

# Does Woody Species Establishment Alter Herbaceous Community Composition of Freshwater Floating Marshes?

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## ABSTRACT

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Floating freshwater marsh communities (flotant) in the Mississippi Deltaic Plain are composed of vegetation rooted in an organic mat that detaches from the underlying mineral substrate and shifts vertically as water levels below rise and drop. Unlike attached marshes dominated by herbaceous species, floating marsh mats are free from the stress of inundation, enabling establishment of woody species. Dynamics of these flotant communities are largely unstudied, and it is unknown whether invasion by woody species alters their structure and composition. To study the potential effects of woody species invasion on herbaceous community characteristics, we compared open herbaceous marsh, sparse scrub-shrub, and dense scrub-shrub thickets at Jean Lafitte National Historical Park and Preserve in coastal Louisiana. We found that species richness and composition differed significantly among the three marsh types. Herbaceous communities lacking shrub canopies had the lowest richness and were dominated by emergent species typical of freshwater marsh. Richness and composition of sparse scrub-shrub thickets were intermediate between open marsh and dense thickets. The latter had the greatest species richness with assemblages more typical of forest understories, as well as aquatic species that occurred where holes in the floating mat formed. *Morella cerifera* (wax myrtle), an actinorhizal shrub, was the dominant woody species and formed the shrub stratum in sparse and dense thickets; the exotic *Triadica sebifera* created a low-stature overstory. Bryophytes colonized the bases and lower stems of both species. We found 35 additional vascular plant species in the thickets, including two other exotics, *Alternanthera philoxeroides* and *Salvinia molesta*. Establishment of woody species in flotant marsh adds structural complexity and appears to drive compositional changes in the herbaceous community toward a combination of woodland and aquatic assemblages. The longevity of the woody phase in flotant marsh and the long-term ecological consequences of widespread *Triadica sebifera* invasion are unknown.

**ADDITIONAL INDEX WORDS:** *Chinese tallow, coastal Louisiana, floating marsh, flotant, fresh bulltongue, fresh maidencane, invasive species, Morella cerifera, ordination, Panicum hemitomon, Triadica sebifera, scrub-shrub, wax myrtle, wetland.*

## INTRODUCTION

Freshwater marshes are ecologically and commercially important ecosystems covering approximately 383,000 ha along Louisiana's coast (GOSSELINK, COLEMAN, and STEWART, 1998). They provide critical habitat for numerous species and buffer the rapidly subsiding coastline from storm and wave action that can exacerbate erosion and sediment loss. Despite the numerous goods and services they provide, these marshes are being lost at an alarming rate (WILSON 2004). A combination of anthropogenic and natural factors including extensive canal systems, decreased sediment input, subsidence, and eustatic sea-level rise contributes to these trends (DAY *et al.*, 2000, 2001; TURNER, 1997, 2001).

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Remaining freshwater marshes support a very diverse plant community (SASSER and GOSSELINK, 1984; SASSER *et al.*, 1996; VISSER *et al.*, 1998) that may be attached, floating, or a complex mosaic of the two. The floating marshes (hereafter referred to as "flotant") are extensive, and it has been estimated that they once covered as much as 100,000 ha in Louisiana (O'NEILL, 1949; RUSSELL, 1942). In the flotant marsh, plants are rooted in an organic mat that detaches from the substrate and shifts vertically as water levels below rise and drop (SWARZENSKI *et al.*, 1991). Thus, hydrology and nutrient inputs may differ from attached marsh in that flooding of the mat surface does not occur (SASSER, GOSSELINK, and SHAFFER, 1991). Mat thickness and buoyancy can vary considerably and depend upon both below-ground biomass allocation and morphology of the constituent species (SASSER *et al.*, 1996), as well as abiotic factors such as salinity and hydrology. Typically, the column of water underneath the mat grades into an organic sludge and then into an underlying clay substrate (SWARZENSKI *et al.*, 1991).



Both attached and floating freshwater herbaceous marshes of the Mississippi Deltaic Plain are generally dominated by the same suite of species (VISSER *et al.*, 1998), despite the fact that several authors have stated that floating marshes in the northern Gulf Coast may differ functionally from their attached counterparts, particularly in hydrology and nutrient cycling (SASSER and GOSSELINK, 1984; SASSER, GOSSELINK, and SHAFFER, 1991; SASSER *et al.*, 1996). The hydrologic differences may indirectly lead to divergence in composition between floating and nonfloating marsh over time. Unlike in attached marshes, less flood-tolerant woody species can establish (WILLIAMSON, BARKER, and LONGSTRETH, 1984) and may proliferate (SHIRLEY and BATTAGLIA, 2006) in floating marsh vegetation because it rises and falls with water levels below and is free from the stress of inundation. Large-stature woody species appear to be excluded, however, and some small-stature trees and shrubs that establish may eventually exceed the flotation capacity of the mat, become flooded, and die (WILLIAMSON, BARKER, and LONGSTRETH, 1984). The actinorhizal shrub *Morella cerifera* (WILNHOLDS and YOUNG, 2000) is a dominant woody invader in the floating marsh (SASSER *et al.*, 1995; WILLIAMSON, BARKER, and LONGSTRETH, 1984), and is believed to establish in thick mats of *Panicum hemitomon* (fresh maidencane) marsh (SASSER *et al.*, 1995, 1996) in the absence of fire. This species is also commonly found in other coastal areas such as barrier islands that fringe the Atlantic and Gulf coasts (TOLLIVER, MARTIN, and YOUNG, 1997; YOUNG, ERIKSON, and SEMONES, 1994; YOUNG, SHAO, and BRINSON, 1995a; YOUNG, SHAO, and PORTER, 1995b) and in attached marshes at higher elevations (CHERRY and GOUGH, 2006).

MITSCHE and GOSSELINK (2000) suggest that the floatant marsh may represent a relatively stable end point of succession because the rising and falling vegetation is not subject to flooding stress and the dominant mat-forming grass species can continue indefinitely building/replacing the organic mat. In the model of possible relations among floating marsh types developed by SASSER *et al.* (1996), invasion by woody species is acknowledged and the *M. cerifera* type is depicted as one possible end point. The vegetation and dynamics of these communities are largely unstudied, however, and it is unknown whether invasion by woody species, which affect resource availability and microclimate, alters the structure and composition of the rest of the community. To our knowledge, there are no studies in the literature that explicitly include comparisons of open herbaceous marsh with scrub-shrub floatant assemblages. There are also no reports documenting changes in community composition after large-scale declines in shrub populations, although WILLIAMSON, BARKER, and LONGSTRETH (1984) speculate that floatant community dynamics are cyclic. Further, we could find no detailed descriptions of species composition in floating scrub-shrub assemblages.

Since the 1950s, woody species have been spreading and perhaps displacing freshwater herbaceous species in several protected floatant marshes in this region (SHIRLEY and BATTAGLIA, 2006; WILLIAMSON, BARKER, and LONGSTRETH, 1984). Fire suppression has been the policy since park establishment in 1974, so the marshes at Jean Lafitte National

Historical Park and Preserve offer a glimpse of this scrub-shrub floatant assemblage (SHIRLEY and BATTAGLIA, 2006) that is relatively uncommon in the present-day landscape. The primary objective of this study was to compare the herbaceous community composition between open herbaceous floatant assemblages and those invaded by woody species. We hypothesized that establishment of woody species would drive changes in herbaceous species composition away from that of open herbaceous marsh such that assemblages with woody canopies would differ from those without. A secondary objective was to provide a description of the vegetation in the scrub-shrub thickets.

## METHODS

### Site Description

The study site is located in the Barataria Preserve Unit of Jean Lafitte National Historical Park and Preserve in Jefferson Parish, south of New Orleans, Louisiana, U.S.A. (Figure 1). The preserve contains 7487 ha of bottomland hardwood, swamp forest, and marsh communities. The marsh occupies approximately two-thirds of the area and on the east grades into bottomland hardwoods and swamp forest that occupy the backswamp of Bayou des Familles, an old distributary of the Mississippi River (SWANSON, 1991). On the west, the marsh is bordered by Lake Salvador (Figure 1). Within the marsh proper, a network of canals, dug for oil exploration and pre-dating park establishment, traverses and partitions the marsh. These features may accelerate subsidence (TURNER, 1997), alter hydrology and natural fire frequency, and permit saltwater intrusion when freshwater flow is low (SASSER *et al.*, 1986). In addition, many of the spoilbanks lining the canals are dominated by the exotic invasive *Triadica sebifera* (BATTAGLIA, unpublished data).

### Vegetation Sampling and Data Analysis—Marsh Grid

In May 2001, we conducted a vegetation survey of the marsh at the Barataria Preserve. We sampled a 500 × 250 m grid that covers this area (Figure 1) but excluded the narrow band of oligohaline marsh that is dominated by halophytic species, *e.g.*, *Spartina patens* and *Distichlis spicata*, and borders the lake. At each grid intersection, we established a 25-m-radius circular plot and recorded presence/absence of all vascular plant species and *Sphagnum* spp. (total plots included in this study = 186).

The four tree and shrub species found in the grid plots were, in order of abundance, *M. cerifera*, *T. sebifera*, *Ilex cassine*, and *Acer rubrum*. We organized all plots in floatant marsh with differing levels of woody invasion into three categories depending on the presence and abundance of *M. cerifera*, by far the dominant woody species. Plots were coded as follows: (a) dense *M. cerifera* (shrub cover ≥ 25%) (D); (b) sparse *M. cerifera* (shrub cover < 25%) (S); and (c) freshwater herbaceous marsh (shrub cover = 0%) (F). Species richness was compared across the three floatant marsh categories using one-way analysis of variance (ANOVA) and Tukey's multiple means tests where warranted.

Trends in species composition were explored using non-

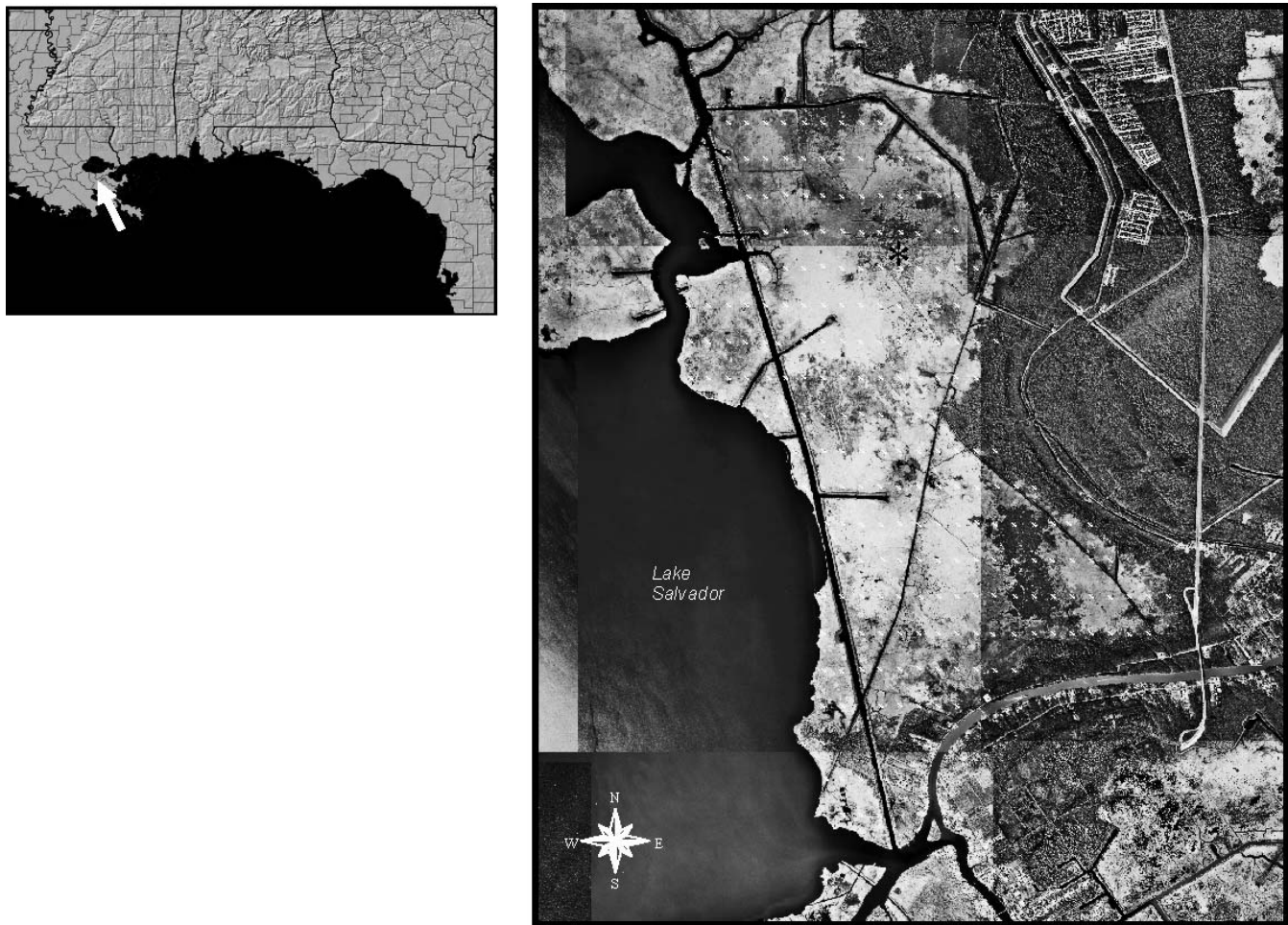


Figure 1. Sampling grid points in the marsh at the Barataria Preserve Unit are indicated by circles. General location of the intensively sampled scrub-shrub thicket plots is represented by an asterisk. Inset depicts northern Gulf of Mexico and location of the study site, approximately 11.3 km south of New Orleans, Louisiana, U.S.A.

metric multidimensional scaling (NMDS) (MINCHIN, 1987). The ordination, based on presence/absence data, was performed in one to four dimensions, in each case using 100 random initial configurations. We excluded woody species from the presence/absence matrix in the multivariate analyses because we were interested in exploring the relationship between woody species presence/abundance and composition of the herbaceous assemblages.

Analysis of similarities (ANOSIM) was used to test for differences in species composition among D, S, and F plots. ANOSIM is a nonparametric technique that uses the ranks of the dissimilarities and compares the mean rank of between-group dissimilarities to the mean rank of within-group dissimilarities (CLARKE, 1993). The significance of the difference is tested using a random permutation test (1000 permutations) that simulates the null hypothesis of no difference. The NMDS ordination and ANOSIM were performed using the DECODA package (MINCHIN, 1989). Where compositional divergence was indicated, we selected several species that ex-

hibited apparent responses to increasing shrub cover and used contingency table analysis to determine whether presence/absence of each species was statistically independent of vegetation category.

#### Vegetation Sampling and Data Analysis—Scrub-Shrub Thicket Plots

In August 2000, we established eight 4 m × 40 m permanent plots to intensively sample the vegetation of the sparse and dense scrub-shrub thickets (Figure 1). Plots were located where thickets were relatively homogeneous in canopy condition and sufficiently extensive to accommodate plot size. All plots had a canopy, but canopy openness varied among them depending on shrub density and cover. Four plots were established in areas where the shrub canopy was sparse (<25% cover) and four plots were established where the shrub canopy was dense (≥25% cover). Each of the plots was subdivided into eight 2 × 10 m subplots in which stems of all shrub

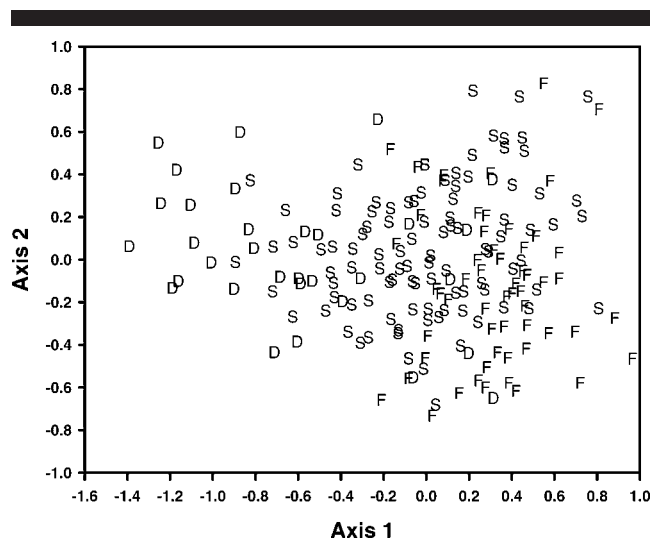


Figure 2. Two-dimensional NMDS ordination of plant species composition data from 186 circular plots established in the marsh at Barataria Preserve (stress = 0.23). Woody species were excluded from the analysis. D = dense thicket; S = sparse thicket; and F = freshwater herbaceous marsh.

and tree species  $\geq 1$  m in height were counted, and their basal diameter measured.

At each of the eight plots, four of the eight subplots were selected in which to establish a series of 1-m<sup>2</sup> quadrats for quantifying cover of all species. To prevent damage to herbaceous species related to our foot traffic, we established cover quadrats along the outside boundaries of the subplots at every 2-m interval (total  $n = 160$ ) and always  $\leq 2$  m perpendicular to the subplot boundary. Cover was estimated and assigned for each taxon using a modified Braun-Blanquet scale (MUELLER-DUMBOIS and ELLENBERG, 1974). Nonvascular taxa, with the exception of *Sphagnum* spp., were grouped as Bryophyta (non-*Sphagnum*). The scale used is as follows: 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, 7 = 96–99%, 8 = >99%.

T-tests (SAS version 8.02) were used to compare basal area and density of the dominant woody species between sparse and dense plots. Average cover of taxa, on the basis of cover quadrats, was summarized in a list for each of the eight plots.

## RESULTS

The one-way ANOVA revealed significant overall differences in species richness among the three vegetation groups (df = 2;  $F = 17.99$ ;  $p < 0.0001$ ). On the basis of Tukey's multiple means tests, we found a statistically significant increase in richness from open herbaceous marsh ( $9.24 \pm 0.42$ , mean  $\pm$  SE) to sparse scrub-shrub ( $11.44 \pm 0.33$ ) to dense thickets ( $13.4 \pm 0.63$ ).

The two-dimensional NMDS ordination (stress = 0.23) suggested compositional separation among the dense thickets (D), sparse thickets (S), and open herbaceous (F) floatant plots (Figure 2). The compositional trend consisted of an ordering of F, S, and D plots. The F plots overlapped least with D plots,

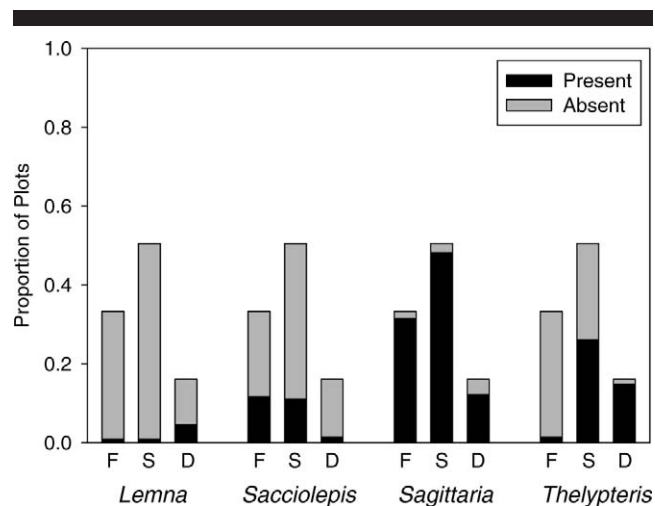


Figure 3. Proportion of plots in which four select species (*Lemna minor*, *Sacciolepis striata*, *Sagittaria lancifolia*, and *Thelypteris palustris*) were present or absent in the three vegetation categories. Total number of plots in each category is as follows: open freshwater herbaceous (F) = 62 plots; sparse scrub-shrub (S) = 94 plots; and dense scrub-shrub (D) = 30 plots.

whereas S plots were in the middle and overlapped with both. ANOSIM results confirmed overall differences among the three groups ( $R = 0.2621$ ,  $p < 0.0001$ ), and subsequent pairwise comparisons revealed significant differences between each pair (F&S:  $R = 0.1192$ ,  $p < 0.0001$ ; F&D:  $R = 0.5973$ ,  $p < 0.0001$ ; S&D:  $R = 0.3379$ ,  $p < 0.0001$ ). Using the classification system of VISSER *et al.* (1998), much of the open herbaceous portion of the marsh can be classified as fresh bulltongue (*Sagittaria lancifolia*). Although some emergent species such as *Sacciolepis striata* (df = 2,  $\chi^2 = 7.6369$ ,  $p = 0.0220$ ) and *Sagittaria lancifolia* (df = 2,  $\chi^2 = 12.8578$ ,  $p = 0.0016$ ) were more likely to occur in the absence of shrub cover (Figure 3), divergence among assemblages was largely driven by species becoming more common with woody canopy cover. Taxa more typical of forest-marsh ecotones such as the fern *Thelypteris palustris* (df = 2,  $\chi^2 = 71.0379$ ,  $p < 0.0001$ ) increased in frequency with shrub cover. Forest understory species including *Woodwardia areolata*, *Rubus trivialis*, and *Sphagnum* spp. only occurred in dense shrub cover. *Lemna minor* (df = 2,  $\chi^2 = 29.2038$ ,  $p < 0.0001$ ), a floating aquatic species, was also positively associated with dense canopies (Figure 3).

In addition to compositional divergence, the marsh assemblages differed in vertical structure. The F plots consisted of only one herbaceous stratum, whereas the S and D communities had an additional shrub canopy dominated by *M. cerifera* and a low-stature tree layer dominated by *T. sebifera*. In the shrub layer, the basal area of *M. cerifera* ranged from 3.8 to 35.5 m<sup>2</sup>/ha (Figure 4). Average density was 14,437.5 stems/ha and ranged from 5813 to 27,625 stem/ha. As expected, basal area ( $t = -5.91$ ,  $p = 0.001$ ) and density ( $t = -2.63$ ,  $p = 0.039$ ) were significantly higher in the dense thicket stands. Size class distributions of sparse and dense areas had the same basic shape, with the majority of individuals in the smaller size classes (Figure 5). The sparse stands,

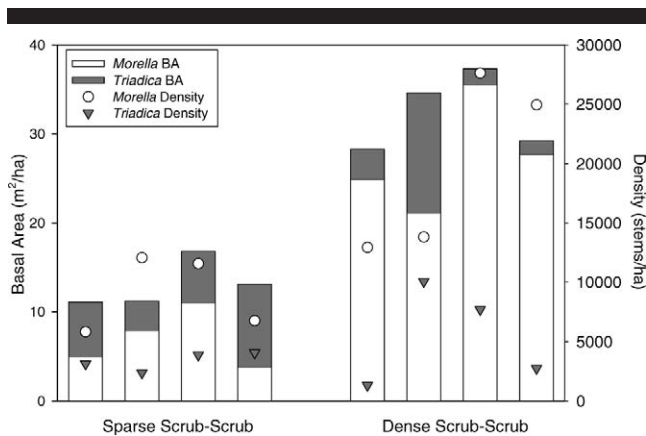


Figure 4. Estimated basal area (m<sup>2</sup>/ha) and density (stems/ha) of dominant canopy species in each of the eight 160 m<sup>2</sup> scrub-shrub thicket plots. Basal area estimates are calculated from basal diameters of all stems. *Acer rubrum* and *Ilex cassine*, two minor components of the canopy, are not presented here.

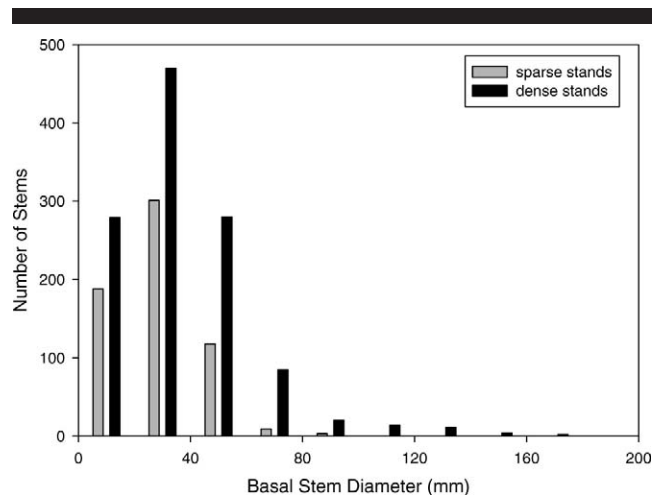


Figure 5. Frequency distributions of live *Morella cerifera* stem diameters in four sparse and four dense canopy stands.

however, had very few individuals in the larger size classes ( $\geq 70$  mm basal diameter) compared with the dense stands. The basal area of *T. sebifera* ranged from 1.5 to 6.1 m<sup>2</sup>/ha, and density ranged from 2375 to 10,062.5 stems/ha (Figure 4). This exotic was virtually ubiquitous where scrub-shrub occurred, and basal area ( $t = 0.35$ ,  $p = 0.74$ ) and density ( $t = -1.0$ ,  $p = 0.39$ ) did not differ between dense and sparse thickets. Basal area and density were not estimated for *A. rubrum* and *I. cassine*, which were minor components of the canopy. An *A. rubrum* tree (diameter at breast height [DBH] = 11.4) was found in one plot. An *I. cassine* tree (DBH = 10.8 cm) was found in one plot, and a small sapling was present in two other plots.

A total of 37 vascular plant taxa was found in the cover plots of the intensively sampled thickets (Table 1). Of the 35 herbaceous taxa, 32 are emergent, two are floating-leaved aquatics (*L. minor* and *Salvinia molesta*), and one is a submerged aquatic (*Myriophyllum spicatum*). *Salvinia molesta* and the emergent *Alternanthera philoxeroides* are exotics. Other species observed in the main plots that were not present in cover quadrats include *Azolla caroliniana*, *Cephalanthus occidentalis* (seedlings), *Dichromena colorata*, *Leersia hexandra*, *Limnobium spongia*, *Pluchea odorata*, *Sacciolepis striata*, and *Zizaniopsis miliacea*.

Differences in woody canopy density were related to distributions of several understory taxa (Table 1). For example, *Sagittaria lancifolia*, a dominant herbaceous species in sparse thickets, was virtually absent in dense stands. *Bacopa monnieri*, *Phyla lanceolata*, *Polygonum punctatum*, and the exotic *Alternanthera philoxeroides* were present only in the sparse canopy sites. Bryophytes were more common in dense thickets, including *Sphagnum* spp., which frequently carpeted the understories of dense shrub stands. In addition, several unidentified liverworts and mosses were abundant on the lower stems and bases of the woody stems.

## DISCUSSION

Flotant marsh vegetation that rises and falls with water levels below is free from the stress of inundation, and it has therefore been suggested that flotant marsh may be a stable end point of succession (MITSCH and GOSSELINK, 2000). Because of the properties of the floating mat, however, shrub and small-stature tree species can establish and proliferate (SHIRLEY and BATTAGLIA, 2006; SASSER *et al.*, 1995; WILLIAMSON, BARKER, and LONGSTRETH, 1984), forming thickets. We found that scrub-shrub thickets were often surrounded by *Panicum hemitomon* (maidencane), which supports the hypothesis that stands of this species are suitable invasion sites for *M. cerifera* (SASSER *et al.*, 1995, 1996). The results of this study also suggest that the addition of a woody canopy drives changes in the structure and composition of the community. Eventually the shrubs and trees are thought to exceed the flotation capacity of the mat, leading to localized flooding as the mat is pushed downward into the water column and eventual death of the stems (WILLIAMSON, BARKER, and LONGSTRETH, 1984). Mortality of individual stems produces relatively small gaps, similar to those in thickets of Atlantic Coast barrier islands (CRAWFORD and YOUNG, 1998), which are then recolonized by emergent marsh dominants such as *Panicum hemitomon* and *Sagittaria lancifolia* (BATTAGLIA, personal observation), apparently restarting the cycle (WILLIAMSON, BARKER, and LONGSTRETH, 1984). Rather than stable and unchanging, flotant marsh appears to be a very dynamic community with a tendency toward cyclic trends, at least in the absence of other disturbances to the community.

Infrequent and large-scale disturbances may have a large impact on flotant dynamics. Hurricanes, for example, can cause considerable damage (STONE *et al.*, 1997) by inverting, crinkling, or otherwise disturbing the floating mat. Fire is also known to be an important disturbance in coastal marsh (FORD and GRACE, 1998), and it is likely that fires in the past either started in the marsh proper or occasionally swept

Table 1. Average cover of plant taxa adjacent to each 4 × 40 m plot. Means are based upon cover class midpoints from a modified Braun-Blanquet scale. Midpoints for each species were averaged over 20 1-m<sup>2</sup> cover quadrats that parallel the main axis of each plot. Nonvascular taxa, with the exception of *Sphagnum* spp., are grouped as Bryophyta (non-Sphagnum). Plots with sparse shrub canopies are coded as "S", and plots with dense shrub canopies are coded as "D". Nomenclature follows Godfrey and Wooten (1981) and Correll and Correll (1972) for ferns.

Taxa	Thicket plots							
	S	S	S	S	D	D	D	D
<i>Acer rubrum</i> L.	0	0.15	0	0	0.03	0	0	0
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	0.48	0.15	0.98	0.03	0	0	0	0
<i>Andropogon virginicus</i> L.	3.6	14.4	0.78	1.65	11.9	3.48	4.08	0.15
<i>Bacopa monnieri</i> (L.) Pennell	2.18	0.75	0.38	0.2	0	0	0	0
<i>Boehmeria cylindrica</i> (L.) Sw.	1	0.03	0.05	0.43	0	0.2	0.05	0
(Non-Sphagnum) bryophytes	0.03	3.55	0.9	0	9.2	0.18	12.15	26.75
<i>Carex</i> spp. L.	0.03	0.75	0	0	0	0	0	0
<i>Cyperus</i> spp. L.	2.05	1.23	1.55	0.38	0	0.15	0.03	0.05
<i>Decodon verticillata</i> (L.) Ell.	0.25	1.95	0	1.18	20.53	6.8	0	0
<i>Eleocharis</i> spp. R. Br.	8.2	5.45	0.35	14.93	0	0	0.33	0.28
<i>Eupatorium capillifolium</i> (Lam.) Small	0	1.05	0	0	0	0	0.03	0.08
<i>Hydrocotyle verticillata</i> Thunb.	1.13	3.55	0.38	0.65	0.03	0.5	1.28	1.63
<i>Hypericum mutilum</i> L.	0.03	0.15	0.05	0.15	0.03	0	0	0
<i>Ilex cassine</i> L.	0	0	0	0	0.05	0.05	0	0.38
<i>Ipomoea sagittata</i> Poir. in Lam.	0.25	0	0.15	0.05	0	0	0	0
<i>Juncus effusus</i> L.	0	0	0.03	0	0	0.75	0	0
<i>Kosteleskya virginica</i> L.	0	0	0.03	0	0.03	0	0	0
<i>Lemna minor</i> L.	0	0.48	0.05	0	0	0	0.18	0.03
<i>Ludwigia alternifolia</i> L.	1.3	0	0.05	0.08	0	0.05	0.03	0
<i>Morella cerifera</i> L.	0.325	0	0	0	0	0	0	0
<i>Myriophyllum spicatum</i> L.	0	0.75	0	0	0	0	0	0
<i>Osmunda regalis</i> L.	0.33	0	0	0	0	0	0	0
<i>Panicum hemitomon</i> Schult.	11.85	42.93	38.43	5.33	0	4.43	46.53	56.95
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	0	1.9	0	0	0	0	0	0
<i>Phyla lanceolata</i> (Michx.) Greene	0.5	0.3	0.25	1	0	0	0	0
<i>Polygonum punctatum</i> Ell.	0.7	0.18	0.18	0.65	0	0	0	0
<i>Pontederia cordata</i> L.	0	0	0	0.3	0	0	0	0
<i>Rhynchospora</i> spp. Vahl	0	3.75	0	0	2.28	3.9	0	0.15
<i>Rubus trivialis</i> Michx.	0	0	0	0	0.08	0.05	0	0
<i>Sagittaria lancifolia</i> L.	6.48	13.65	10.2	14.7	0	0.3	0.75	0.9
<i>Salvinia molesta</i> Mitchell	0.18	7.53	0.3	0	0	0.75	1.88	0.75
<i>Triadica sebifera</i> (L.) Small	6.08	0	5.55	0.63	5	8.8	0	0
<i>Saururus cernuus</i> L.	0.88	0	0	0.4	0.03	0	0	0
<i>Smilax bona-nox</i> L.	0	0.15	0.03	0	0.03	0	0	0
<i>Sphagnum</i> spp. L.	0	1.88	4.18	0	0	0	20.83	0.33
<i>Thelypteris palustris</i> Schott	8.25	16.73	3.45	7.83	1.95	14.25	9.98	17
<i>Typha latifolia</i> L.	0	0	0	1.05	0	0	0	0
<i>Vigna luteola</i> (Jacq.) Benth.	0	0	0	0.05	0	0	0	0
<i>Woodwardia areolata</i> (L.) T. Moore	0	0.45	0	0	9.4	0.05	0.3	0.63

down from the forests during droughts. Interestingly, the role of woody species has received little attention in float marshes and may have gone largely unstudied because many of these marshes today are frequently burned by land managers or hunters (SASSER and GOSELINK, 1984; SASSER *et al.*, 1995; WILLIAMSON, BARKER, and LONGSTRETH, 1984). Although *M. cerifera*, for example, is often included in species lists, it is rarely abundant in the modern landscape (SASSER and GOSELINK, 1984; VISSER *et al.*, 1998, 1999; but see SASSER *et al.*, 1996). With frequent fire, woody species might be excluded indefinitely, resulting in a relatively stable community dominated by herbaceous species such as *Panicum hemitomon* (MITSCH and GOSELINK, 2000). Suppression of fire in marshes, such as those in Barataria Preserve, may have enabled the spread of woody species such as *M. cerifera* (SHIRLEY and BATTAGLIA, 2006; SASSER *et al.*, 1996). In Florida's Indian River Lagoon, for example, reduced fire frequencies have been associated with invasion of brackish and sa-

line marshes by woody species, including *M. cerifera* and the invasive *Schinus terebrinifolia* (SCHMALZER, 1995).

In this study, we also found that exotic species pose a potential threat to the biological integrity of these marshes. *Morella cerifera* was the dominant woody species in the float marsh, but the second most common woody species was the exotic *Triadica sebifera* (Chinese tallow). Although uncommon in the open herbaceous marsh, it was frequent and abundant in sparse and dense thickets. The severity of the threat posed by *T. sebifera* to the float marsh remains unclear, as it appears to simply add another stratum above the shrub layer. It is a major concern, however, because it is known to be a successful and aggressive invader in a wide array of other communities in the southeastern and south-central United States (MATLACK, 2002), including coastal prairies, upland pine forests (BARRILLEAUX and GRACE, 2000; RENNE, SPIRA, and BRIDGES, 2001; SIEMANN and ROGERS, 2003), and bottomland forests (DENSLOW and BATTAGLIA, 2002).

We did not find complete turnover of species among the three vegetation categories (F, S, and D), and indeed there was much overlap of species. Many of the vascular species in the scrub-shrub thickets were also present in open herbaceous plots, and appear in published species lists of herbaceous floating marsh sites in the area (SASSER *et al.*, 1995, 1996; VISSER *et al.*, 1998). Although a few species did completely drop out of the community with canopy development, the divergence was mostly related to increasing frequencies of species not common in the open herbaceous marsh.

With increased woody canopy cover, the herbaceous marsh assemblage essentially became an understory. Thus, it is not surprising that species more typical of forest understories became increasingly common at the expense of more light-demanding marsh species. The understory fern and vine species may be more shade-tolerant or able to thrive where dominant marsh grasses, sedges, and broad-leaved macrophytes are less abundant. In scrub-shrub assemblages, and particularly where the canopy was dense, the floating mat was often carpeted with *Sphagnum* spp. Other moss and liverwort species colonized the bases and lower stems of the woody stems, resulting in an overall increase in bryophyte abundance with the enhanced structural diversity. Vertical patterning in bryophyte communities is known from forest communities (KUUSINEN, 1996; MCGEE and KIMMERER, 2002), but to our knowledge, this is the first report of bryophyte establishment in coastal marshes.

We did not anticipate the high frequency of submerged and floating-leaved aquatics in thickets since these species usually occur in open water bodies with little to no canopy. In fact, the aquatic species were not found throughout the thicket understory, but rather mostly restricted to holes in the mat, which were widespread in dense thickets. The small pools were common near the bases of larger woody stems, suggesting that the woody biomass was beginning to exceed the mat's ability to stay afloat (WILLIAMSON, BARKER, and LONGSTRETH, 1984). Another possibility is that decomposition of the mat may be accelerated where there is an abundance of the actinorhizal *M. cerifera* (WIJNHOLDS and YOUNG, 2000), because nitrogen is considered to be one of the limiting factors in this oligotrophic ecosystem (SASSER, GOSSELINK, and SHAFFER, 1991). Nonetheless, the mat under dense woody canopies was more often than not perforated with holes, indicating signs of breakup. In most cases where emergent marsh dominants were recolonizing small canopy gaps, holes in the mat were also present. Our study suggests that the perforated mat condition may be a phase of floatant dynamics.

Establishment of canopy-forming woody species increases overall plant diversity of the marsh community, but they may also be important for many animal species as well. Woody species are rare in the marsh and are largely confined to neighboring swamp forests and isolated clumps of relict *Taxodium distichum* (bald cypress) near the subsiding forest-marsh interface. Establishment of *M. cerifera* provides essential habitat and cover for many species of wildlife (KWIT *et al.*, 2004; WILLIAMSON, BARKER, and LONGSTRETH, 1984) that are otherwise absent in expanses of herbaceous marsh. Relatively isolated from predatory fish, small pools in the

dense thickets support larval amphibians (BATTAGLIA, personal observation). Alligators are known to use thickets as nesting sites (PALMER and MAZZOTTI, 2004). Snakes and lizards are year-round residents, and numerous resident bird and mammal species utilize the scrub for cover and food (BATTAGLIA, personal observation). The scrub-shrub thickets may also provide essential food resources for migratory waterfowl (ZOLLER, 2004) before and after the energetically expensive migration over the Gulf of Mexico (LEBERG, SPENGLER, and BARROW, 1996).

## CONCLUSIONS

The herbaceous stratum of floatant marsh assemblages that had a woody canopy differed significantly from that of open herbaceous marshes. Our results suggest that establishment of woody species in the floatant marsh drives changes in herbaceous community structure and composition, leading to higher overall diversity. With woody establishment, ferns, vines, and *Sphagnum* spp. more typical of forest understories established on the mat and aquatic species in mat holes. Liverworts and other mosses also became more abundant by colonizing the bases of woody stems. More research is needed to evaluate the effects of larger-scale disturbances (hurricanes and fires) on these apparently cyclic trends in the floatant community, as well as those of the invasive *T. sebifera*. Whether this widespread exotic has cyclic dynamics as well or persists and spreads is unknown but may have long-term implications for the floatant community.

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