Degradation of Baldcypress–Water Tupelo Swamp to Marsh and Open Water in Southeastern Louisiana, U.S.A.: An Irreversible Trajectory?

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ABSTRACT

SHAFFER, G.P.; WOOD, W.B.; HOEPPNER, S.S.; PERKINS, T.E.; ZOLLER, J., and KANDALEPAS, D., 2009. Degradation of baldcypress–water tupelo swamp to marsh marsh and open water in Southeastern Louisiana, U.S.A.: an irreversible trajectory? *Journal of Coastal Research*, 54(00), 000–000. West Palm Beach (Florida), ISSN 0749-0208.

1 In general, many of the swamps of coastal Louisiana, U.S.A., are highly degraded, and several are converting to marsh and open water. The initial purpose of this study was to determine the feasibility, and potential benefits, of reintroducing waters of the Mississippi River into the degraded Maurepas swamp, located in the Pontchartrain Basin of southeastern Louisiana. Early in the year 2000, 20 sites were selected in three different habitat types characterized by moving freshwater (throughput sites), stagnant, nearly permanently flooded (relict sites), and areas prone to saltwater intrusion events (degraded sites). Paired 625-m^2 plots were outfitted with litter-fall traps, herbaceous subplots, and wells for measuring interstitial soil salinity. From 2000–2006, diameter growth was followed for 2219 trees, and herbaceous production was estimated using mid- and late-growing season clip plots. Overall, primary production was dominated by trees early in the study, but switched to herbaceous vegetation as parts of the ecosystem converted from swamp to marsh. Salt stress was the primary cause of tree mortality in areas of low density, whereas stagnant standing water and nutrient deprivation appear to be the largest stressors at interior (relict) sites. The 2005 hurricanes caused wind throw of up to 100% of midstory trees in areas of low canopy density and was negligible when basal areas of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) were greater than 30 m^2 ha^{-1}. Using spectral signatures of the 625-m^2 plots, the aerial extent of habitat types revealed that the vast majority of the Maurepas swamp is either relict or degraded. Without a river reintroduction in the near future, as well as harnessing other point and nonpoint sources of freshwater, the Maurepas swamp will continue its clear trajectory to marsh and open water.

ADDITIONAL INDEX WORDS: *Coastal forested wetlands,* Taxodium distichum–Nyssa aquatica *swamp, wetland loss, saltwater intrusion, hydrologic alteration, Mississippi River reintroduction, river diversion.*

INTRODUCTION

Historically, the wetlands of the upper Lake Pontchartrain Basin, located in southeastern Louisiana, U.S.A., were 90% baldcypress–water tupelo (*Taxodium distichum–Nyssa aquatica*) swamps (Saucier, 1963). The extent of swamp has been radically reduced by multiple stressors such as logging, development, hydrologic alteration, nutrient deprivation, and saltwater intrusion. Much of the remaining swamp is in a state of deterioration (Chambers *et al.,* 2005) and several restoration projects are planned (Coast 2050, 1998).

Despite its degraded condition, the Maurepas swamp complex is the second largest contiguous coastal forest in Louisiana, consisting of 77,550 ha of swamp and 5204 ha of fresh or oligohaline marsh (Coast 2050, 1998). As in most of deltaic Louisiana, leveeing the Mississippi River has removed a once reliable source of freshwater, nutrients, and sediments, and enabled periodic encroachment of saltwater from the Gulf of Mexico (Day *et al.,* 2000, 2007). Construction of massive canals, such as the Mississippi River Gulf Outlet (MRGO, Shaffer *et al.* this volume), combined with sea level rise, have further exacerbated the frequency and intensity of saltwater intrusion events. As a result, most of the Maurepas swamp appears to be in transition to marsh and open water. Several restoration projects have been proposed to combat swamp loss, the most promising of which involve reintroductions of Mississippi River water. This study was initiated to document the extent of swamp degradation and to quantify the potential benefits of a river reintroduction into the southwestern Maurepas swamp (Day *et al.,* 2004; Shaffer *et al.,* 2003).

The geologic development of most of coastal Louisiana occurred through a series of delta lobe shifts of the Mississippi River, which occurred roughly once every 1000 years (Coleman, Roberts, and Stone, 1998; Day, *et al.,* 2007; Scruton, 1960). Lakes Pontchartrain and Maurepas were

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formed during the evolution of two separate delta lobes over the past 4000 years. The Cocodrie lobe expanded over the area where New Orleans presently resides, forming the lakes' southern shores. The St. Bernard lobe then completed the lakes' eastern shoreline (Frazier, 1967; Saucier, 1963).

Wood from the vast virgin stands of baldcypress became the dominant cash crop in Louisiana during the eighteenth century (Mattoon, 1915). However, it was not until the 1890s that large-scale clear-cutting of the baldcypress swamps became possible due to the invention of pullboats and skidders, which increased the accessibility of interior swamps (Mancil, 1980). Most of the old-growth baldcypress had been clear cut by the early twentieth century. Most areas in the Pontchartrain Basin regenerated as second-growth baldcypress–water tupelo swamps. By the mid-1960s, however, many areas in the basin started to convert to marsh and open water (Barras, Bourgeois, and Handley, 1994).

The second-growth swamps in coastal Louisiana have now become merchantable, and harvesting interests have been renewed. These renewed logging interests have generated opposition from scientists and the general public. Several studies of Mississippi River deltaic swamps indicate that many of these swamps are not sustainable (Chambers *et al.,* 2005; Conner and Day, 1992; Hoeppner, 2002; Hoeppner, Shaffer, and Perkins, 2008; Pezeshki, DeLaune, and Patrick, 1990; Shaffer *et al.,* 2003) and exhibit little natural regeneration (Conner and Day, 1976; Shaffer *et al.,* 2003). To address the issue of the conflicting pressures of logging versus restoration, the governor of Louisiana convened a group of forested wetland ecologists to provide science-based interim guidelines for coastal swamp conservation and utilization (Chambers *et al.,* 2005). As part of this effort, we identified and mapped the extent of potentially sustainable, relict, and degraded swamp in the upper Lake Pontchartrain Basin and will present that herein.

The main objective of this study is to compare the primary production of woody and herbaceous vegetation throughout a 7-year duration that experienced periods of severe drought, normal weather conditions, and Hurricanes Katrina and Rita in 2005. By following changes in abiotic and biotic factors influencing swamp production over multiple years, this study should enable crisp quantification of benefits that restoration projects (such as Mississippi River reintroductions and using other point and nonpoint freshwater resources) will have on ecosystem function.

MATERIALS AND METHODS

Study Site

The study area is located in the upper Pontchartrain Basin, a marginal deltaic basin that was enclosed by the progradation of the St. Bernard delta complex some 2500 years ago. Regional estimates place relative sea-level rise (RSLR) between 3.6 and 4.5 mm y^{-1} in this basin (Penland and Ramsey, 1990). To accurately characterize the Maurepas swamp, we selected 20 study sites with paired 625-m^2 plots in the southern wetlands of Lake Maurepas. These sites were chosen to capture three different hydrological regimes within the swamp, namely stagnant, nearly permanently flooded interior sites (relict), sites near the margin of Lake Maurepas that are prone to severe saltwater intrusion events (degraded), and sites receiving reliable nonpoint sources of freshwater runoff (throughput) (Figure 1). To determine the validity of the *a priori* habitat type groupings, we used multinomial regressions on the 2000 and 2001 environmental data (for details, see Statistical Analysis). Taken together, all study sites characterize an area roughly 180 km^2 in size.

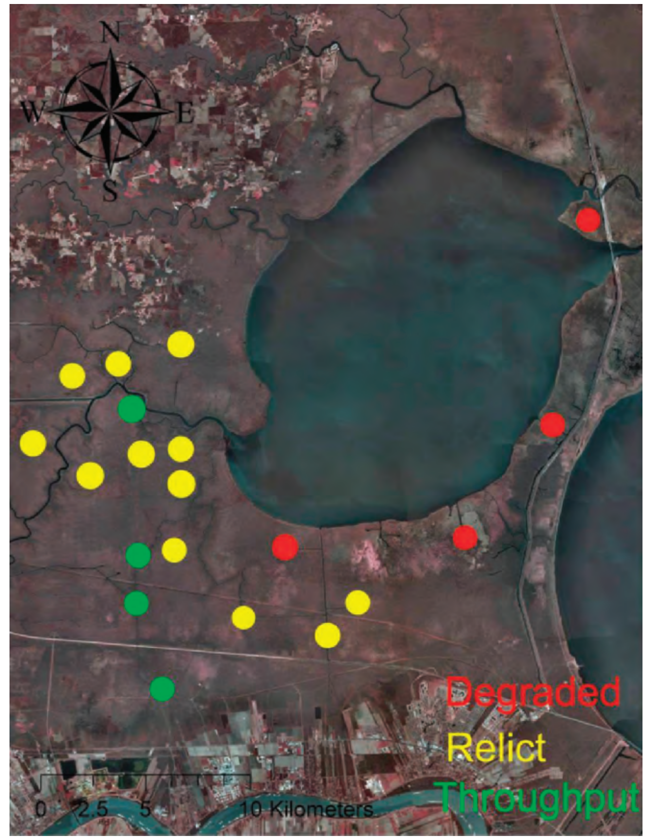

Figure 1. The Maurepas swamps rim the margin of Lake Maurepas in southeastern Louisiana, and are bounded by urban development to the north, west, and south. Twenty sites were selected to represent the three major habitat types: throughput sites (green), relict sites (yellow), and degraded swamp sites (red).

Environmental Covariables

Abiotic variables, including soil water salinity, light penetration, pH, bulk density, redox potential (Eh), sulfide, nitrate, ammonia, and phosphate concentrations, were monitored at the 20 study sites (Shaffer *et al.,* 2003). Of these, soil salinity, light penetration, and bulk density were the most important predictors of herbaceous and tree production so we will limit description to these.

To measure soil salinity, we inserted two 1 m × 6 cm diameter PVC wells 0.75 m into the ground at each of the 40 stations. Wells were capped at both ends. Horizontal slits were cut into the wells every 2 cm from a depth of 5 cm to a depth of 70 cm below the soil surface to enable groundwater to enter. Wells were outfitted with plastic skirts at the soil surface to prevent rainwater seepage (Thomson, 2000). Each well was completely evacuated and allowed to refill before salinity measurements were taken (using a YSI salinity–conductivity–temperature meter). Well-water salinity was measured during most site visits and averaged to yield a measure of yearly mean salinity at each study plot.

Soil cores for bulk density analysis were collected during the fall sampling period in 2001 and 2002, using an aluminum soil corer with a 1.6 cm inner diameter. Samples were collected by coring to a depth of 10 cm, carefully removing the soil corer from the surrounding substrate, and extruding the cores into plastic sample bags. To minimize the influence of microscale heterogeneity of soil strength, we took five replicate cores at two locations within each study plot. The five replicate cores were combined into a single sample in the field, while the two pooled samples from different locations within the same study plot were processed independently. Each sample was dried to constant mass at 65°C in a ventilated oven before soil core weights were measured. Light penetration was measured in the center of each of four 16-m^2 herbaceous plots within each station, using a spherical crown microdensiometer.

Herbaceous Vegetation

Within each of the 40 permanent stations, four 4 m $\times$ 4 m (16 m^2) permanent herbaceous plots were established 5 m in from the diagonal corners of each station. A 4-m^2 plot was established in the center of each 16-m^2 plot for cover value estimates and biomass clip plots. Each year cover values were obtained by two independent estimates during summer and fall. Percentage cover of vegetation by species was determined by ocular estimation in 5% increments. Each year understory primary production was estimated within each herbaceous plot by clipping two randomly chosen (nonrepeating) replicate subplots (of 0.25 m^2 area) twice during the growing season (Whigham *et al.,* 1978; Wohlgemuth, 1988). The pseudoreplicate subplots were pooled on site during the May–June (summer) sampling and again during late September–early October (fall). Plant material was clipped at the soil surface, placed in a labeled bag, and transported to the lab, where it remained in cold storage until it could be oven dried and weighed. Annual aboveground herbaceous production was estimated by summing the summer and fall biomass estimates. Indeed, a turnover study on *Sagittaria lancifolia* (a dominant herbaceous species in the study area) on the Manchac land bridge, during 2005 and 2006, indicated that this species completely replaces itself approximately once per year (2005 mean turnover = 1.094 $\pm$ 0.032 SE; 2006 mean turnover = 1.341 $\pm$ 0.077 SE).

During 2002 and 2003, fifty-six 16 m^2 vegetation plots were used to simulate nutrient loading rates of several different Mississippi River reintroduction scenarios. Four (18-6-12 timed-release Osmocote) fertilizer levels were applied to simulate (a) current conditions (*i.e.*, no fertilizer addition), (b) a loading rate of 11.25 g N m^2 y^{-1}, or a discharge of 42.5 m^3 s^{-1} (Lane *et al.,* 2003) during the spring, (c) twice that during the spring, and (d) twice that during both spring and fall to simulate a river reintroduction operating during the entire growing season. Half of the plots at each fertilizer level were outfitted with herbivore-exclusion cages to prevent herbivory, primarily by nutria and deer.

Forest Vegetation

All trees greater than 5 cm diameter within each of the two 625 m^2 plots at each of 20 study sites in the Maurepas swamp were tagged using 8-penny galvanized nails and prenumbered 5-cm metal ID tags in February and March of 2000. Trees were tagged at breast height, unless the fluting bases of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) or the complex branching structure of shrubs such as wax myrtle (*Morella cerifera*) required the tags to be somewhat higher. Using fiberglass metric diameter tapes, initial tree diameters of 1860 tagged trees were measured during February and March of 2000 at the bottom of the freely hanging metal tags. Nails were placed at the same height 180° from the tags to improve precision of subsequent measurements. During late fall, 2000–2006, diameter measures were taken of all tagged trees. Throughout the study many trees suffered mortality and many saplings grew to the 5 cm tagging size such that a total of 2219 trees were tagged in all. Prior to analysis, the diameter data were harmonized following the guidelines of Sheil (1995).

Tree primary production was measured through the collection of annual litter fall and the measurement of annual tree diameter growth (Brown, 1981; Conner and Day, 1992; Mitsch and Ewel, 1979) at the 40 study plots. Five litter-fall traps were installed at approximately even spacing at each of the two stations at 20 study sites to yield a total of 200 litter traps deployed. Each of these traps was 0.25 m^2 in area and was constructed to catch biomass in a fine (1 mm) mesh approximately 1 m above the ground to prevent loss from flooding events. The litter was collected frequently during site visits, which occurred as often as once every 2 weeks or as infrequently as once every 2 months during periods of the growing season when few leaves were falling (*i.e.*, spring, summer). During or after collection, the litter from each of the five litter traps at each plot was combined to yield one total sample of litter per plot because the five traps are considered pseudoreplicates. For this study, we use the term "litter" for leaves, flowers, fruits, and seeds. Collected litter was then dried to constant mass at 65°C. After drying, the litter was sorted into *T. distichum, N. aquatic,* and "other" litter. This enabled us to monitor production effects at the species level for at least the two most dominant tree species in the swamp. The vast majority of other stems were midstory swamp red maple [*Acer rubrum* (var. *drummondii*)] and ash (*Fraxinus pennsylvanica* and *F. profunda*).

Each year, tree diameter was used to calculate tree wood biomass using published regression formulas (Clark, Phillips, and Frederick, 1985; Muzika, Gladden, and Haddock, 1987; Scott, Sharitz, and Lee, 1985). Wood production was calculated as the difference in wood biomass per year. Wood production per tree was then summed by species category per plot and then converted to total wood production per square meter per year (g m^{-2} y^{-1}).

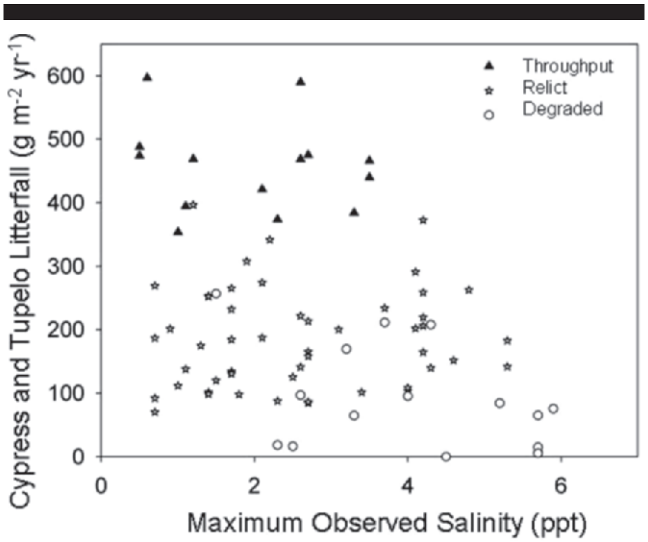

Figure 2. Results of multinomial logistic regressions classifying three *a priori* habitat types by maximum observed soil salinity and annual cypress and tupelo litter production. Clear separation occurs between throughput and degraded sites with some relict sites sharing attributes with each.

Mapping Habitat Types

To determine the spatial extent of the three habitat types (degraded, relict, and throughput), we used spectral signatures of our 625-m^2 stations to extrapolate areally over the Manchac–Maurepas wetlands. A Landsat 7 Thematic Mapper image of the upper Lake Pontchartrain Basin from May 21, 2002, was imported into ERDAS Imagine 8.7 (Leica-Geosystems, 2004) for analysis. In a supervised classification, we used the coordinates and known habitat types from 30 of our 40 field plots as training sites to identify the signature profiles of the *a priori* vegetation types discussed, plus bottomland hardwood forest. The 30 field plots chosen as training sites were those that displayed clear separation in the multinomial logistic regressions (Figure 2). Unsupervised classification was then used to classify all of the remaining pixels. The final classification was then verified by conducting field trips to many locations not used as training sites within each habitat type and showing the map to local authorities familiar with the area.

Statistical Analysis

All statistical analyses were performed using SYSTAT 10.2 (Wilkenson, 2001) and SAS 9.1.2 for Windows (SAS Institute Inc., 2000–2004). Stepwise multinomial logistic regressions were used to evaluate *a priori* site groupings (degraded, relict, throughput). To avoid tolerance problems, we screened variables for multicollinearity by principal components analysis prior to their use in the logistic regressions. Variables with high collinearity were combined as factor scores. Principal components analysis utilized a varimax rotation and minimum eigenvalue of 1.0 (Hair *et al.,* 1998). Primary production data that included tree species (baldcypress, water tupelo, and other [mostly swamp red maple and ash]) were subjected to a repeated measures analysis of covariance design with experimental (sites) and sampling (stations within sites) error terms. Interaction terms and higher order nested terms were pooled with the appropriate error term when nonsignificant F values were less than 1.70. Comparisons of herbaceous production with tree production required summing over tree species categories. Potential covariables included light penetration, bulk density, interstitial salinity, and woody basal area. Linear contrasts were used to address specific *a priori* hypotheses. In addition, wood and litter production also were analyzed as total (all species) wood and litter production per square meter per year, again with bulk density, interstitial salinity, light penetration, and basal area as potential covariables. Finally, herbaceous, wood, and litter production were combined for total primary production and analyzed for site grouping differences. Unless otherwise noted, all statistical findings were significant at a Bonferroni-protected $\alpha = 0.05$ level (Zar, 1996).

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964) was used to determine the nature of the temporal trajectory of the tree and herbaceous vegetation of the Maurepas swamp and to determine the crispness in habitat separation of the three habitat types (degraded, relict, and throughput) over the study period. The ANOSIM test in Primer 6 (Clarke and Warwick, 2006) revealed a significant difference among habitat types (ANOSIM Global R = 0.42); therefore, we used NMS in Primer 6 to describe these differences. We used the BEST procedure with the BVSTEP option to determine the most influential factors in our classification.

RESULTS

Habitat Type Groupings

The separate multinomial logistic regression models of habitat type were both significant (year 2000: likelihood ratio $\chi^2 = 54.15$, df = 2, $p < 0.001$; year 2001: likelihood ratio $\chi^2 = 48.77$, df = 2, $p < 0.001$). In both data sets, we only retained annual maximum observed salinity and the combined amount of baldcypress and water tupelo litterfall as significant predictors of habitat type. The multinomial logistic models correctly classified 38 out of 40 field plots with the 2000 data and 36 out of 40 field plots with the 2001 data. The separation of throughput and degraded swamp sites was strong, while the distinction between relict swamp and either throughput or degraded swamp was ambiguous at some sites (Figure 2), leading us to drop 10 of the 40 sites as training sites in the remote sensing analysis.

Environmental Variables

Salinity followed a U-shaped pattern from 2000 to 2006 (quadratic contrast $F_{1,259} = 406.16$, $p < 0.00001$; Figure 3) with the highest salinities occurring during the severe drought of 1999–2000 followed by 2006, another drought year. Overall, salinity was highest at degraded sites and lowest at throughput sites (linear contrast $F_{1,259} = 168.92$, $p < 0.00001$). Soil salinity also was found to decrease with

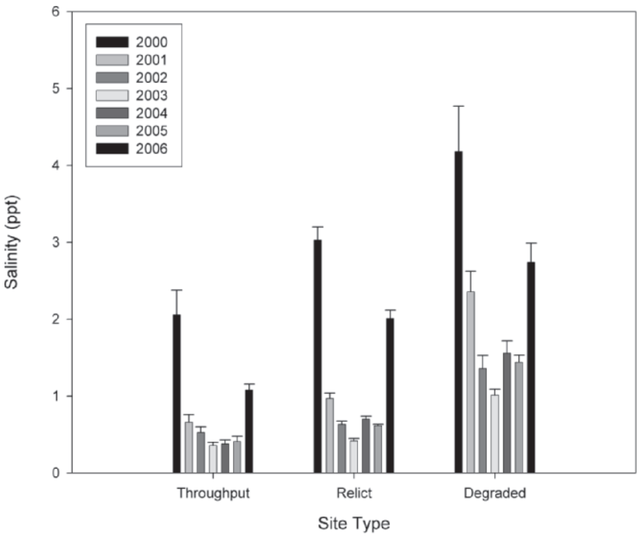

Figure 3. The average observed soil salinity in the Maurepas swamps was greatly elevated during a severe drought in 1999–2000, then declined gradually through 2003 and increased as a result of drought in 2006. This effect was greatest at the degraded sites located near Pass Manchac, which is the main saltwater conduit into the system.

increasing distance from Pass Manchac, as well as with increasing distance from the margin of Lake Maurepas into the interior swamp.

Bulk densities differed among site groupings ($F_{2,277}$ = 72.28, $p < 0.00001$; Figure 4). The highest bulk densities were found at the throughput sites (mean = 0.158 ± 0.013 g cm^{-3}) and the lowest at degraded sites (mean = 0.054 ± 0.001 g cm^{-3}). Relict sites had intermediate bulk densities (mean = 0.086 ± 0.002 g cm^{-3}).

Light penetration followed the opposite pattern of the total basal area of trees per plot (Figure 4), with greater amounts of penetration as the swamp varied from throughput to relict to degraded (linear contrast $F_{2,277}$ = 701.81, $p < 0.00001$). Light penetration continues to increase annually because large trees continue to suffer mortality and recruitment is absent at the degraded sites.

Tree Mortality

The Maurepas swamp is in a steady state of rapid decline, perhaps best shown by the mortality of canopy and midstory trees (Figure 5). Over the past 7 years, nearly 20% of the original 1860 trees in our study plots have suffered mortality, and recruitment of baldcypress and water tupelo saplings is essentially absent. In 2000, almost all of the mortality occurred at the degraded sites, but the highest rates are now experienced in the relict sites, largely because there are very few trees left to die at degraded sites. The few remaining trees at degraded sites are nearly all baldcypress, which is more tolerant to saltwater intrusion events. Mortality is highest for midstory species (Figure 5), nearly all of which are swamp red maple and green and pumpkin ash.

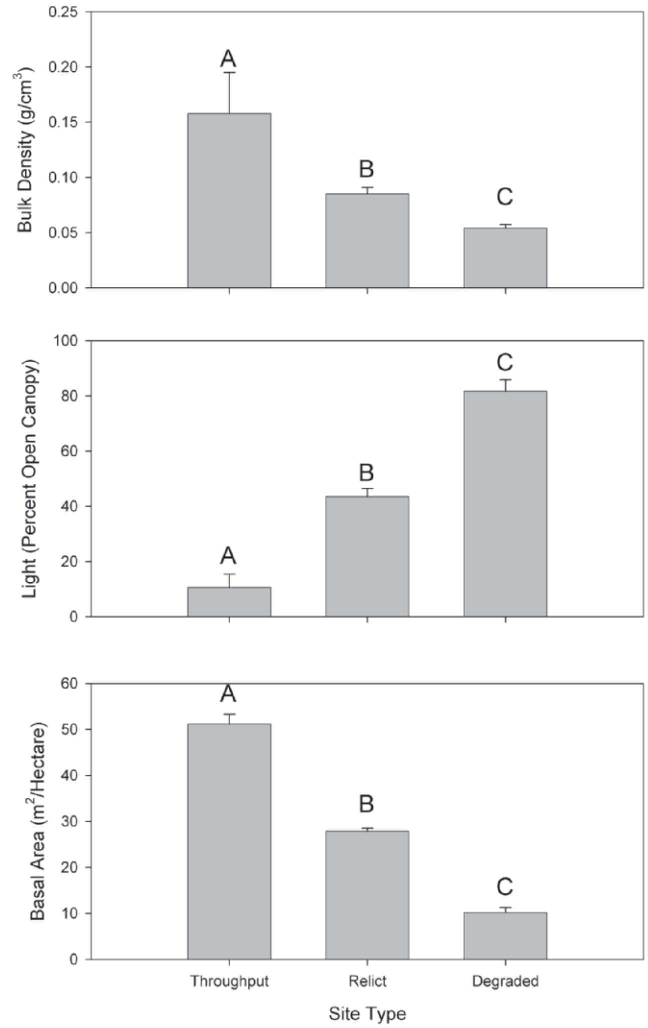

Figure 4. Soil bulk density (g cm^{-3}), light penetration (%), and basal area of trees (m^2 ha^{-1}) summed over each 625-m^2 plot for each of the three habitats. Degraded sites have the weakest soils, and the highest light penetration resulting from mortality of trees. Letters above bars indicate Bonferroni-adjusted significant differences.

Herbaceous Vegetation

Nutrient Enrichment

For the uncaged treatments, nutrient enrichment at all levels had little effect on vegetative biomass production (Figure 6), indicating grazers such as nutria and deer had a large impact on the fertilized plots. The cage effect was highly significant for both 2002 ($F_{1,51}$ = 7.032, p = 0.0102) and 2003 ($F_{1,48}$ = 12.390, p = 0.00084). Although a clear trend of increased vegetation production with increased nutrient enrichment exists for 2002 (Figure 6), the fertilizer effect was not significant ($F_{3,51}$ = 2.080, p = 0.154). By 2003, nutrient augmentation showed a highly significant increase in herbaceous production ($F_{3,48}$ = 4.685, p = 0.0053; Figure 6), with a 50% increase for the loading rate of 11.25 g N m^2 y^{-1} and a 100% increase for the loading rates of 22.5 g N m^2 y^{-1} during

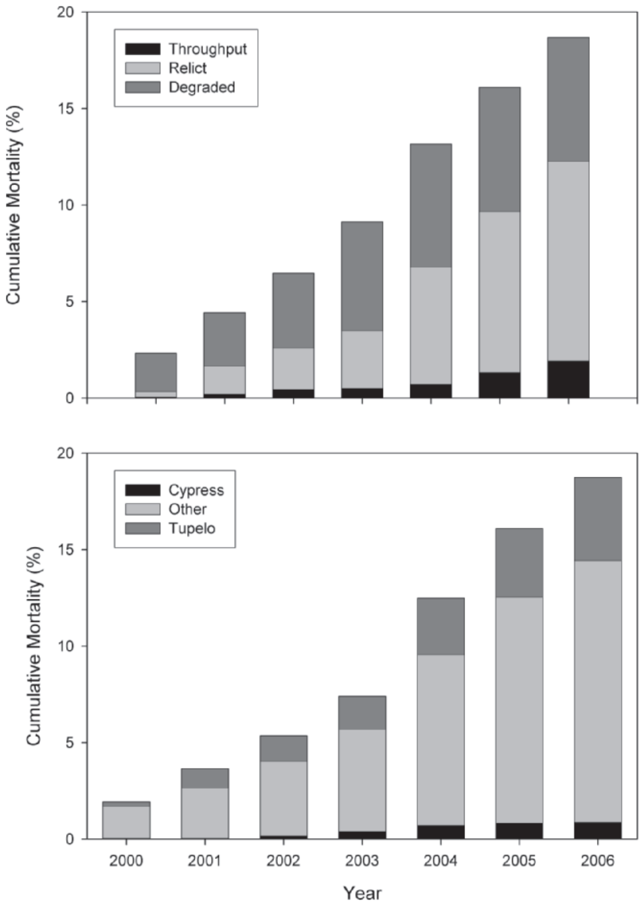

Figure 5. Cumulative percentage mortality occurring in the three habitat types over time. Mortality increases linearly from 2000–2006 and is highest for other species and lowest for baldcypress (*Taxodium distichum*).

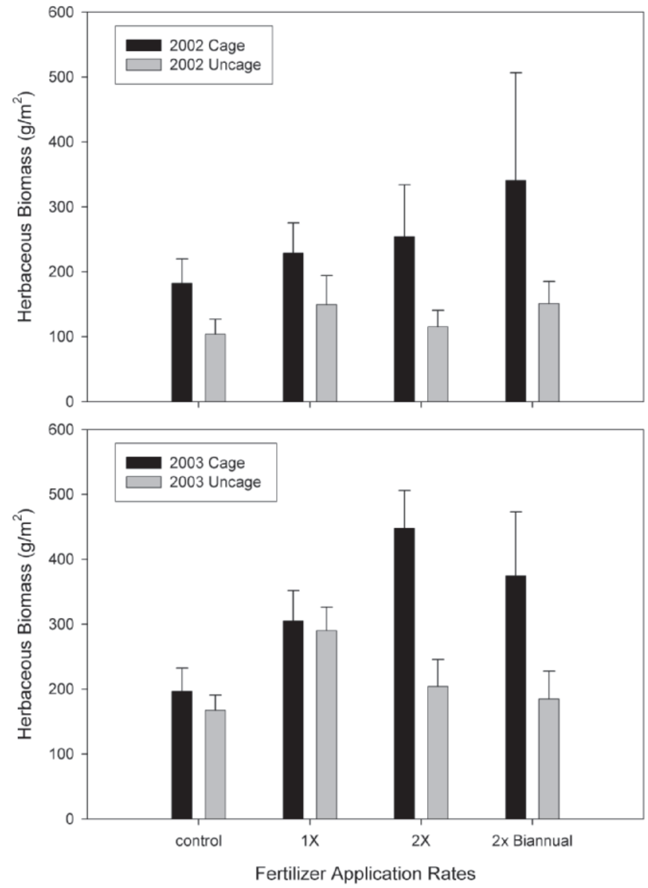

Figure 6. Results of nutrient enrichment experiment with and without herbivore exclusion cages. The 1× treatment simulates a Mississippi River reintroduction discharge of 42.5 $m^3 s^{-1}$ and a loading rate of 11.25 g N $m^{-2} y^{-1}$. The 2× treatment doubles that loading rate, and the 2× biannual treatment applies the timed-release fertilizer in early spring and again in midsummer.

spring (2×) and throughout the growing season (2× biannual), which did not differ from one another.

Annual Production

Herbaceous production was highest at the degraded sites (mean = 697.33 ± SE 71.84 g $m^{-2} y^{-1}$) followed by relict sites (mean = 381.60 ± SE 26.11 g $m^{-2} y^{-1}$), and lowest for throughput sites (64.31 ± SE 13.64 g $m^{-2} y^{-1}$; $F_{2,256} = 3.26$, p = 0.040; Figure 7). There was a strong linear trend of increased herbaceous production from 2000–2006 (linear contrast F = 119.141, $p < 0.00001$). Depressed production in 2001 and 2002 is thought to be a carryover effect from the drought because it took several years for soil salinities to freshen (Figure 3). Higher production in recent years is partially attributable to a shift to more salt tolerant herbaceous species and decreased competition with tree species with continued high mortality rates, especially at the degraded sites.

Most of the herbaceous biomass production could be attributed to 15 dominant ground-cover species, which together represented 97% of the total herbaceous cover throughout the study. Alligatorweed (*Alternanthera philoxeroides*), smartweed (*Polygomum punctatum*), and arrow arum (*Peltandra virginica*) were the most ubiquitous herbaceous species in the swamps of southern Maurepas. Pickerelweed (*Pontederia cordata*) decreased in abundance as habitats became saltier and more open, whereas bulltongue (*Sagitarria lancifolia*) and fall panicum (*Panicum dicotomiflorum*) became more abundant. Maidencane (*Panicum hemitomon*) and spike rush (*Eleocharis* spp.) were generally only present at the interior sites and in ponded areas of degraded sites, and appear to be indicator species of marsh converting to open water.

Primary Production of Trees

Total tree primary production differed between habitat types ($F_{2,126} = 14.126$, $p < 0.00001$; Figure 8) and years ($F_{6,126} = 9.997$, $p = 0.00001$; Figure 7). Bulk density and salinity were significant covariables in the model ($F_{1,256} = 12.940$, $p = 0.00039$, $F_{1,256} = 2.058$, $p = 0.020$, respectively), indicating that tree primary production was higher at sites with higher bulk densities and lower salinities. The highest rates of total tree primary production were found at the

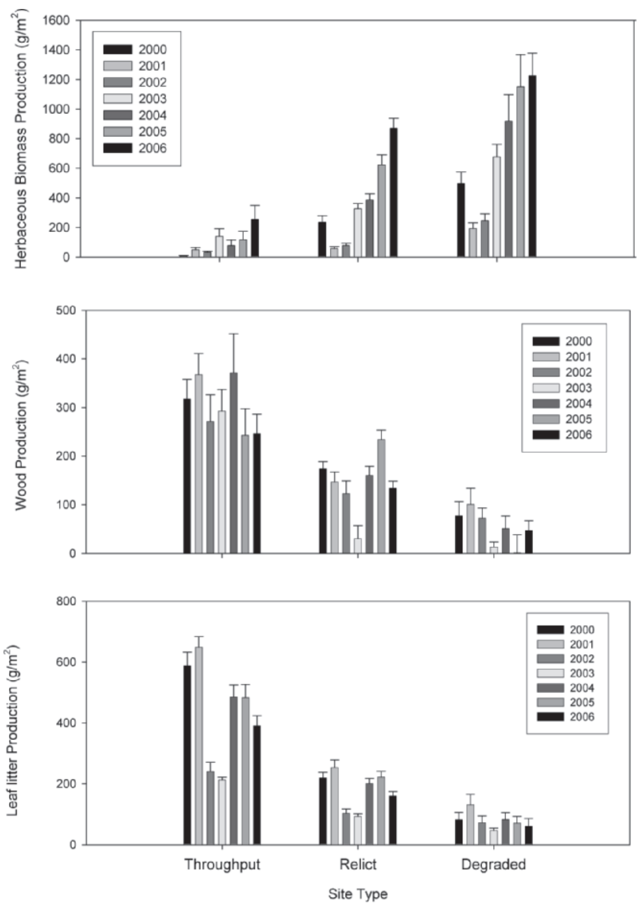

Figure 7. Annual herbaceous production, wood production, and litter production from 2000–2006 for the three habitat types. In general, the trees and ground cover followed inverse patterns through time with production increasing for herbaceous vegetation and decreasing for trees.

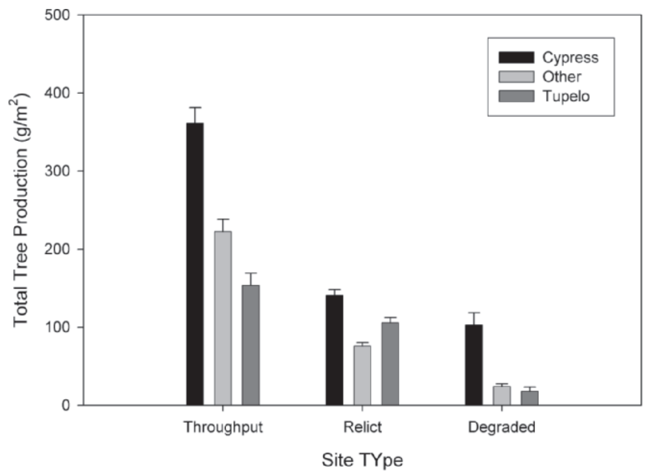

Figure 8. The interaction ($F_{4,651} = 17.43$, $p < 0.00001$) between species grouping and habitat type for total (leaf plus wood) production. Baldcypress production dominates in throughput and degraded habitats, but not in relict habitats.

throughput sites (mean = 737.03 ± SE 37.18 g·m^{-2}·y^{-1}), followed by relict sites (mean = 322.48 ± SE 13.88 g·m^{-2}·y^{-1}), followed by degraded sites (mean = 144.36 ± SE 37.18 g·m^{-2}·y^{-1}). In general, leaf litter and wood production followed similar patterns through time (Figure 7) with the lowest production overall occurring in 2003 (mean = 104.56 ± SE 10.34 g m^{-2} y^{-1}, 73.03 ± SE 24.25 g m^{-2} y^{-1}, respectively). Interestingly, a general increase in production was experienced by the herbaceous community in 2003, whereas the forest community continued to decline until 2004.

For total annual (leaf plus wood) tree production, an interaction existed between habitat type and the three categories of species (F = 17.34, $p < 0.00001$; Figure 8). The interaction occurred for relict sites where baldcypress had similar growth rates as water tupelo as well as in the other category. Although baldcypress was the least abundant species of the three categories at almost all sites (Hoeppner, 2002; Hoeppner, Shaffer, and Perkins, 2008), it had nearly twice the average growth rate (mean = 171.83 ± SE 8.33 g m^{-2} y^{-1}) as water tupelo (96.46± SE 5.70 g m^{-2} y^{-1}) or other (mean = 91.10 ± SE 5.53 g m^{-2} y^{-1}).

Total Primary Production

In a period of only 7 years, the Maurepas swamp has switched from an ecosystem dominated by tree production to one dominated by herbaceous production (Figure 9). From 2000–2003, overall production was similar, with a decrease in tree production compensated for by an increase in ground cover production. Overall production from 2004–2006 was significantly greater than that of 2000–2003, yet tree production continued to fluctuate around 400 g m^{-2} y^{-1}.

The BVSTEP routine (Clarke and Warwick, 2006) determined that the combination of factors that best described community structure was total tree production and herbaceous production (Spearman correlation ρ = 0.964; Figure 10). These two factors separated the throughput sites from the degraded sites, with relict sites containing some overlap with both, as in the logistic regressions (Figure 2). The ordination, based on nonmetric multidimensional scaling, shows a striking temporal trajectory from less forestlike characteristics to more marshlike characteristics (Figure 10). Degraded sites became completely dominated by herbaceous vegetation from 2000–2006, relict sites late in the study transitioned toward degraded sites early in the study, and throughput sites transitioned toward relict sites following the severe drought (*i.e.*, 2002), and late in the study.

The 2005 Hurricanes

The 2005 hurricanes appear to have decreased canopy tree production primarily by snapping limbs, whereas midstory trees suffered extensive wind throw where canopy basal areas fell below about 30 m^2 ha^{-1} (Figure 11; sites with basal areas less than 30 m^2 ha^{-1} that fell on the *x*-axis had lost all midstory trees prior to the 2005 hurricanes as a result of saltwater intrusion). Degraded sites suffered 100% loss of midstory species, whereas throughput sites, with many more

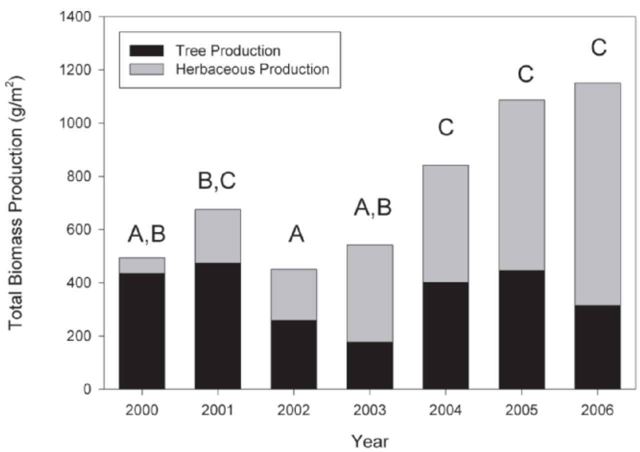

Figure 9. Overall (herbaceous plus tree) annual primary production averaged across habitat types from 2000–2006 with trees fluctuating between 200–400 g m^{-2} y^{-1} and ground cover showing a linear increase.

midstory stems, suffered very low mortality because of wind throw (Figure 12).

Spatial Extent of Degraded, Relict, and Thoughput Swamp

Overall, the mapped landscape was dominated by relict swamp, and the habitat types followed known salinity gradients (Figure 13). Only 13% (12,547 ha) of the mapped area classified as throughput swamp and was found in narrow strips contiguous with reliable sources of flowing freshwater. Without exception, areas that classified as degraded swamps were located near Lake Pontchartrain or along the margin of Lake Maurepas (Figure 13). These areas are prone to saltwater intrusion events from Lake Pontchartrain and totaled roughly 16% (15,168 ha) of the classified habitat. The remainder of the classified wetlands was identified as relict swamp (67%, 63,247 ha) and was generally located in hydrologically isolated areas that are nearly permanently flooded or in close proximity to the lake margin.

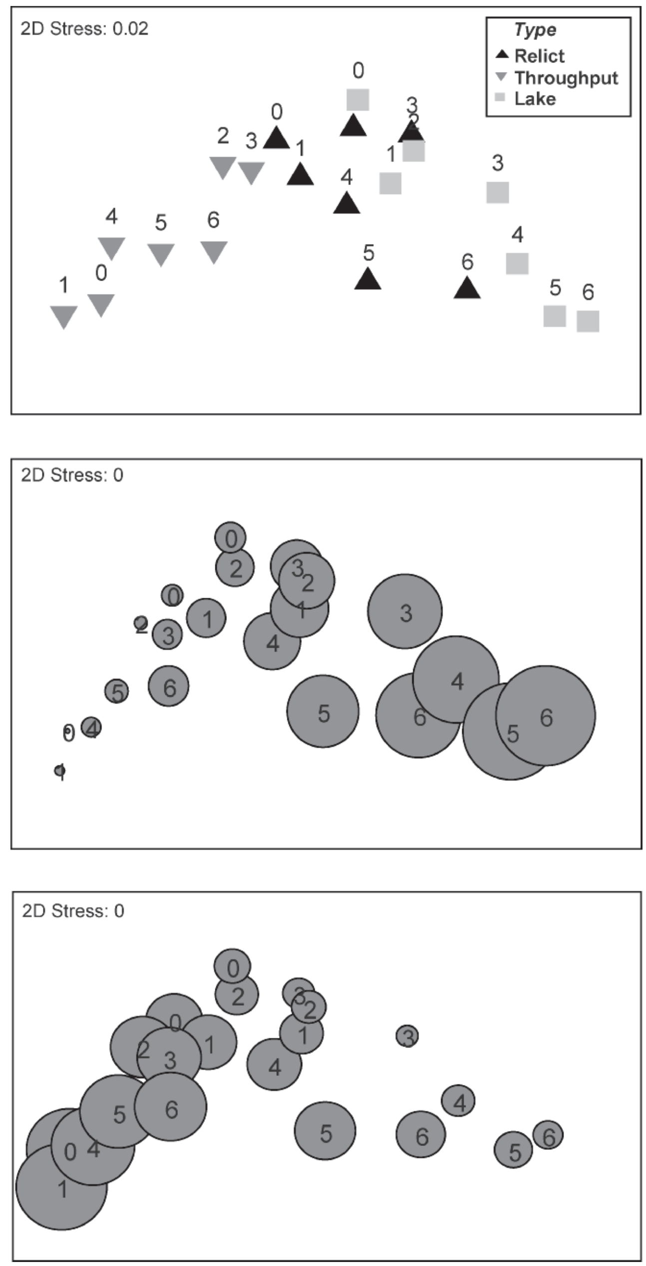

Figure 10. Overall tree and herbaceous production for each of the 20 sites was measured each year from 2000–2006. The 20 sites were grouped into three habitat types (throughput, relict, and degraded) and analyzed using nonmetric multidimensional scaling (NMS). Axis 1 separates throughput sites (the most treed sites) on the left from degraded (marshlike) sites on the right, with relict forming a tree–herbaceous gradient (shown on top). Herbaceous production is highest in degraded sites (shown in middle). Tree production is highest in throughput sites (shown in bottom). Numbers 0–6 represent years 2000 to 2006. Each year is represented within each habitat type.

DISCUSSION

Flooding has doubled in the Manchac Wildlife Management Area adjacent to the Maurepas swamp since 1955 because of sea-level rise and subsidence (Thomson, Shaffer, and McCorquodale, 2002). Currently, the Maurepas swamps are often lower in elevation than the lake, rendering flooding semipermanent. Furthermore, flood control levees and abandoned raised railroad tracks have impounded much of the remaining swamps, causing throughput to be low. These swamps have been cut off from the sustaining spring floods of the Mississippi River for over a century and are in varying states of decline. Until this study was undertaken, the decline was evidenced by qualitative information such as dead and dying canopies of the predominant water tupelo trees. We now have quantitative information that allows us to compute the likely benefits of a future with a reintroduction of Mississippi River water into the southwestern Maurepas swamp in comparison to the continued demise of the swamp ecosystem in a future without such a project (Shaffer *et al.,* 2003).

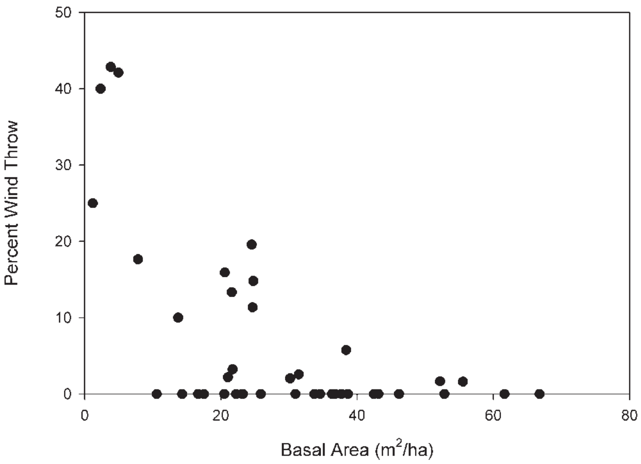

Figure 11. Percentage of midstory species wind thrown by the 2005 hurricanes (*y*-axis) across different basal areas of baldcypress–water tupelo canopy trees. Wind throw increases dramatically when the basal area of canopy trees decreases below about 30 m^2 ha^{-1}. Points on *x*-axis below 30 m^2 ha^{-1} have no midstory trees left to lose.

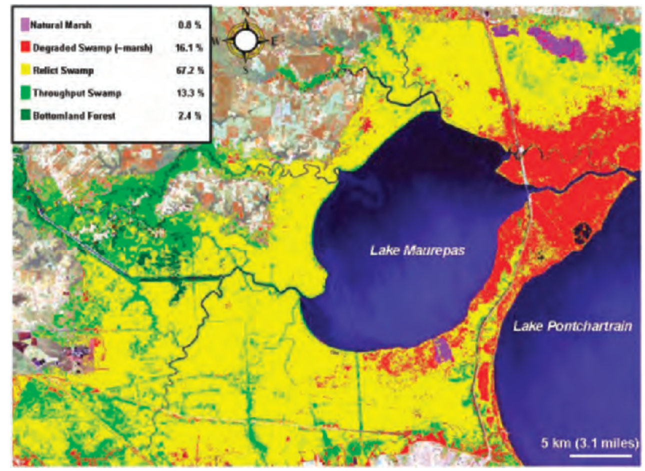

Figure 13. Habitat type classification of the wetlands in the Upper Lake Pontchartrain Basin, Louisiana. Habitats include natural marsh (purple), swamp that has degraded to marsh during the past half-century (red), relict swamps (yellow), potentially sustainable throughput swamps (bright green), and bottomland hardwood forests (dark green).

The Maurepas swamps are characterized by nutrient poor waters with nitrate levels less than 1% of those found in the Mississippi River (Lane *et al.,* 2003). In addition, the soils are of extremely low strength indicative of stress such as saltwater intrusion events that typically occur during late summer and fall. The mean salinity of lake water measured at the Manchac bridge also has increased gradually, beginning in the early 1960s with the opening of the MRGO (Shaffer *et al.,* 2009; Thomson, Shaffer, and McCorquodale, 2002). Severe increases in salinity, like those experienced during the droughts in 1999 and 2000, may be prevented or greatly ameliorated by the increased freshwater throughput that the proposed river reintroduction would offer. It is likely that the influences of freshening would be felt in wetlands as distant as Lake Pontchartrain (Figure 13) because the smallest proposed diversion of 42.5 m^3 s^{-1} would replace all of the water in Lake Maurepas twice each year, and it can only exit to Lake Pontchartrain through Pass Manchac and North Pass.

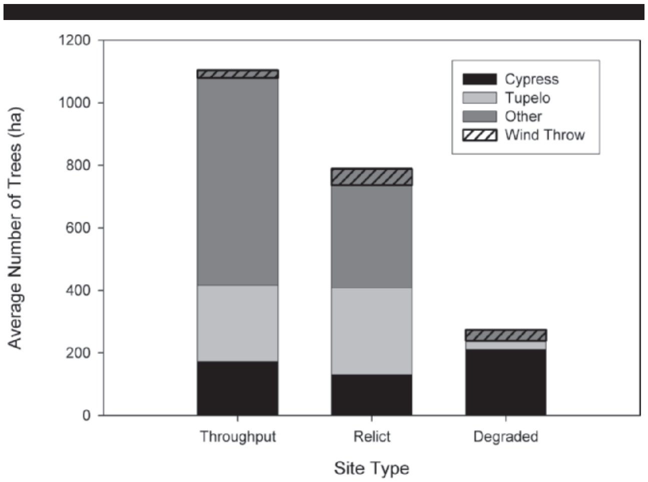

Figure 12. Average number of individuals of baldcypress, water tupelo, and other (mostly swamp red maple and ash) species at each habitat type. Hatched areas show number of wind thrown midstory trees, demonstrating that throughput sites, with the highest number of trees in the other grouping, suffered very low mortality from the 2005 hurricanes.

The soil characteristics at the majority of the study sites are indicative of a lack of riverine influence (lack of sediment input and throughput) as evidenced by high soil organic matter content and low bulk density values (DeLaune, Buresh, and Patrick, 1979; Hatton, 1981; Messina and Conner, 1998). With the exception of throughput sites, soil bulk densities are in the range of those typically found in fresh and oligohaline marshes that are located interior of streamside hydrology effects (Hatton, 1981). This agrees with the continued mortality of trees and the conversion of the system to a more herbaceous plant community.

Our study, and previous studies by Boshart (1997), Effler, Goyer, and Lenhard (2006), Greene (1994), and Myers, Shaffer, and Llewellyn (1995) indicate that the herbaceous and woody vegetation in the Maurepas swamp is nutrient starved. The dramatic increases in herbaceous standing crop with increased nutrient loading were only evidenced in caged plots because herbivores targeted the vegetation with increased protein content in uncaged, fertilized plots. Fertilizing at a loading rate of 22.5 g N m^{-2} y^{-1}, which simulates a river diversion of 85 m^3 s^{-1}, more than doubled biomass production, when compared with caged control plots. Although the second application of fertilizer during the summer did not increase production over a single application, it is during the fall that saltwater intrusion events generally occur. Therefore engineering the river reintroduction to allow for fall operation remains an important design feature.

The difference in forest structure among different areas in the Maurepas swamp also is an indication of the health and

Table 1. *Measurements of swamp primary production from several different studies including the Maurepas swamp.*

Forest Type (State)	Tree Standing Biomass (kg m^{-2})	Litterfall (g·m^{-2}·y^{-1})	Stem Growth (g·m^{-2}·y^{-1})	Above-Ground NPP[1] (g·m^{-2}·y^{-1})	Reference
Reference locations					
Cypress–tupelo (LA)	37.5[2]	620	500	1120	Conner and Day (1976)
Impounded managed swamp (LA)	32.8[2,3]	550	1230	1780	Conner *et al.* (1981)
Impounded stagnant swamp (LA)	15.9[2,3]	330	560	890	Conner *et al.* (1981)
Tupelo stand (LA)	36.2[2]	379	—	—	Conner and Day (1982)
Cypress stand (LA)	27.8[2]	562	—	—	Conner and Day (1982)
Nutrient-poor cypress swamp (GA)	30.7[4]	328	353	681	Schlesinger (1978)
Stagnant cypress swamp (KY)	9.4	63	142	205	Taylor (1985), Mitsch *et al.* (1991)
Sewage enriched cypress strand (FL)	28.6	650	640	1290	Nessel (1978)
Near-continuously flooded cypress–ash swamp (LA)	—	553[5]	443[4]	996	Megonigal *et al.* (1997)[5]
Near-continuously flooded riverine cypress–tupelo swamp (SC)	—	438[5]	216[4]	654	Megonigal *et al.* (1997)[5]
Naturally flooded swamp (LA)	—	487[5]	338[4]	825	Megonigal *et al.* (1997)[5]
Periodically flooded riverine swamp (LA)	—	725[5]	430[4]	1155	Megonigal *et al.* (1997)[5]
Frequently flooded swamp (SC)	—	—	—	1887	Muzika *et al.* (1987)
Maurepas Swamp locations (this study)					
Relict sites	11.68[7]	179.2	143.3[4,7,8]	322.5[6]	
Degraded sites	4.7	78.0	66.4[4,7,8]	144.4[6]	
Throughput sites	23.26[7]	435.7	301.4[4,7,8]	737.0[6]	
Total average	12.65[7]	203.8	155.6[4,7,8]	359.4[6]	

[1] NPP = net primary productivity = litterfall + stem growth.
[2] Trees defined as >2.54 cm DBH (diameter at breast height).
[3] Cypress, tupelo, ash only.
[4] Trees defined as >10 cm DBH.
[5] Litterfall does not include woody litter.
[6] All values are presented as averages of two replicate plots in two consecutive years.
[7] Averages of three to six sites with two substations each.
[8] Cypress, tupelo, ash, maple, and blackgum, where present.

future of these sites. Overall, the overstory is dominated by either water tupelo, baldcypress, or both, while the midstory is largely dominated by high numbers of swamp red maple, pumpkin ash and green ash, all of which are more shade tolerant than either of the dominants (Fowells, 1965). Similar observations have been made in comparable swamps in the Barataria Basin (Conner and Day, 1976). Wax mytle (*Morella cerifera*), Chinese tallow (*Triadica sebiferum*), and black willow (*Salix nigra*) dominate the midstory in areas of disturbance that were characterized by more open canopies and measurable saltwater intrusion effects. Shrub–scrub habitats are often observed on the transitional edges between marshes and forested wetlands or uplands (Barras, Bourgeois, and Handley, 1994; White, 1983). Diamond oak (*Quercus obtusa*), pumpkin ash, and green ash were found in greater abundance at sites characterized by higher bulk densities, which were indicative of increased throughput and generally less flooding. These observations support similar findings from wetland plant ordinations by White (1983) in the Pearl River, Louisiana, and Rheinhardt *et al.,* (1998) in the forested riverine wetlands of the inner coastal plain of North Carolina. Because Chinese tallow has been found to be more shade, flood, and salt tolerant (Conner and Askew, 1993; Jones, Sharitz, and McLeod, 1989) than several other native wetland tree species, this invasive species may become more dominant in the coastal wetlands of the southeastern United States (Conner and Askew, 1993).

Stem densities at throughput sites are similar to densities reported for impounded (Conner and Day, 1992; Conner, Gosselink, and Parrondo, 1981) or continuously flooded (Dicke and Toliver, 1990) swamps throughout Louisiana, whereas stem densities at relict sites are less than those reported for impounded swamps (Table 1). Average stem densities at degraded sites are not even half of those reported for impounded swamp sites, most likely because neither water tupelo, ash, nor swamp red maple have salt tolerances that could withstand the chronic salinity conditions of 2–4 ppt found at these sites. Conner, McCloed, and McCarron (1997) and Pezeshki (1989) reported that these species showed signs of stress and reduced growth at salinities as low as 2–3 ppt. Black gum (*Nyssa sylvatica* var. *biflora*) seedlings experienced 100% mortality when exposed to chronic flooding with 2 ppt (McCarron, McLeod, and Conner, 1998). Likewise, the relatively low stem densities observed at the relict swamp sites (Table 1) are primarily the result of the decreased abundance of ash and swamp red maple in the impounded and stagnant hydrologic regimes characteristic of these sites. In general, basal area followed very similar patterns as stem density. During our 7-year study, nearly 20% of the monitored trees suffered mortality, with mortality as high as 87% at one degraded site.

In terms of above-ground net tree primary production, only the most productive sites of the Maurepas swamp compare well with natural, periodically flooded baldcypress–water tupelo swamps (Carter *et al.,* 1973; Conner and Day, 1976; Conner, Gosselink, and Parrondo, 1981; Megonigal *et al.,* 1997), and then only during years of normal precipitation. The vast majority of the Maurepas swamp is either relict or degraded (Figure 13), and these areas range in total tree production between swamps that have been identified as either nutrient-poor and stagnant (Schlesinger, 1978), just stagnant (Mitsch, Taylor, and Benson, 1991; Taylor, 1985), or near-continuously flooded baldcypress swamps (Megonigal *et al.,* 1997). The remarkable linear increase of herbaceous production at relict and, more emphatically, degraded sites from 2000–2006 is a strong indication that these forested wetlands are converting to marshes (Barras, Bourgeois, and Handley, 1994). We believe that the increased herbaceous production in 2006 was largely a result of the 2005 hurricanes because up to 1 cm of sedimentation occurred (Turner *et al.,* 2006) at sites near the lake margin and light penetration was increased by wind throw of midstory species. We expect this trend to reverse itself as the marsh degrades, just as it has on the nearby Manchac land bridge.

Overall, baldcypress was the most productive species in the Maurepas, while water tupelo was the second most productive. This finding agrees with the observation that these two species are the canopy dominants, make up the majority of the basal area found at each site, and are the most flood-tolerant tree species in this ecosystem (Hook, 1984). Furthermore, the higher biomass production of baldcypress also agrees with several studies that reported baldcypress seedlings to be more tolerant of low salinity and permanent flooding than water tupelo, swamp red maple, and ash (Conner, McCleod, and McCarron, 1997; Dickson and Broyer, 1972; Keeland and Sharitz, 1990; Pezeshki, 1989).

The Maurepas swamps are nearly continuously flooded and largely impounded, which prevents seed germination and recruitment of baldcypress and water tupelo (Conner and Day, 1976, 1988; DuBarry, 1963; Harms, 1973; Myers, Shaffer, and Llewellyn, 1995; Souther and Shaffer, 2000; Williston, Shropshire, and Balmer, 1980). Modeling efforts by Conner and Brody (1989) have shown that even though baldcypress and water tupelo are flood tolerant (Brown, 1981; Carter *et al.,* 1973; Conner, Gosselink, and Parrondo, 1981; Mitsch and Rust, 1984), the total basal area of both will decline if water levels continue to rise. Thus, continuous flooding, though not immediately detrimental to these swamps, will lead to their gradual death over time (Conner and Brody, 1989; Conner and Day, 1988, 1992; Harms *et al.,* 1980; Mitsch and Rust, 1984). The different habitat types identified within the Maurepas swamp (Figure 13) appear to be in various stages along this trajectory of swamp decline, ranging from the continuously flooded but productive throughput sites to the impounded, flood and/or salinity stressed relict and degraded sites, respectively.

Hurricane Impacts

Only live oak (*Quercus virginica*) and palms are more resistant to wind throw than baldcypress and water tupelo (Williams *et al.,* 1999). Baldcypress–water tupelo swamps fared far better than other forest types in Hurricanes Camille (Touliatos and Roth, 1971), Andrew (Doyle *et al.,* 1995), and Hugo (Gresham, Williams, and Lipscomb, 1991; Putz and Sharitz, 1991). In addition, fresh, oligohaline, and brackish marshes suffered vastly greater loss in Hurricanes Katrina and Rita than did baldcypress–water tupelo swamps (Barras, 2006). Hurricane Katrina caused wind throws of an estimated 320 million bottomland hardwood trees in the Pearl River Basin, while contiguous swamps remained largely intact (Chambers *et al.,* 2007). The Maurepas swamp was no different with respect to canopy species that suffered zero wind throw, but a relationship was found between canopy basal area and wind throw of midstory species, in particular swamp red maple. As basal areas of canopy species dropped below about 30 m^2 ha^{-1}, a linear increase in wind-thrown midstory trees existed (Figure 11). At the degraded sites, all of the midstory trees were lost to the 2005 hurricanes (Figure 12), whereas throughput sites, containing a far greater number of midstory stems, lost very few individuals. It appears that the extensive lateral root systems of baldcypress and water tupelo hold the entire ecosystem together when canopy trees are dense.

In terms of flood- and wind-damage reduction, baldcypress–water tupelo swamps appear to be far superior to other wetland habitat types, even mangrove forests that were instrumental in protecting villages during the recent Asian tsunami (Danielsen *et al.,* 2005; Williams *et al.,* 1999). We need to rethink coastal restoration and management strategies, tailoring them to storm-protection alternatives (Boesch *et al.,* 2006; Costanza, Mitsch, and Day, 2006; Day *et al.,* 2007; Lopez, 2006) that include restoring historic levels of baldcypress–water tupelo swamps.

Reversing the Trajectory of Decline

In summary, the Maurepas swamp is characterized by nutrient poor waters, soils of extremely low strength, nearly permanent flooding in most areas, and saltwater intrusions that generally occur during the late summer and fall seasons. The Maurepas swamp is nitrogen limited, and nutrient stress is potentially as important as salt or flood stress. Furthermore, recruitment of baldcypress and water tupelo saplings throughout the swamp is very low, certainly not sufficient to sustain the aerial extent of current forest. Most of the Maurepas swamp appears to be converting to marsh and open water, primarily due to the lack of riverine input. Salt stress is killing trees proximal to the lake, whereas stagnant standing water and nutrient deprivation appear to be the largest stressors at interior sites.

Although baldcypress–water tupelo swamps are extremely resistant to wind throw and deep flooding, they are less resistant to saltwater intrusion and thus require a reliable source of freshwater for system flushing following tropical storm events and during droughts. Swamps can survive short-term salinity pulses (Allen, Chambers, and McKinney, 1994; Campo, 1996; Conner *et al.* 1997). We are in the process of building a geographic information system that contains all substantial point and nonpoint freshwater sources, including urban and agricultural runoff, storm water pumps, noncontact industrial cooling water, municipal wastewater treatment facilities, and potential Mississippi River diversion sites. At present, most of these sources are input to the basin to maximize drainage efficiency. Freshwater is routed into ditches and canals that carry it directly to the lakes, bypassing wetland contact. This creates a "lose–lose" situation because potential for eutrophication is maximized and the wetlands remain nutrient starved. In contrast, rerouting the water to maximize sheet flow would improve water quality, increase wetland net primary production, and decrease saltwater intrusion (Shaffer and Day, 2007). Furthermore, implementation of the proposed Mississippi River reintroductions at Violet, Bonnet Carre, La Branche, and two in the Maurepas swamp (Coast 2050, 1998) will greatly enhance restoration of historic salinity regimes. In addition to the benefits mentioned, increasing swamp acreage will decrease storm damage, may lead to net sediment accretion, will increase carbon sequestration (Trettin and Jorgensen, 2003), enhance biodiversity, and improve several of the "multiple lines of defense" proposed by Lopez (2006). Of historic significance is the current closure of the Mississippi River Gulf Outlet (USACE 2007), which will help approximate historic salinity regimes and further assist in storm-damage reduction (Shaffer *et al.,* 2009).

One concern that managers and the general public have with restoring repressed swamps is the amount of time required for swamplike characteristics to emerge and manifest. Fortunately, given favorable hydrologic and nutrient conditions, baldcypress and water tupelo seedlings can reach greater than 10 m heights within one decade. For example, a pilot planting of baldcypress seedlings at the Caernarvon diversion (Krauss *et al.,* 2000) has yielded trees over 10 m tall in a decade, and all of these resisted wind throw during the hurricanes of 2005. In conclusion, if we are to reverse the trajectory of decline of coastal Louisiana swamps, we must find, and wisely use, point and nonpoint sources of fresh water currently being wasted.

Despite the degraded condition of the majority of the baldcypress–water tupelo swamps of the upper Lake Pontchartrain Basin, healthy areas of swamp still exist. Without exception, each of these swamps receives some form of reliable high-quality, nutrient-rich fresh water. These forests are either receiving nonpoint sources of fresh water from urban areas (*e.g.,* forests of Hope Canal and Alligator Island), high quality river water (*e.g.,* forests of Pearl River), or secondarily treated sewage effluent (*e.g.,* forests of Bayou Chinchuba). Restoration efforts that include the proper combination of river diversions, treated sewage effluent assimilation wetlands, and rerouted nonpoint source freshwater, should enable restoration of Lake Pontchartrain Basin's swamps (Shaffer and Day, 2007).

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Degradation of Baldcypress–Water Tupelo Swamp to Marsh and Open Water in Southeastern Louisiana, U.S.A.: An Irreversible Trajectory?

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ABSTRACT

SHAFFER, G.P.; WOOD, W.B.; HOEPPNER, S.S.; PERKINS, T.E.; ZOLLER, J., and KANDALEPAS, D., 2009. Degradation of baldcypress–water tupelo swamp to marsh marsh and open water in Southeastern Louisiana, U.S.A.: an irreversible trajectory? *Journal of Coastal Research*, 54(00), 000–000. West Palm Beach (Florida), ISSN 0749-0208.

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In general, many of the swamps of coastal Louisiana, U.S.A., are highly degraded, and several are converting to marsh and open water. The initial purpose of this study was to determine the feasibility, and potential benefits, of reintroducing waters of the Mississippi River into the degraded Maurepas swamp, located in the Pontchartrain Basin of southeastern Louisiana. Early in the year 2000, 20 sites were selected in three different habitat types characterized by moving freshwater (throughput sites), stagnant, nearly permanently flooded (relict sites), and areas prone to saltwater intrusion events (degraded sites). Paired 625-m^2 plots were outfitted with litter-fall traps, herbaceous subplots, and wells for measuring interstitial soil salinity. From 2000–2006, diameter growth was followed for 2219 trees, and herbaceous production was estimated using mid- and late-growing season clip plots. Overall, primary production was dominated by trees early in the study, but switched to herbaceous vegetation as parts of the ecosystem converted from swamp to marsh. Salt stress was the primary cause of tree mortality in areas of low density, whereas stagnant standing water and nutrient deprivation appear to be the largest stressors at interior (relict) sites. The 2005 hurricanes caused wind throw of up to 100% of midstory trees in areas of low canopy density and was negligible when basal areas of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) were greater than 30 m^2 ha^{-1}. Using spectral signatures of the 625-m^2 plots, the aerial extent of habitat types revealed that the vast majority of the Maurepas swamp is either relict or degraded. Without a river reintroduction in the near future, as well as harnessing other point and nonpoint sources of freshwater, the Maurepas swamp will continue its clear trajectory to marsh and open water.

ADDITIONAL INDEX WORDS: *Coastal forested wetlands,* Taxodium distichum–Nyssa aquatica *swamp, wetland loss, saltwater intrusion, hydrologic alteration, Mississippi River reintroduction, river diversion.*

INTRODUCTION

Historically, the wetlands of the upper Lake Pontchartrain Basin, located in southeastern Louisiana, U.S.A., were 90% baldcypress–water tupelo (*Taxodium distichum–Nyssa aquatica*) swamps (Saucier, 1963). The extent of swamp has been radically reduced by multiple stressors such as logging, development, hydrologic alteration, nutrient deprivation, and saltwater intrusion. Much of the remaining swamp is in a state of deterioration (Chambers *et al.*, 2005) and several restoration projects are planned (Coast 2050, 1998).

Despite its degraded condition, the Maurepas swamp complex is the second largest contiguous coastal forest in Louisiana, consisting of 77,550 ha of swamp and 5204 ha of fresh or oligohaline marsh (Coast 2050, 1998). As in most of deltaic Louisiana, leveeing the Mississippi River has removed a once reliable source of freshwater, nutrients, and sediments, and enabled periodic encroachment of saltwater from the Gulf of Mexico (Day *et al.*, 2000, 2007). Construction of massive canals, such as the Mississippi River Gulf Outlet (MRGO, Shaffer *et al.* this volume), combined with sea level rise, have further exacerbated the frequency and intensity of saltwater intrusion events. As a result, most of the Maurepas swamp appears to be in transition to marsh and open water. Several restoration projects have been proposed to combat swamp loss, the most promising of which involve reintroductions of Mississippi River water. This study was initiated to document the extent of swamp degradation and to quantify the potential benefits of a river reintroduction into the southwestern Maurepas swamp (Day *et al.*, 2004; Shaffer *et al.*, 2003).

The geologic development of most of coastal Louisiana occurred through a series of delta lobe shifts of the Mississippi River, which occurred roughly once every 1000 years (Coleman, Roberts, and Stone, 1998; Day, *et al.*, 2007; Scruton, 1960). Lakes Pontchartrain and Maurepas were

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formed during the evolution of two separate delta lobes over the past 4000 years. The Cocodrie lobe expanded over the area where New Orleans presently resides, forming the lakes' southern shores. The St. Bernard lobe then completed the lakes' eastern shoreline (Frazier, 1967; Saucier, 1963).

Wood from the vast virgin stands of baldcypress became the dominant cash crop in Louisiana during the eighteenth century (Mattoon, 1915). However, it was not until the 1890s that large-scale clear-cutting of the baldcypress swamps became possible due to the invention of pullboats and skidders, which increased the accessibility of interior swamps (Mancil, 1980). Most of the old-growth baldcypress had been clear cut by the early twentieth century. Most areas in the Pontchartrain Basin regenerated as second-growth baldcypress–water tupelo swamps. By the mid-1960s, however, many areas in the basin started to convert to marsh and open water (Barras, Bourgeois, and Handley, 1994).

The second-growth swamps in coastal Louisiana have now become merchantable, and harvesting interests have been renewed. These renewed logging interests have generated opposition from scientists and the general public. Several studies of Mississippi River deltaic swamps indicate that many of these swamps are not sustainable (Chambers *et al.,* 2005; Conner and Day, 1992; Hoeppner, 2002; Hoeppner, Shaffer, and Perkins, 2008; Pezeshki, DeLaune, and Patrick, 1990; Shaffer *et al.,* 2003) and exhibit little natural regeneration (Conner and Day, 1976; Shaffer *et al.,* 2003). To address the issue of the conflicting pressures of logging versus restoration, the governor of Louisiana convened a group of forested wetland ecologists to provide science-based interim guidelines for coastal swamp conservation and utilization (Chambers *et al.,* 2005). As part of this effort, we identified and mapped the extent of potentially sustainable, relict, and degraded swamp in the upper Lake Pontchartrain Basin and will present that herein.

The main objective of this study is to compare the primary production of woody and herbaceous vegetation throughout a 7-year duration that experienced periods of severe drought, normal weather conditions, and Hurricanes Katrina and Rita in 2005. By following changes in abiotic and biotic factors influencing swamp production over multiple years, this study should enable crisp quantification of benefits that restoration projects (such as Mississippi River reintroductions and using other point and nonpoint freshwater resources) will have on ecosystem function.

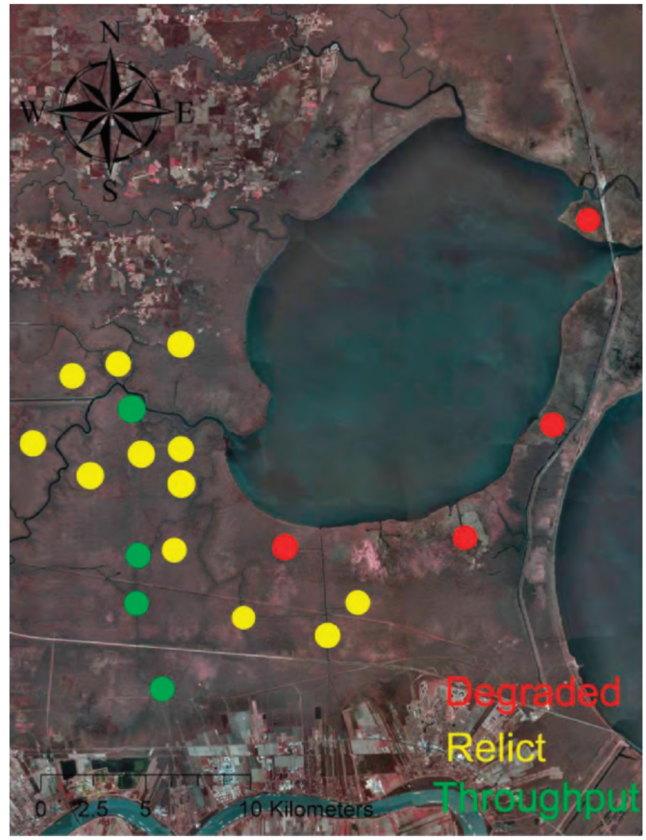

Figure 1. The Maurepas swamps rim the margin of Lake Maurepas in southeastern Louisiana, and are bounded by urban development to the north, west, and south. Twenty sites were selected to represent the three major habitat types: throughput sites (green), relict sites (yellow), and degraded swamp sites (red).

MATERIALS AND METHODS

Study Site

The study area is located in the upper Pontchartrain Basin, a marginal deltaic basin that was enclosed by the progradation of the St. Bernard delta complex some 2500 years ago. Regional estimates place relative sea-level rise (RSLR) between 3.6 and 4.5 mm y^{-1} in this basin (Penland and Ramsey, 1990). To accurately characterize the Maurepas swamp, we selected 20 study sites with paired 625-m^2 plots in the southern wetlands of Lake Maurepas. These sites were chosen to capture three different hydrological regimes within the swamp, namely stagnant, nearly permanently flooded interior sites (relict), sites near the margin of Lake Maurepas that are prone to severe saltwater intrusion events (degraded), and sites receiving reliable nonpoint sources of freshwater runoff (throughput) (Figure 1). To determine the validity of the *a priori* habitat type groupings, we used multinomial regressions on the 2000 and 2001 environmental data (for details, see Statistical Analysis). Taken together, all study sites characterize an area roughly 180 km^2 in size.

Environmental Covariables

Abiotic variables, including soil water salinity, light penetration, pH, bulk density, redox potential (Eh), sulfide, nitrate, ammonia, and phosphate concentrations, were monitored at the 20 study sites (Shaffer *et al.,* 2003). Of these, soil salinity, light penetration, and bulk density were the most important predictors of herbaceous and tree production so we will limit description to these.

To measure soil salinity, we inserted two 1 m × 6 cm diameter PVC wells 0.75 m into the ground at each of the 40 stations. Wells were capped at both ends. Horizontal slits were cut into the wells every 2 cm from a depth of 5 cm to a depth of 70 cm below the soil surface to enable groundwater to enter. Wells were outfitted with plastic skirts at the soil surface to prevent rainwater seepage (Thomson, 2000). Each well was completely evacuated and allowed to refill before salinity measurements were taken (using a YSI salinity–conductivity–temperature meter). Well-water salinity was measured during most site visits and averaged to yield a measure of yearly mean salinity at each study plot.

Soil cores for bulk density analysis were collected during the fall sampling period in 2001 and 2002, using an aluminum soil corer with a 1.6 cm inner diameter. Samples were collected by coring to a depth of 10 cm, carefully removing the soil corer from the surrounding substrate, and extruding the cores into plastic sample bags. To minimize the influence of microscale heterogeneity of soil strength, we took five replicate cores at two locations within each study plot. The five replicate cores were combined into a single sample in the field, while the two pooled samples from different locations within the same study plot were processed independently. Each sample was dried to constant mass at 65°C in a ventilated oven before soil core weights were measured. Light penetration was measured in the center of each of four 16-m^2 herbaceous plots within each station, using a spherical crown microdensiometer.

Herbaceous Vegetation

Within each of the 40 permanent stations, four 4 m × 4 m (16 m^2) permanent herbaceous plots were established 5 m in from the diagonal corners of each station. A 4-m^2 plot was established in the center of each 16-m^2 plot for cover value estimates and biomass clip plots. Each year cover values were obtained by two independent estimates during summer and fall. Percentage cover of vegetation by species was determined by ocular estimation in 5% increments. Each year understory primary production was estimated within each herbaceous plot by clipping two randomly chosen (nonrepeating) replicate subplots (of 0.25 m^2 area) twice during the growing season (Whigham *et al.,* 1978; Wohlgemuth, 1988). The pseudoreplicate subplots were pooled on site during the May–June (summer) sampling and again during late September–early October (fall). Plant material was clipped at the soil surface, placed in a labeled bag, and transported to the lab, where it remained in cold storage until it could be oven dried and weighed. Annual aboveground herbaceous production was estimated by summing the summer and fall biomass estimates. Indeed, a turnover study on *Sagittaria lancifolia* (a dominant herbaceous species in the study area) on the Manchac land bridge, during 2005 and 2006, indicated that this species completely replaces itself approximately once per year (2005 mean turnover = 1.094 ± 0.032 SE; 2006 mean turnover = 1.341 ± 0.077 SE).

During 2002 and 2003, fifty-six 16 m^2 vegetation plots were used to simulate nutrient loading rates of several different Mississippi River reintroduction scenarios. Four (18-6-12 timed-release Osmocote) fertilizer levels were applied to simulate (a) current conditions (*i.e.*, no fertilizer addition), (b) a loading rate of 11.25 g N m^2 y^{-1}, or a discharge of 42.5 m^3 s^{-1} (Lane *et al.,* 2003) during the spring, (c) twice that during the spring, and (d) twice that during both spring and fall to simulate a river reintroduction operating during the entire growing season. Half of the plots at each fertilizer level were outfitted with herbivore-exclusion cages to prevent herbivory, primarily by nutria and deer.

Forest Vegetation

All trees greater than 5 cm diameter within each of the two 625 m^2 plots at each of 20 study sites in the Maurepas swamp were tagged using 8-penny galvanized nails and prenumbered 5-cm metal ID tags in February and March of 2000. Trees were tagged at breast height, unless the fluting bases of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) or the complex branching structure of shrubs such as wax myrtle (*Morella cerifera*) required the tags to be somewhat higher. Using fiberglass metric diameter tapes, initial tree diameters of 1860 tagged trees were measured during February and March of 2000 at the bottom of the freely hanging metal tags. Nails were placed at the same height 180° from the tags to improve precision of subsequent measurements. During late fall, 2000–2006, diameter measures were taken of all tagged trees. Throughout the study many trees suffered mortality and many saplings grew to the 5 cm tagging size such that a total of 2219 trees were tagged in all. Prior to analysis, the diameter data were harmonized following the guidelines of Sheil (1995).

Tree primary production was measured through the collection of annual litter fall and the measurement of annual tree diameter growth (Brown, 1981; Conner and Day, 1992; Mitsch and Ewel, 1979) at the 40 study plots. Five litter-fall traps were installed at approximately even spacing at each of the two stations at 20 study sites to yield a total of 200 litter traps deployed. Each of these traps was 0.25 m^2 in area and was constructed to catch biomass in a fine (1 mm) mesh approximately 1 m above the ground to prevent loss from flooding events. The litter was collected frequently during site visits, which occurred as often as once every 2 weeks or as infrequently as once every 2 months during periods of the growing season when few leaves were falling (*i.e.*, spring, summer). During or after collection, the litter from each of the five litter traps at each plot was combined to yield one total sample of litter per plot because the five traps are considered pseudoreplicates. For this study, we use the term "litter" for leaves, flowers, fruits, and seeds. Collected litter was then dried to constant mass at 65°C. After drying, the litter was sorted into *T. distichum, N. aquatic,* and "other" litter. This enabled us to monitor production effects at the species level for at least the two most dominant tree species in the swamp. The vast majority of other stems were midstory swamp red maple [*Acer rubrum* (var. *drummondii*)] and ash (*Fraxinus pennsylvanica* and *F. profunda*).

Each year, tree diameter was used to calculate tree wood biomass using published regression formulas (Clark, Phillips, and Frederick, 1985; Muzika, Gladden, and Haddock, 1987; Scott, Sharitz, and Lee, 1985). Wood production was calculated as the difference in wood biomass per year. Wood production per tree was then summed by species category per plot and then converted to total wood production per square meter per year (g m^{-2} y^{-1}).

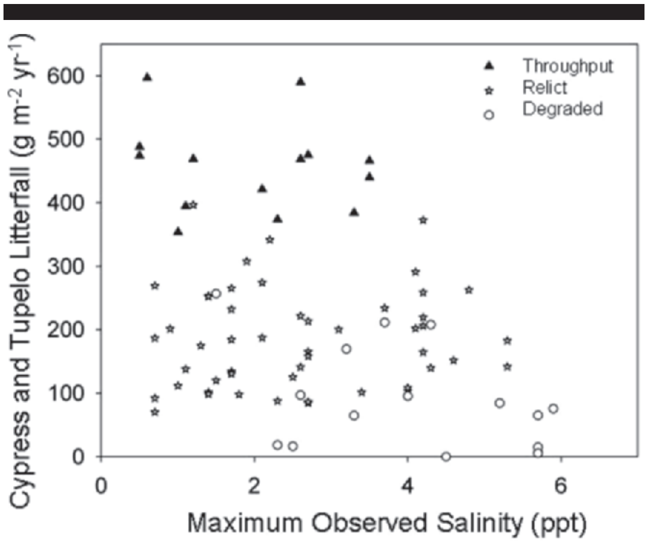

Figure 2. Results of multinomial logistic regressions classifying three *a priori* habitat types by maximum observed soil salinity and annual cypress and tupelo litter production. Clear separation occurs between throughput and degraded sites with some relict sites sharing attributes with each.

Mapping Habitat Types

To determine the spatial extent of the three habitat types (degraded, relict, and throughput), we used spectral signatures of our 625-m^2 stations to extrapolate areally over the Manchac–Maurepas wetlands. A Landsat 7 Thematic Mapper image of the upper Lake Pontchartrain Basin from May 21, 2002, was imported into ERDAS Imagine 8.7 (Leica-Geosystems, 2004) for analysis. In a supervised classification, we used the coordinates and known habitat types from 30 of our 40 field plots as training sites to identify the signature profiles of the *a priori* vegetation types discussed, plus bottomland hardwood forest. The 30 field plots chosen as training sites were those that displayed clear separation in the multinomial logistic regressions (Figure 2). Unsupervised classification was then used to classify all of the remaining pixels. The final classification was then verified by conducting field trips to many locations not used as training sites within each habitat type and showing the map to local authorities familiar with the area.

Statistical Analysis

All statistical analyses were performed using SYSTAT 10.2 (Wilkenson, 2001) and SAS 9.1.2 for Windows (SAS Institute Inc., 2000–2004). Stepwise multinomial logistic regressions were used to evaluate *a priori* site groupings (degraded, relict, throughput). To avoid tolerance problems, we screened variables for multicollinearity by principal components analysis prior to their use in the logistic regressions. Variables with high collinearity were combined as factor scores. Principal components analysis utilized a varimax rotation and minimum eigenvalue of 1.0 (Hair *et al.,* 1998). Primary production data that included tree species (baldcypress, water tupelo, and other [mostly swamp red maple and ash]) were subjected to a repeated measures analysis of covariance design with experimental (sites) and sampling (stations within sites) error terms. Interaction terms and higher order nested terms were pooled with the appropriate error term when nonsignificant F values were less than 1.70. Comparisons of herbaceous production with tree production required summing over tree species categories. Potential covariables included light penetration, bulk density, interstitial salinity, and woody basal area. Linear contrasts were used to address specific *a priori* hypotheses. In addition, wood and litter production also were analyzed as total (all species) wood and litter production per square meter per year, again with bulk density, interstitial salinity, light penetration, and basal area as potential covariables. Finally, herbaceous, wood, and litter production were combined for total primary production and analyzed for site grouping differences. Unless otherwise noted, all statistical findings were significant at a Bonferroni-protected $\alpha = 0.05$ level (Zar, 1996).

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964) was used to determine the nature of the temporal trajectory of the tree and herbaceous vegetation of the Maurepas swamp and to determine the crispness in habitat separation of the three habitat types (degraded, relict, and throughput) over the study period. The ANOSIM test in Primer 6 (Clarke and Warwick, 2006) revealed a significant difference among habitat types (ANOSIM Global R = 0.42); therefore, we used NMS in Primer 6 to describe these differences. We used the BEST procedure with the BVSTEP option to determine the most influential factors in our classification.

RESULTS

Habitat Type Groupings

The separate multinomial logistic regression models of habitat type were both significant (year 2000: likelihood ratio $\chi^2 = 54.15$, df = 2, $p < 0.001$; year 2001: likelihood ratio $\chi^2 = 48.77$, df = 2, $p < 0.001$). In both data sets, we only retained annual maximum observed salinity and the combined amount of baldcypress and water tupelo litterfall as significant predictors of habitat type. The multinomial logistic models correctly classified 38 out of 40 field plots with the 2000 data and 36 out of 40 field plots with the 2001 data. The separation of throughput and degraded swamp sites was strong, while the distinction between relict swamp and either throughput or degraded swamp was ambiguous at some sites (Figure 2), leading us to drop 10 of the 40 sites as training sites in the remote sensing analysis.

Environmental Variables

Salinity followed a U-shaped pattern from 2000 to 2006 (quadratic contrast $F_{1,259} = 406.16$, $p < 0.00001$; Figure 3) with the highest salinities occurring during the severe drought of 1999–2000 followed by 2006, another drought year. Overall, salinity was highest at degraded sites and lowest at throughput sites (linear contrast $F_{1,259} = 168.92$, $p < 0.00001$). Soil salinity also was found to decrease with

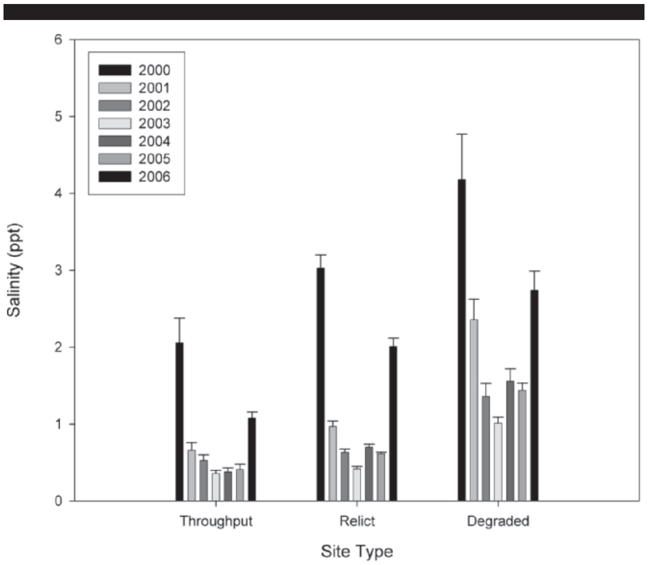

Figure 3. The average observed soil salinity in the Maurepas swamps was greatly elevated during a severe drought in 1999–2000, then declined gradually through 2003 and increased as a result of drought in 2006. This effect was greatest at the degraded sites located near Pass Manchac, which is the main saltwater conduit into the system.

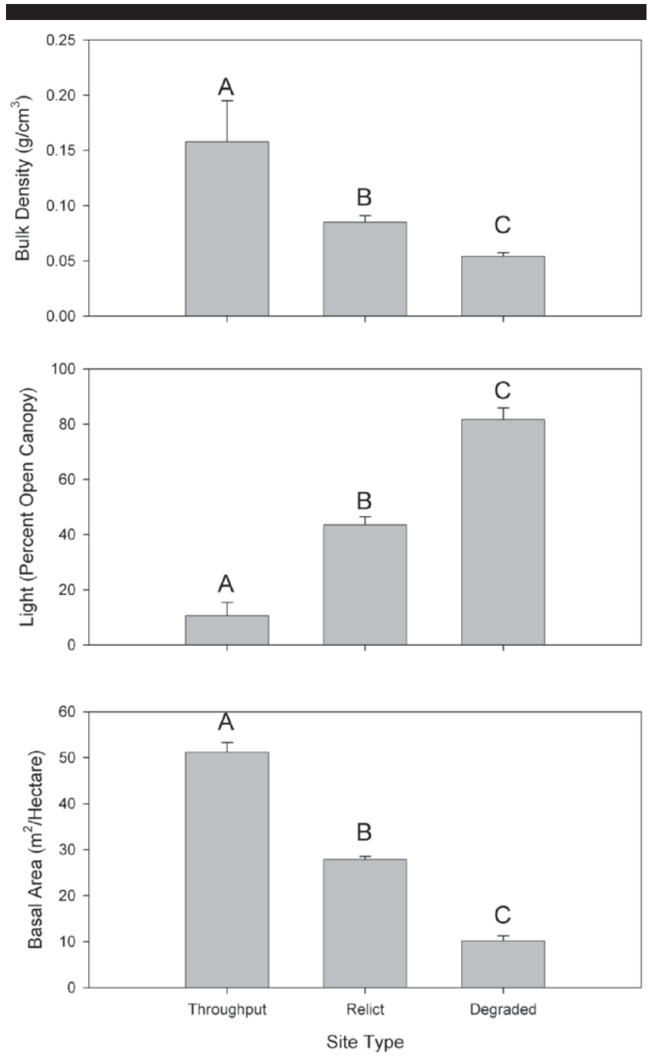

Figure 4. Soil bulk density (g cm^{-3}), light penetration (%), and basal area of trees (m^2 ha^{-1}) summed over each 625-m^2 plot for each of the three habitats. Degraded sites have the weakest soils, and the highest light penetration resulting from mortality of trees. Letters above bars indicate Bonferroni-adjusted significant differences.

increasing distance from Pass Manchac, as well as with increasing distance from the margin of Lake Maurepas into the interior swamp.

Bulk densities differed among site groupings ($F_{2,277}$ = 72.28, $p < 0.00001$; Figure 4). The highest bulk densities were found at the throughput sites (mean = 0.158 ± 0.013 g cm^{-3}) and the lowest at degraded sites (mean = 0.054 ± 0.001 g cm^{-3}). Relict sites had intermediate bulk densities (mean = 0.086 ± 0.002 g cm^{-3}).

Light penetration followed the opposite pattern of the total basal area of trees per plot (Figure 4), with greater amounts of penetration as the swamp varied from throughput to relict to degraded (linear contrast $F_{2,277}$ = 701.81, $p < 0.00001$). Light penetration continues to increase annually because large trees continue to suffer mortality and recruitment is absent at the degraded sites.

Tree Mortality

The Maurepas swamp is in a steady state of rapid decline, perhaps best shown by the mortality of canopy and midstory trees (Figure 5). Over the past 7 years, nearly 20% of the original 1860 trees in our study plots have suffered mortality, and recruitment of baldcypress and water tupelo saplings is essentially absent. In 2000, almost all of the mortality occurred at the degraded sites, but the highest rates are now experienced in the relict sites, largely because there are very few trees left to die at degraded sites. The few remaining trees at degraded sites are nearly all baldcypress, which is more tolerant to saltwater intrusion events. Mortality is highest for midstory species (Figure 5), nearly all of which are swamp red maple and green and pumpkin ash.

Herbaceous Vegetation

Nutrient Enrichment

For the uncaged treatments, nutrient enrichment at all levels had little effect on vegetative biomass production (Figure 6), indicating grazers such as nutria and deer had a large impact on the fertilized plots. The cage effect was highly significant for both 2002 ($F_{1,51}$ = 7.032, p = 0.0102) and 2003 ($F_{1,48}$ = 12.390, p = 0.00084). Although a clear trend of increased vegetation production with increased nutrient enrichment exists for 2002 (Figure 6), the fertilizer effect was not significant ($F_{3,51}$ = 2.080, p = 0.154). By 2003, nutrient augmentation showed a highly significant increase in herbaceous production ($F_{3,48}$ = 4.685, p = 0.0053; Figure 6), with a 50% increase for the loading rate of 11.25 g N m^2 y^{-1} and a 100% increase for the loading rates of 22.5 g N m^2 y^{-1} during

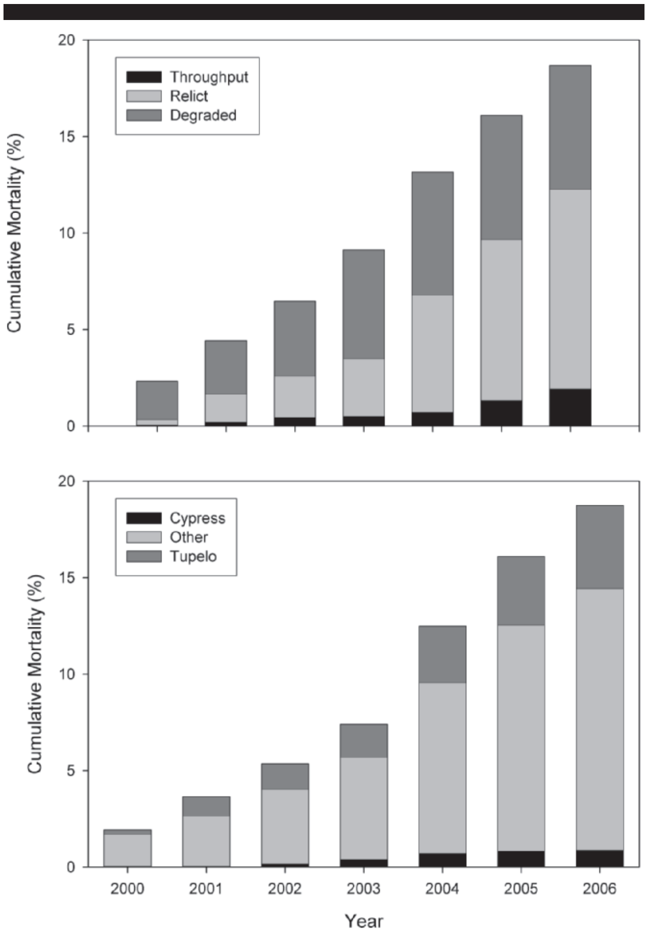

Figure 5. Cumulative percentage mortality occurring in the three habitat types over time. Mortality increases linearly from 2000–2006 and is highest for other species and lowest for baldcypress (*Taxodium distichum*).

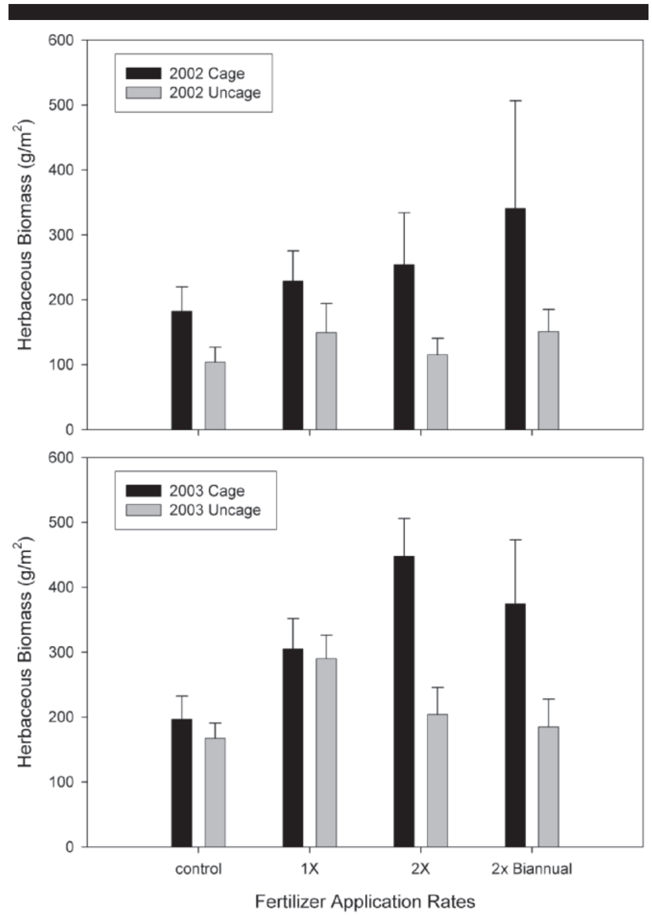

Figure 6. Results of nutrient enrichment experiment with and without herbivore exclusion cages. The 1× treatment simulates a Mississippi River reintroduction discharge of 42.5 $m^3 s^{-1}$ and a loading rate of 11.25 g N $m^{-2} y^{-1}$. The 2× treatment doubles that loading rate, and the 2× biannual treatment applies the timed-release fertilizer in early spring and again in midsummer.

spring (2×) and throughout the growing season (2× biannual), which did not differ from one another.

Annual Production

Herbaceous production was highest at the degraded sites (mean = 697.33 ± SE 71.84 g $m^{-2} y^{-1}$) followed by relict sites (mean = 381.60 ± SE 26.11 g $m^{-2} y^{-1}$), and lowest for throughput sites (64.31 ± SE 13.64 g $m^{-2} y^{-1}$; $F_{2,256} = 3.26$, p = 0.040; Figure 7). There was a strong linear trend of increased herbaceous production from 2000–2006 (linear contrast F = 119.141, $p < 0.00001$). Depressed production in 2001 and 2002 is thought to be a carryover effect from the drought because it took several years for soil salinities to freshen (Figure 3). Higher production in recent years is partially attributable to a shift to more salt tolerant herbaceous species and decreased competition with tree species with continued high mortality rates, especially at the degraded sites.

Most of the herbaceous biomass production could be attributed to 15 dominant ground-cover species, which together represented 97% of the total herbaceous cover throughout the study. Alligatorweed (*Alternanthera philoxeroides*), smartweed (*Polygomum punctatum*), and arrow arum (*Peltandra virginica*) were the most ubiquitous herbaceous species in the swamps of southern Maurepas. Pickerelweed (*Pontederia cordata*) decreased in abundance as habitats became saltier and more open, whereas bulltongue (*Sagitarria lancifolia*) and fall panicum (*Panicum dicotomiflorum*) became more abundant. Maidencane (*Panicum hemitomon*) and spike rush (*Eleocharis* spp.) were generally only present at the interior sites and in ponded areas of degraded sites, and appear to be indicator species of marsh converting to open water.

Primary Production of Trees

Total tree primary production differed between habitat types ($F_{2,126} = 14.126$, $p < 0.00001$; Figure 8) and years ($F_{6,126} = 9.997$, $p = 0.00001$; Figure 7). Bulk density and salinity were significant covariables in the model ($F_{1,256} = 12.940$, $p = 0.00039$, $F_{1,256} = 2.058$, $p = 0.020$, respectively), indicating that tree primary production was higher at sites with higher bulk densities and lower salinities. The highest rates of total tree primary production were found at the

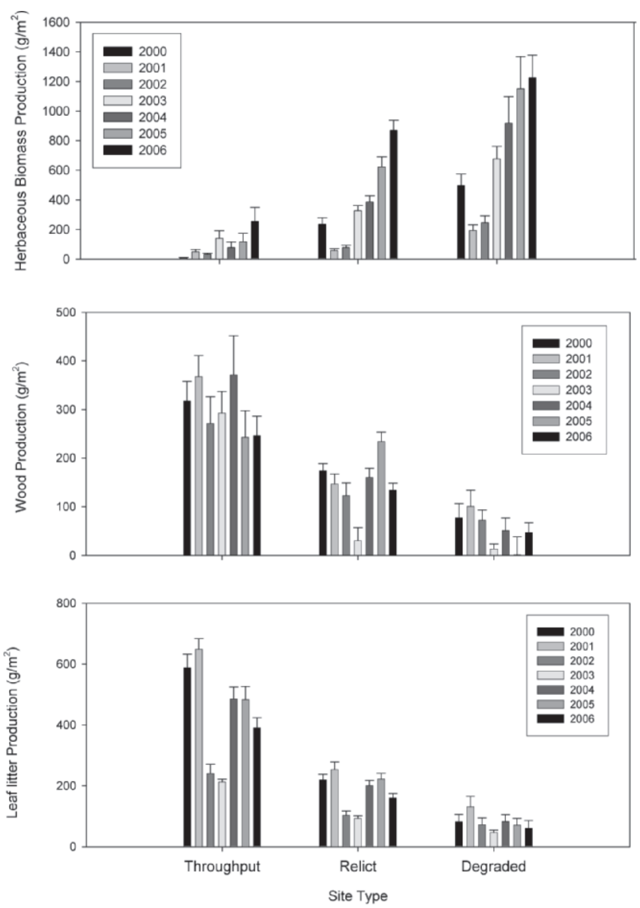

Figure 7. Annual herbaceous production, wood production, and litter production from 2000–2006 for the three habitat types. In general, the trees and ground cover followed inverse patterns through time with production increasing for herbaceous vegetation and decreasing for trees.

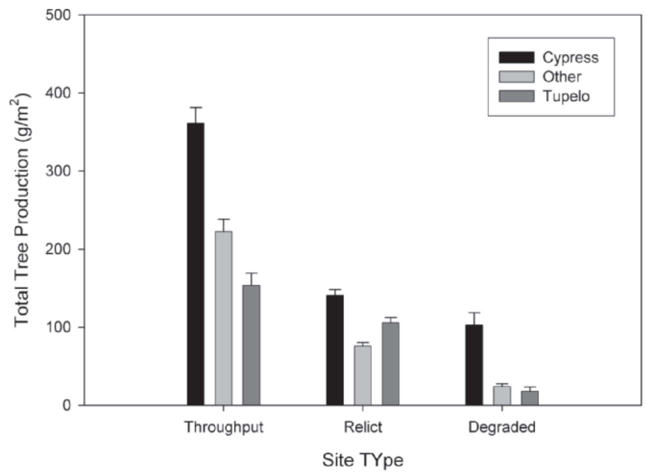

Figure 8. The interaction ($F_{4,651}$ = 17.43, $p < 0.00001$) between species grouping and habitat type for total (leaf plus wood) production. Baldcypress production dominates in throughput and degraded habitats, but not in relict habitats.

throughput sites (mean = 737.03 ± SE 37.18 g·m^{-2}·y^{-1}), followed by relict sites (mean = 322.48 ± SE 13.88 g·m^{-2}·y^{-1}), followed by degraded sites (mean = 144.36 ± SE 37.18 g·m^{-2}·y^{-1}). In general, leaf litter and wood production followed similar patterns through time (Figure 7) with the lowest production overall occurring in 2003 (mean = 104.56 ± SE 10.34 g m^{-2} y^{-1}, 73.03 ± SE 24.25 g m^{-2} y^{-1}, respectively). Interestingly, a general increase in production was experienced by the herbaceous community in 2003, whereas the forest community continued to decline until 2004.

For total annual (leaf plus wood) tree production, an interaction existed between habitat type and the three categories of species (F = 17.34, $p < 0.00001$; Figure 8). The interaction occurred for relict sites where baldcypress had similar growth rates as water tupelo as well as in the other category. Although baldcypress was the least abundant species of the three categories at almost all sites (Hoeppner, 2002; Hoeppner, Shaffer, and Perkins, 2008), it had nearly twice the average growth rate (mean = 171.83 ± SE 8.33 g m^{-2} y^{-1}) as water tupelo (96.46± SE 5.70 g m^{-2} y^{-1}) or other (mean = 91.10 ± SE 5.53 g m^{-2} y^{-1}).

Total Primary Production

In a period of only 7 years, the Maurepas swamp has switched from an ecosystem dominated by tree production to one dominated by herbaceous production (Figure 9). From 2000–2003, overall production was similar, with a decrease in tree production compensated for by an increase in ground cover production. Overall production from 2004–2006 was significantly greater than that of 2000–2003, yet tree production continued to fluctuate around 400 g m^{-2} y^{-1}.

The BVSTEP routine (Clarke and Warwick, 2006) determined that the combination of factors that best described community structure was total tree production and herbaceous production (Spearman correlation ρ = 0.964; Figure 10). These two factors separated the throughput sites from the degraded sites, with relict sites containing some overlap with both, as in the logistic regressions (Figure 2). The ordination, based on nonmetric multidimensional scaling, shows a striking temporal trajectory from less forestlike characteristics to more marshlike characteristics (Figure 10). Degraded sites became completely dominated by herbaceous vegetation from 2000–2006, relict sites late in the study transitioned toward degraded sites early in the study, and throughput sites transitioned toward relict sites following the severe drought (*i.e.*, 2002), and late in the study.

The 2005 Hurricanes

The 2005 hurricanes appear to have decreased canopy tree production primarily by snapping limbs, whereas midstory trees suffered extensive wind throw where canopy basal areas fell below about 30 m^2 ha^{-1} (Figure 11; sites with basal areas less than 30 m^2 ha^{-1} that fell on the *x*-axis had lost all midstory trees prior to the 2005 hurricanes as a result of saltwater intrusion). Degraded sites suffered 100% loss of midstory species, whereas throughput sites, with many more

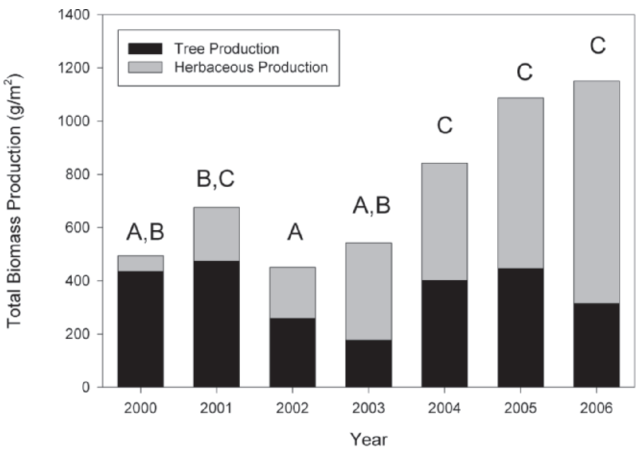

Figure 9. Overall (herbaceous plus tree) annual primary production averaged across habitat types from 2000–2006 with trees fluctuating between 200–400 g m^{-2} y^{-1} and ground cover showing a linear increase.

midstory stems, suffered very low mortality because of wind throw (Figure 12).

Spatial Extent of Degraded, Relict, and Thoughput Swamp

Overall, the mapped landscape was dominated by relict swamp, and the habitat types followed known salinity gradients (Figure 13). Only 13% (12,547 ha) of the mapped area classified as throughput swamp and was found in narrow strips contiguous with reliable sources of flowing freshwater. Without exception, areas that classified as degraded swamps were located near Lake Pontchartrain or along the margin of Lake Maurepas (Figure 13). These areas are prone to saltwater intrusion events from Lake Pontchartrain and totaled roughly 16% (15,168 ha) of the classified habitat. The remainder of the classified wetlands was identified as relict swamp (67%, 63,247 ha) and was generally located in hydrologically isolated areas that are nearly permanently flooded or in close proximity to the lake margin.

DISCUSSION

Flooding has doubled in the Manchac Wildlife Management Area adjacent to the Maurepas swamp since 1955 because of sea-level rise and subsidence (Thomson, Shaffer, and McCorquodale, 2002). Currently, the Maurepas swamps are often lower in elevation than the lake, rendering flooding semipermanent. Furthermore, flood control levees and abandoned raised railroad tracks have impounded much of the remaining swamps, causing throughput to be low. These swamps have been cut off from the sustaining spring floods of the Mississippi River for over a century and are in varying states of decline. Until this study was undertaken, the decline was evidenced by qualitative information such as dead and dying canopies of the predominant water tupelo trees. We now have quantitative information that allows us to compute the likely

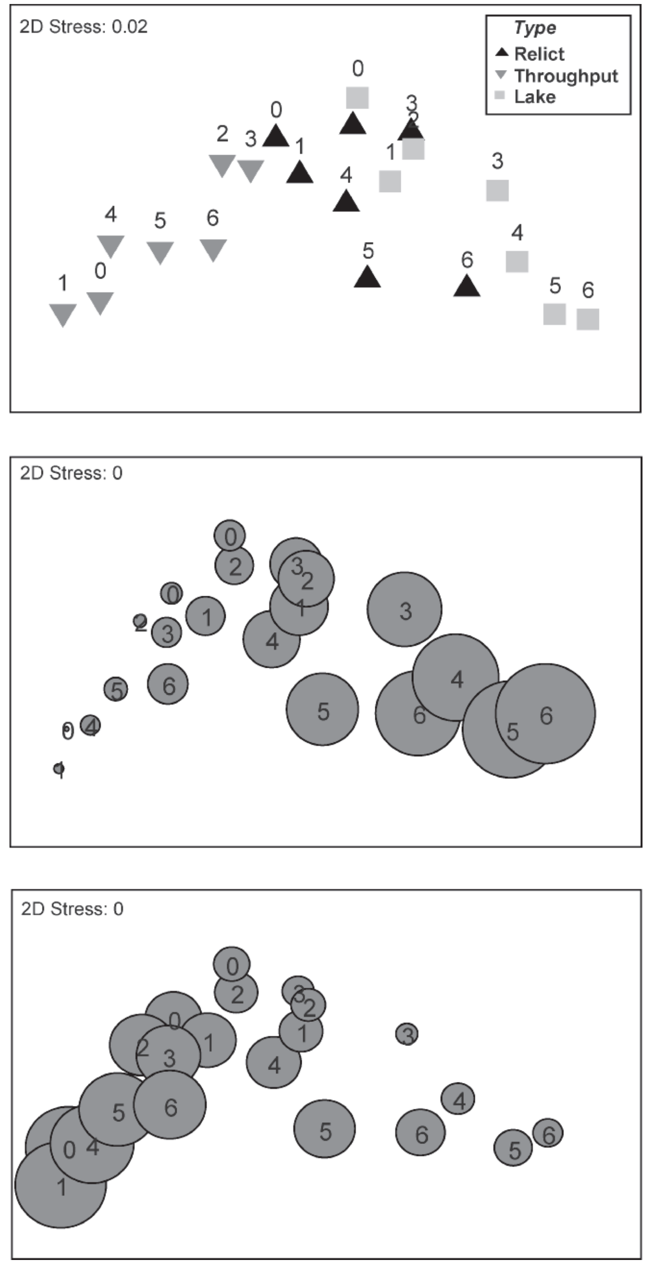

Figure 10. Overall tree and herbaceous production for each of the 20 sites was measured each year from 2000–2006. The 20 sites were grouped into three habitat types (throughput, relict, and degraded) and analyzed using nonmetric multidimensional scaling (NMS). Axis 1 separates throughput sites (the most treed sites) on the left from degraded (marshlike) sites on the right, with relict forming a tree–herbaceous gradient (shown on top). Herbaceous production is highest in degraded sites (shown in middle). Tree production is highest in throughput sites (shown in bottom). Numbers 0–6 represent years 2000 to 2006. Each year is represented within each habitat type.

benefits of a future with a reintroduction of Mississippi River water into the southwestern Maurepas swamp in comparison to the continued demise of the swamp ecosystem in a future without such a project (Shaffer *et al.,* 2003).

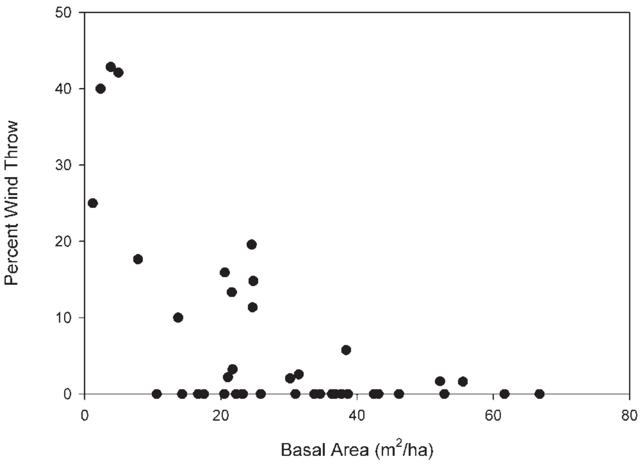

Figure 11. Percentage of midstory species wind thrown by the 2005 hurricanes (y-axis) across different basal areas of baldcypress–water tupelo canopy trees. Wind throw increases dramatically when the basal area of canopy trees decreases below about 30 m^2 ha^{-1}. Points on x-axis below 30 m^2 ha^{-1} have no midstory trees left to lose.

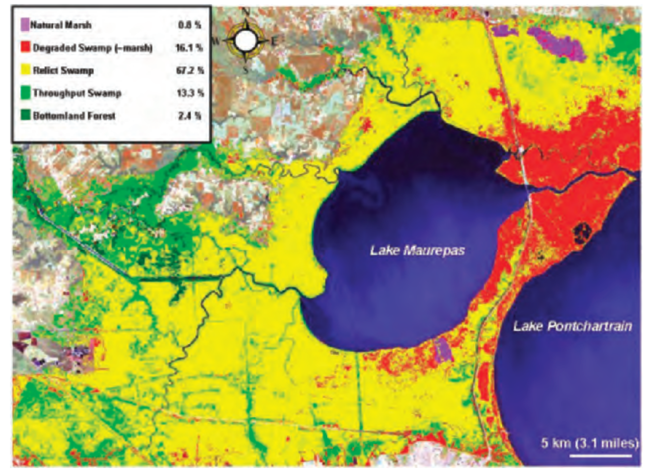

Figure 13. Habitat type classification of the wetlands in the Upper Lake Pontchartrain Basin, Louisiana. Habitats include natural marsh (purple), swamp that has degraded to marsh during the past half-century (red), relict swamps (yellow), potentially sustainable throughput swamps (bright green), and bottomland hardwood forests (dark green).

The Maurepas swamps are characterized by nutrient poor waters with nitrate levels less than 1% of those found in the Mississippi River (Lane *et al.,* 2003). In addition, the soils are of extremely low strength indicative of stress such as saltwater intrusion events that typically occur during late summer and fall. The mean salinity of lake water measured at the Manchac bridge also has increased gradually, beginning in the early 1960s with the opening of the MRGO (Shaffer *et al.,* 2009; Thomson, Shaffer, and McCorquodale, 2002). Severe increases in salinity, like those experienced during the droughts in 1999 and 2000, may be prevented or greatly ameliorated by the increased freshwater throughput that the proposed river reintroduction would offer. It is likely that the influences of freshening would be felt in wetlands as distant as Lake Pontchartrain (Figure 13) because the smallest proposed diversion of 42.5 m^3 s^{-1} would replace all of the water in Lake Maurepas twice each year, and it can only exit to Lake Pontchartrain through Pass Manchac and North Pass.

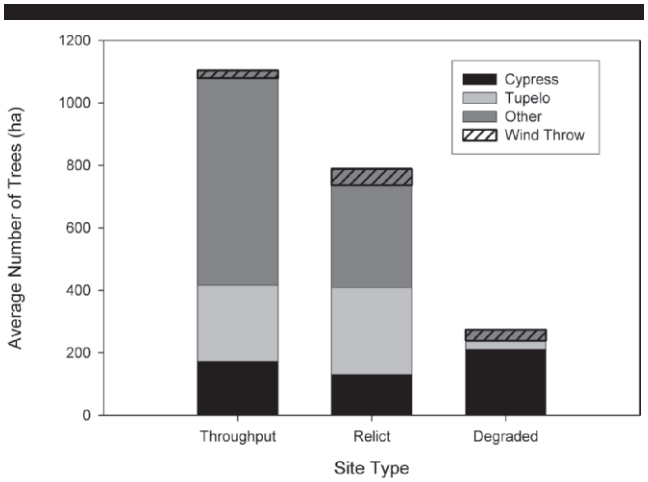

Figure 12. Average number of individuals of baldcypress, water tupelo, and other (mostly swamp red maple and ash) species at each habitat type. Hatched areas show number of wind thrown midstory trees, demonstrating that throughput sites, with the highest number of trees in the other grouping, suffered very low mortality from the 2005 hurricanes.

The soil characteristics at the majority of the study sites are indicative of a lack of riverine influence (lack of sediment input and throughput) as evidenced by high soil organic matter content and low bulk density values (DeLaune, Buresh, and Patrick, 1979; Hatton, 1981; Messina and Conner, 1998). With the exception of throughput sites, soil bulk densities are in the range of those typically found in fresh and oligohaline marshes that are located interior of streamside hydrology effects (Hatton, 1981). This agrees with the continued mortality of trees and the conversion of the system to a more herbaceous plant community.

Our study, and previous studies by Boshart (1997), Effler, Goyer, and Lenhard (2006), Greene (1994), and Myers, Shaffer, and Llewellyn (1995) indicate that the herbaceous and woody vegetation in the Maurepas swamp is nutrient starved. The dramatic increases in herbaceous standing crop with increased nutrient loading were only evidenced in caged plots because herbivores targeted the vegetation with increased protein content in uncaged, fertilized plots. Fertilizing at a loading rate of 22.5 g N m^{-2} y^{-1}, which simulates a river diversion of 85 m^3 s^{-1}, more than doubled biomass production, when compared with caged control plots. Although the second application of fertilizer during the summer did not increase production over a single application, it is during the fall that saltwater intrusion events generally occur. Therefore engineering the river reintroduction to allow for fall operation remains an important design feature.

The difference in forest structure among different areas in the Maurepas swamp also is an indication of the health and

Table 1. *Measurements of swamp primary production from several different studies including the Maurepas swamp.*

Forest Type (State)	Tree Standing Biomass (kg m^{-2})	Litterfall (g·m^{-2}·y^{-1})	Stem Growth (g·m^{-2}·y^{-1})	Above-Ground NPP[1] (g·m^{-2}·y^{-1})	Reference
Reference locations					
Cypress–tupelo (LA)	37.5[2]	620	500	1120	Conner and Day (1976)
Impounded managed swamp (LA)	32.8[2,3]	550	1230	1780	Conner *et al.* (1981)
Impounded stagnant swamp (LA)	15.9[2,3]	330	560	890	Conner *et al.* (1981)
Tupelo stand (LA)	36.2[2]	379	—	—	Conner and Day (1982)
Cypress stand (LA)	27.8[2]	562	—	—	Conner and Day (1982)
Nutrient-poor cypress swamp (GA)	30.7[4]	328	353	681	Schlesinger (1978)
Stagnant cypress swamp (KY)	9.4	63	142	205	Taylor (1985), Mitsch *et al.* (1991)
Sewage enriched cypress strand (FL)	28.6	650	640	1290	Nessel (1978)
Near-continuously flooded cypress–ash swamp (LA)	—	553[5]	443[4]	996	Megonigal *et al.* (1997)[5]
Near-continuously flooded riverine cypress–tupelo swamp (SC)	—	438[5]	216[4]	654	Megonigal *et al.* (1997)[5]
Naturally flooded swamp (LA)	—	487[5]	338[4]	825	Megonigal *et al.* (1997)[5]
Periodically flooded riverine swamp (LA)	—	725[5]	430[4]	1155	Megonigal *et al.* (1997)[5]
Frequently flooded swamp (SC)	—	—	—	1887	Muzika *et al.* (1987)
Maurepas Swamp locations (this study)					
Relict sites	11.68[7]	179.2	143.3[4,7,8]	322.5[6]	
Degraded sites	4.7	78.0	66.4[4,7,8]	144.4[6]	
Throughput sites	23.26[7]	435.7	301.4[4,7,8]	737.0[6]	
Total average	12.65[7]	203.8	155.6[4,7,8]	359.4[6]	

[1] NPP = net primary productivity = litterfall + stem growth.
[2] Trees defined as >2.54 cm DBH (diameter at breast height).
[3] Cypress, tupelo, ash only.
[4] Trees defined as >10 cm DBH.
[5] Litterfall does not include woody litter.
[6] All values are presented as averages of two replicate plots in two consecutive years.
[7] Averages of three to six sites with two substations each.
[8] Cypress, tupelo, ash, maple, and blackgum, where present.

future of these sites. Overall, the overstory is dominated by either water tupelo, baldcypress, or both, while the midstory is largely dominated by high numbers of swamp red maple, pumpkin ash and green ash, all of which are more shade tolerant than either of the dominants (Fowells, 1965). Similar observations have been made in comparable swamps in the Barataria Basin (Conner and Day, 1976). Wax mytle (*Morella cerifera*), Chinese tallow (*Triadica sebiferum*), and black willow (*Salix nigra*) dominate the midstory in areas of disturbance that were characterized by more open canopies and measurable saltwater intrusion effects. Shrub–scrub habitats are often observed on the transitional edges between marshes and forested wetlands or uplands (Barras, Bourgeois, and Handley, 1994; White, 1983). Diamond oak (*Quercus obtusa*), pumpkin ash, and green ash were found in greater abundance at sites characterized by higher bulk densities, which were indicative of increased throughput and generally less flooding. These observations support similar findings from wetland plant ordinations by White (1983) in the Pearl River, Louisiana, and Rheinhardt *et al.,* (1998) in the forested riverine wetlands of the inner coastal plain of North Carolina. Because Chinese tallow has been found to be more shade, flood, and salt tolerant (Conner and Askew, 1993; Jones, Sharitz, and McLeod, 1989) than several other native wetland tree species, this invasive species may become more dominant in the coastal wetlands of the southeastern United States (Conner and Askew, 1993).

Stem densities at throughput sites are similar to densities reported for impounded (Conner and Day, 1992; Conner, Gosselink, and Parrondo, 1981) or continuously flooded (Dicke and Toliver, 1990) swamps throughout Louisiana, whereas stem densities at relict sites are less than those reported for impounded swamps (Table 1). Average stem densities at degraded sites are not even half of those reported for impounded swamp sites, most likely because neither water tupelo, ash, nor swamp red maple have salt tolerances that could withstand the chronic salinity conditions of 2–4 ppt found at these sites. Conner, McCloed, and McCarron (1997) and Pezeshki (1989) reported that these species showed signs of stress and reduced growth at salinities as low as 2–3 ppt. Black gum (*Nyssa sylvatica* var. *biflora*) seedlings experienced 100% mortality when exposed to chronic flooding with 2 ppt (McCarron, McLeod, and Conner, 1998). Likewise, the relatively low stem densities observed at the relict swamp sites (Table 1) are primarily the result of the decreased abundance of ash and swamp red maple in the impounded and stagnant hydrologic regimes characteristic of these sites. In general, basal area followed very similar patterns as stem density. During our 7-year study, nearly 20% of the monitored trees suffered mortality, with mortality as high as 87% at one degraded site.

In terms of above-ground net tree primary production, only the most productive sites of the Maurepas swamp compare well with natural, periodically flooded baldcypress–water tupelo swamps (Carter *et al.,* 1973; Conner and Day, 1976; Conner, Gosselink, and Parrondo, 1981; Megonigal *et al.,* 1997), and then only during years of normal precipitation. The vast majority of the Maurepas swamp is either relict or degraded (Figure 13), and these areas range in total tree production between swamps that have been identified as either nutrient-poor and stagnant (Schlesinger, 1978), just stagnant (Mitsch, Taylor, and Benson, 1991; Taylor, 1985), or near-continuously flooded baldcypress swamps (Megonigal *et al.,* 1997). The remarkable linear increase of herbaceous production at relict and, more emphatically, degraded sites from 2000–2006 is a strong indication that these forested wetlands are converting to marshes (Barras, Bourgeois, and Handley, 1994). We believe that the increased herbaceous production in 2006 was largely a result of the 2005 hurricanes because up to 1 cm of sedimentation occurred (Turner *et al.,* 2006) at sites near the lake margin and light penetration was increased by wind throw of midstory species. We expect this trend to reverse itself as the marsh degrades, just as it has on the nearby Manchac land bridge.

Overall, baldcypress was the most productive species in the Maurepas, while water tupelo was the second most productive. This finding agrees with the observation that these two species are the canopy dominants, make up the majority of the basal area found at each site, and are the most flood-tolerant tree species in this ecosystem (Hook, 1984). Furthermore, the higher biomass production of baldcypress also agrees with several studies that reported baldcypress seedlings to be more tolerant of low salinity and permanent flooding than water tupelo, swamp red maple, and ash (Conner, McCleod, and McCarron, 1997; Dickson and Broyer, 1972; Keeland and Sharitz, 1990; Pezeshki, 1989).

The Maurepas swamps are nearly continuously flooded and largely impounded, which prevents seed germination and recruitment of baldcypress and water tupelo (Conner and Day, 1976, 1988; DuBarry, 1963; Harms, 1973; Myers, Shaffer, and Llewellyn, 1995; Souther and Shaffer, 2000; Williston, Shropshire, and Balmer, 1980). Modeling efforts by Conner and Brody (1989) have shown that even though baldcypress and water tupelo are flood tolerant (Brown, 1981; Carter *et al.,* 1973; Conner, Gosselink, and Parrondo, 1981; Mitsch and Rust, 1984), the total basal area of both will decline if water levels continue to rise. Thus, continuous flooding, though not immediately detrimental to these swamps, will lead to their gradual death over time (Conner and Brody, 1989; Conner and Day, 1988, 1992; Harms *et al.,* 1980; Mitsch and Rust, 1984). The different habitat types identified within the Maurepas swamp (Figure 13) appear to be in various stages along this trajectory of swamp decline, ranging from the continuously flooded but productive throughput sites to the impounded, flood and/or salinity stressed relict and degraded sites, respectively.

Hurricane Impacts

Only live oak (*Quercus virginica*) and palms are more resistant to wind throw than baldcypress and water tupelo (Williams *et al.,* 1999). Baldcypress–water tupelo swamps fared far better than other forest types in Hurricanes Camille (Touliatos and Roth, 1971), Andrew (Doyle *et al.,* 1995), and Hugo (Gresham, Williams, and Lipscomb, 1991; Putz and Sharitz, 1991). In addition, fresh, oligohaline, and brackish marshes suffered vastly greater loss in Hurricanes Katrina and Rita than did baldcypress–water tupelo swamps (Barras, 2006). Hurricane Katrina caused wind throws of an estimated 320 million bottomland hardwood trees in the Pearl River Basin, while contiguous swamps remained largely intact (Chambers *et al.,* 2007). The Maurepas swamp was no different with respect to canopy species that suffered zero wind throw, but a relationship was found between canopy basal area and wind throw of midstory species, in particular swamp red maple. As basal areas of canopy species dropped below about 30 m^2 ha^{-1}, a linear increase in wind-thrown midstory trees existed (Figure 11). At the degraded sites, all of the midstory trees were lost to the 2005 hurricanes (Figure 12), whereas throughput sites, containing a far greater number of midstory stems, lost very few individuals. It appears that the extensive lateral root systems of baldcypress and water tupelo hold the entire ecosystem together when canopy trees are dense.

In terms of flood- and wind-damage reduction, baldcypress–water tupelo swamps appear to be far superior to other wetland habitat types, even mangrove forests that were instrumental in protecting villages during the recent Asian tsunami (Danielsen *et al.,* 2005; Williams *et al.,* 1999). We need to rethink coastal restoration and management strategies, tailoring them to storm-protection alternatives (Boesch *et al.,* 2006; Costanza, Mitsch, and Day, 2006; Day *et al.,* 2007; Lopez, 2006) that include restoring historic levels of baldcypress–water tupelo swamps.

Reversing the Trajectory of Decline

In summary, the Maurepas swamp is characterized by nutrient poor waters, soils of extremely low strength, nearly permanent flooding in most areas, and saltwater intrusions that generally occur during the late summer and fall seasons. The Maurepas swamp is nitrogen limited, and nutrient stress is potentially as important as salt or flood stress. Furthermore, recruitment of baldcypress and water tupelo saplings throughout the swamp is very low, certainly not sufficient to sustain the aerial extent of current forest. Most of the Maurepas swamp appears to be converting to marsh and open water, primarily due to the lack of riverine input. Salt stress is killing trees proximal to the lake, whereas stagnant standing water and nutrient deprivation appear to be the largest stressors at interior sites.

Although baldcypress–water tupelo swamps are extremely resistant to wind throw and deep flooding, they are less resistant to saltwater intrusion and thus require a reliable source of freshwater for system flushing following tropical storm events and during droughts. Swamps can survive short-term salinity pulses (Allen, Chambers, and McKinney, 1994; Campo, 1996; Conner *et al.* 1997). We are in the process of building a geographic information system that contains all substantial point and nonpoint freshwater sources, including urban and agricultural runoff, storm water pumps, noncontact industrial cooling water, municipal wastewater treatment facilities, and potential Mississippi River diversion sites. At present, most of these sources are input to the basin to maximize drainage efficiency. Freshwater is routed into ditches and canals that carry it directly to the lakes, bypassing wetland contact. This creates a "lose–lose" situation because potential for eutrophication is maximized and the wetlands remain nutrient starved. In contrast, rerouting the water to maximize sheet flow would improve water quality, increase wetland net primary production, and decrease saltwater intrusion (Shaffer and Day, 2007). Furthermore, implementation of the proposed Mississippi River reintroductions at Violet, Bonnet Carre, La Branche, and two in the Maurepas swamp (Coast 2050, 1998) will greatly enhance restoration of historic salinity regimes. In addition to the benefits mentioned, increasing swamp acreage will decrease storm damage, may lead to net sediment accretion, will increase carbon sequestration (Trettin and Jorgensen, 2003), enhance biodiversity, and improve several of the "multiple lines of defense" proposed by Lopez (2006). Of historic significance is the current closure of the Mississippi River Gulf Outlet (USACE 2007), which will help approximate historic salinity regimes and further assist in storm-damage reduction (Shaffer *et al.,* 2009).

One concern that managers and the general public have with restoring repressed swamps is the amount of time required for swamplike characteristics to emerge and manifest. Fortunately, given favorable hydrologic and nutrient conditions, baldcypress and water tupelo seedlings can reach greater than 10 m heights within one decade. For example, a pilot planting of baldcypress seedlings at the Caernarvon diversion (Krauss *et al.,* 2000) has yielded trees over 10 m tall in a decade, and all of these resisted wind throw during the hurricanes of 2005. In conclusion, if we are to reverse the trajectory of decline of coastal Louisiana swamps, we must find, and wisely use, point and nonpoint sources of fresh water currently being wasted.

Despite the degraded condition of the majority of the baldcypress–water tupelo swamps of the upper Lake Pontchartrain Basin, healthy areas of swamp still exist. Without exception, each of these swamps receives some form of reliable high-quality, nutrient-rich fresh water. These forests are either receiving nonpoint sources of fresh water from urban areas (*e.g.,* forests of Hope Canal and Alligator Island), high quality river water (*e.g.,* forests of Pearl River), or secondarily treated sewage effluent (*e.g.,* forests of Bayou Chinchuba). Restoration efforts that include the proper combination of river diversions, treated sewage effluent assimilation wetlands, and rerouted nonpoint source freshwater, should enable restoration of Lake Pontchartrain Basin's swamps (Shaffer and Day, 2007).

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