Leaf area allometrics and morphometrics in baldcypress. *Can. J. For. Res.* 45 (8), 963–969.
- Allen, S.T., Keim, R.F., Dean, T.J., 2019. Contrasting effects of flooding on tree growth and stand density determine aboveground production, in baldcypress forests. *For. Ecol. Manage.* 432, 345–355.
- Asner, G.P., Scurlock, J.M., Hicke, A.J., 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Glob. Ecol. Biogeogr.* 12 (3), 191–205.
- Asner, G.P., Powell, G.V., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., et al., 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proc. Natl. Acad. Sci.* 107 (38), 16738–16742.
- Barras, J.A., Bourgeois, P.E., Handley, L. R. (1994). Land loss in coastal Louisiana 1956–90. National Biology Survey, National Wetlands Research Center Open File Report 94-01.
- Baustian, M.M., Stagg, C.L., Perry, C.L., Moss, L.C., Carruthers, T.J., Allison, M., 2017. Relationships between salinity and short-term soil carbon accumulation rates from marsh types across a landscape in the Mississippi River Delta. *Wetlands* 37 (2), 313–324.
- Coastal Protection and Restoration Authority of Louisiana, 2017. Louisiana's comprehensive master plan for a sustainable coast. Baton Rouge, LA: OTS-State Printing.
- Coleman, J.M., Huh, O.K., Braud Jr., D., 2008. Wetland loss in world deltas. *J. Coastal Res.* 21 (1), 1–14.
- Coleman, J.M., Roberts, H.H., Stone, G.W., 1998. Mississippi River delta: an overview. *J. Coastal Res.* 14 (3), 699–716.
- Conner, W.H., Buford, M.A., 1998. Southern deepwater swamps. In: Messina, M.G., Conner, W.H. (Eds.), *Southern Forested Wetlands Ecology and Management*. CRC Press, Boca Raton, FL.
- Conner, W.H., Day, J.W., 1976. Productivity and composition of a baldcypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. *Am. J. Bot.* 63 (10), 1354–1364.
- Conner, W.H., Gosselink, J.G., Parrondo, R.T., 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. *Am. J. Bot.* 68 (3), 320–331.
- Couvillion, B.R., Barras, J.A., Steyer, G.D., Sleavin, W., Fischer, M., Beck, H., et al., 2011. Land Area Change in Coastal Louisiana from 1932 to 2010: US Geological Survey Scientific Investigations Map 3164.
- Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States. US Department of the Interior, US Fish and Wildlife Service.
- Craig, N.J., Turner, R.E., Day, J.W., 1979. Land loss in coastal Louisiana (USA). *Environ. Manage.* 3 (2), 133–144.

- Day, J.W., Britsch, L.D., Hawes, S.R., Shaffer, G.P., Reed, D.J., Cahoon, D., 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. *Estuaries* 23 (4), 425–438.
- Day Jr, J.W., Ko, J.Y., Rybczyk, J., Sabins, D., Bean, R., Berthelot, G., et al., 2004. The use of wetlands in the Mississippi Delta for wastewater assimilation: a review. *Ocean Coast. Manag.* 47 (11–12), 671–691.
- Day, J.W., Boesch, D.F., Clairain, E.J., Kemp, G.P., Laska, S.B., Mitsch, W.J., et al., 2007. Restoration of the Mississippi Delta: lessons from hurricanes Katrina and Rita. *science* 315 (5819), 1679–1684.
- Day, J., Hunter, R., Keim, R.F., DeLaune, R., Shaffer, G., Evers, E., et al., 2012. Ecological response of forested wetlands with and without large-scale Mississippi River input: implications for management. *Ecol. Eng.* 46, 57–67.
- DeLaune, R.D., Pezeshki, S.R., 2003. The role of soil organic carbon in maintaining surface elevation in rapidly subsiding US Gulf of Mexico coastal marshes. *Water Air Soil Pollut. Focus* 3 (1), 167–179.
- Donnelly, J.P., Bertness, M.D., 2001. Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. *Proc. Natl. Acad. Sci.* 98 (25), 14218–14223.
- Doughty, C.L., Langley, J.A., Walker, W.S., Feller, I.C., Schaub, R., Chapman, S.K., 2016. Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries Coasts* 39 (2), 385–396.
- Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Change* 3 (11), 961.
- Dybala, K.E., Matzek, V., Gardali, T., Seavy, N.E., 2018. Carbon sequestration in riparian forests: a global synthesis and meta-analysis. *Glob. Change Biol.* 25, 57–67.
- Effler, R.S., Goyer, R.A., 2006. Baldcypress and water tupelo sapling response to multiple stress agents and reforestation implications for Louisiana swamps. *For. Ecol. Manage.* 226 (1–3), 330–340.
- Eggler, W.A., Moore, W.G., 1961. The vegetation of Lake Chicot, Louisiana, after eighteen years impoundment. *Southwestern Nat.* 6, 175–183.
- Engle, V.D., 2011. Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. *Wetlands* 31 (1), 179–193.
- Giosan, L., Syvitski, J., Constantinescu, S., Day, J., 2014. Climate change: protect the world's deltas. *Nat. News* 516 (7529), 31.
- Gresham, C.A., Williams, T.M., Lipscomb, D.J., 1991. Hurricane Hugo wind damage to southeastern US coastal forest tree species. *Biotropica* 420–426.
- Hsueh, Y.H., Chambers, J.L., Krauss, K.W., Allen, S.T., Keim, R.F., 2016. Hydrologic exchanges and baldcypress water use on deltaic hummocks, Louisiana, USA. *Ecology* 9 (8), 1452–1463.
- Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S., Schneider, R.L., 1994. Woody plant regeneration in four floodplain forests. *Ecol. Monogr.* 64 (3), 345–367.
- Keim, R.F., Chambers, J.L., Hughes, M.S., Nyman, J.A., Miller, C.A., Amos, B.J., et al., 2006. Ecological consequences of changing hydrological conditions in wetland forests of coastal Louisiana. In: Xu, X.J., Singh, V.P. (Eds.), *Coastal Environment and Water Quality*. Water Resources Publications, Highlands Ranch, CO.
- Keim, R.F., Dean, T.J., Chambers, J.L., Conner, W.H., 2010. Stand density relationships in baldcypress. *For. Sci.* 56 (4), 336–343.
- Keim, R.F., Izdepski, C.W., Day, J.W., 2012. Growth responses of baldcypress to wastewater nutrient additions and changing hydrologic regime. *Wetlands* 32 (1), 95–103.
- Keim, R.F., Zoller, J.A., Braud, D.H., Edwards, B.L., 2013. Classification of forested wetland degradation using ordination of multitemporal reflectance. *Wetlands* 33 (6), 1103–1115.
- Kirwan, M.L., Guntenspergen, G.R., Morris, J.T., 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Glob. Change Biol.* 15 (8), 1982–1989.
- Ko, J.Y., Day, J.W., 2004. A review of ecological impacts of oil and gas development on coastal ecosystems in the Mississippi Delta. *Ocean Coast. Manag.* 47 (11–12), 597–623.
- Kolker, A.S., Allison, M.A., Hameed, S., 2011. An evaluation of subsidence rates and sea-level variability in the northern Gulf of Mexico. *Geophys. Res. Lett.* 38 (21).
- Krauss, K.W., Duberstein, J.A., Doyle, T.W., Conner, W.H., Day, R.H., Inabinette, L.W., Whitbeck, J.L., 2009. Site condition, structure, and growth of baldcypress along tidal/non-tidal salinity gradients. *Wetlands* 29 (2), 505–519.
- Krauss, K.W., Noe, G.B., Duberstein, J.A., Conner, W.H., Stagg, C.L., Cormier, N., et al., 2018. The role of the upper tidal estuary in wetland blue carbon storage and flux. *Global Biogeochem. Cycles* 32 (5), 817–839.
- Louisiana Oil Spill Coordinator's Office, 2007. *Landsat Thematic Mapper Satellite Image 2005, UTM Zone 15 NAD83*. Baton Rouge, LA: Louisiana Oil Spill Coordinator's Office. http://lagic.lsu.edu/data/losco/landsat5tm_la_lsu_2005_faq.html.
- Mattoon, W.R., 1915. *The southern cypress* (No. 272). US Department of Agriculture.
- Meadows, J.S., Burkhardt, E.C., Johnson, R.L., Hodges, J.D., 2001. A numerical rating system for crown classes of southern hardwoods. *South. J. Appl. For.* 25 (4), 154–158.
- Middleton, B.A., 2009. Regeneration potential of *Taxodium distichum* swamps and climate change. *Plant Ecol.* 202 (2), 257.
- Moerschbacher, M.K., Keim, R.F., Day, J.W., 2016. Estimating carbon stocks in uneven-aged bottomland hardwood forest stands in south Louisiana. In: *Proceedings of the 18th biennial southern silvicultural research conference*. Technical Report SRS-212. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.
- Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83 (10), 2869–2877.
- Muzika, R.M., Gladden, J.B., Haddock, J.D., 1987. Structural and functional aspects of succession in southeastern floodplain forests following a major disturbance. *Am. Midl. Nat.* 117, 1–9.
- Paola, C., Twilley, R.R., Edmonds, D.A., Kim, W., Mohrig, D., Parker, G., et al., 2011. Natural processes in delta restoration: Application to the Mississippi Delta. *Ann. Rev. Mar. Sci.* 3, 67–91.
- Penland, S., Boyd, R., Suter, J.R., 1988. Transgressive depositional systems of the Mississippi Delta plain; a model for barrier shoreline and shelf sand development. *J. Sediment. Res.* 58 (6), 932–949.
- Pezeshki, S.R., DeLaune, R.D., Patrick Jr, W.H., 1990. Flooding and saltwater intrusion: potential effects on survival and productivity of wetland forests along the US Gulf Coast. *For. Ecol. Manage.* 33, 287–301.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- Roberts, H.H., 1997. Dynamic changes of the Holocene Mississippi River delta plain: the delta cycle. *J. Coastal Res.* 13, 605–627.
- Scott, M.L., Sharitz, R.R., Lee, L.C., 1985. Disturbance in a cypress-tupelo wetland: an interaction between thermal loading and hydrology. *Wetlands* 5 (1), 53–68.
- Shaffer, G.P., Wood, W.B., Hoepfner, S.S., Perkins, T.E., Zoller, J., Kandalepas, D., 2009. Degradation of baldcypress–water tupelo swamp to marsh and open water in southeastern Louisiana, USA: an irreversible trajectory? *J. Coastal Res. Spec. Issue* 54, 152–165.
- Shaffer, G.P., Day, J.W., Kandalepas, D., Wood, W.B., Hunter, R.G., Lane, R.R., Hillmann, E.R., 2016. Decline of the Maurepas Swamp, Pontchartrain Basin, Louisiana, and approaches to restoration. *Water* 8 (3), 101.
- Shirley, L.J., Battaglia, L.L., 2006. Assessing vegetation change in coastal landscapes of the northern Gulf of Mexico. *Wetlands* 26 (4), 1057–1070.
- Stagg, C.L., Krauss, K.W., Cahoon, D.R., Cormier, N., Conner, W.H., Swarzenski, C.M., 2016. Processes contributing to resilience of coastal wetlands to sea-level rise. *Ecosystems* 19 (8), 1445–1459.
- Swift, M.J., Heal, O.W., Anderson, J.M., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. Univ of California Press, Berkeley.
- Syvitski, J.P., Kettner, A.J., Overeem, I., Hutton, E.W., Hannon, M.T., Brakenridge, G.R., et al., 2009. Sinking deltas due to human activities. *Nat. Geosci.* 2 (10), 681.
- Tessler, Z.D., Vörösmarty, C.J., Grossberg, M., Gladkova, I., Aizenman, H., Syvitski, J.P.M., Fofoula-Georgiou, E., 2015. Profiling risk and sustainability in coastal deltas of the world. *Science* 349 (6248), 638–643.