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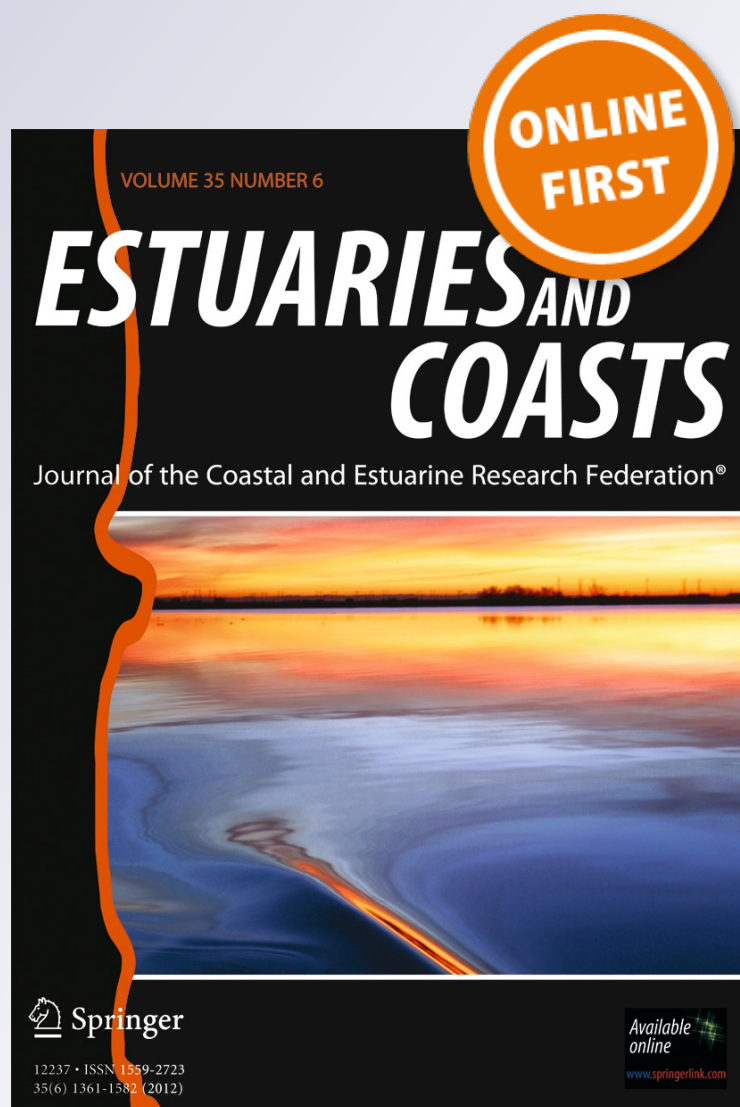
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Vegetation Dynamics in a Tidal Freshwater Wetland: A Long-Term Study at Differing Scales

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Abstract Tidal freshwater wetlands are complex, species-rich ecosystems located at the interface between tidal estuaries and nontidal rivers. This study conducted on the Patuxent River estuary in Maryland was designed to assess vegetation dynamics over several decades to determine if there were directional changes in the dominant communities. Aerial photographs (1970, 1989, and 2007) documented broad-scale spatial changes in major plant communities. The coverage of areas dominated by *Nuphar lutea* and *Phragmites australis* expanded; mixed vegetation and scrub–shrub habitats were essentially unchanged; and *Typha* and *Zizania aquatica* communities fluctuated in coverage. Data collected between 1988 and 2010 from permanent plots and transects were used to examine fine-scale changes. Shifts in the importance of some species through time were observed, but there were no directional changes in community species composition. The lack of directional change as measured at a fine scale is characteristic of tidal freshwater wetlands in which variations in the abundance of individual species, especially annuals, are responsible for most short-term change in species composition. Changes in the composition of plant communities are interpreted as responses to variations in vertical accretion,

stability of habitat types, invasive plant species, and herbivores. In the future, vegetation changes are likely to occur as a result of the intrusion of brackish water and increased flooding associated with global climate change and sea level rise. This long-term study establishes a baseline from which potential future changes to tidal freshwater wetlands can be better understood.

Keywords Tidal freshwater wetlands · Plant communities · Succession · Annuals · Perennials · Patuxent River · Sea level rise

Introduction

Tidal freshwater wetlands are located at the interface between nontidal freshwater riverine ecosystems and estuarine intertidal wetlands (Anderson et al. 1968; Simpson et al. 1983; Odum 1988; Pasternack and Brush 1998; Barendregt et al. 2009), and because of their position in the coastal landscape, they have been directly and indirectly impacted by human activities. In Europe, humans have managed tidal freshwater wetlands for thousands of years, resulting in significant losses, primarily due to reclamation schemes (Zonneveld and Barendregt 2009). In North America, tidal freshwater wetlands have been impacted by human activities for hundreds of years, especially changes that converted wetlands into agricultural fields (e.g., Baden et al. 1975) or that increased sedimentation associated with forest clearing and subsequent increases in farming activities, and the consequences of the development of major urban centers (Khan and Brush 1994; Hilgartner and Brush 2006). Dams and eutrophication have had major impacts on tidal freshwater wetlands in North America and Europe over the past several hundred years (e.g., Simpson et al. 1983; Orson et al. 1992; Leck and Crain 2009; Van den Bergh et al. 2009). Tidal freshwater wetlands will continue to be impacted

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by changing environmental conditions associated with rising sea levels and the subsequent intrusion of brackish water (Boesch 2008; Neubauer and Craft 2009; Perry et al. 2009).

Analyses of pollen, seeds, and nutrient concentrations in sediment cores have demonstrated that there have been major changes in the vegetation of tidal freshwater wetlands that have been associated with the direct and indirect factors cited above (e.g., Khan and Brush 1994; Hilgartner and Brush 2006). For example, on the Patuxent River, the rates of sedimentation following forest clearing increased over fivefold from the 1600s to the mid-1800s, converting open water areas to low marsh and causing low marsh areas to change to high marsh (Khan and Brush 1994). In contrast, there have been few studies (see succeeding references provided) of vegetation changes in tidal freshwater wetlands over shorter time scales, especially changes that might be associated with the increasing rate of sea level rise. Plant communities in tidal freshwater wetlands may also be influenced by other climate change factors, such as decreasing freshwater input from rivers (Scavia et al. 2002), rising atmospheric CO₂ levels (Neubauer and Craft 2009; Sharpe and Baldwin 2009), and intrusion of brackish water into freshwater habitats (Brinson et al. 1985; Perry and Hershner 1999; Whigham et al. 2009).

Other factors make tidal freshwater wetlands ideal for studying the consequences of changing environmental conditions. These wetlands are composed of a diversity of plant communities that are distributed over a tidally influenced gradient of low to high marsh habitats (Simpson et al. 1983; Odum et al. 1984) and are influenced by a series of biogeomorphic controls (Pasternack et al. 2000; Pasternack and Brush 2001, 2002).

The importance or relevance of autogenic successional processes in the dynamics of tidal freshwater wetland vegetation over shorter time periods have rarely, to our knowledge, been examined, but paleoecological studies suggest that, in modern times, communities have been relatively stable in terms of species composition (Hilgartner and Brush 2006). The few studies of vegetation changes over time based on sampling plots in the field have focused on changes in vegetation following the intrusion of brackish water due to sea level rise (e.g., Brinson et al. 1985; Perry and Hershner 1999; Krauss and Duberstein 2010; Schuyler et al. 1993) or to the extraction of groundwater (Higinbotham et al. 2004). In contrast, Salter and Baden (1994) found little evidence for vegetation changes over a 20-year period following the abandonment of wetlands that had been converted into rice fields in South Carolina, but Field and Philip (2000) used aerial photos of a series of Delaware River freshwater tidal wetlands to determine that low marsh increased from 9 % in 1977 to 34 % in 1998. Rice et al. (2000) examined a sequence of aerial photographs taken over a span of 60 years and found no evidence of succession resulting in the shift of herb-dominated communities toward dominance by woody species or the

replacement of *Phragmites*-dominated areas by other types of herb-dominated communities.

Tidal freshwater wetland plant communities are characterized by a high diversity of annual and perennial plant species resulting in dramatic seasonal changes in species' dominance patterns (e.g., Whigham and Simpson 1978; Simpson et al. 1983). Some researchers have described distinct communities (Odum et al. 1984; Pasternack et al. 2000), but others have found a lack of marked zonation patterns (Leck et al. 2009; Perry et al. 2009). These characteristics make it difficult to assess long-term trends in species abundance or shifts in species distribution, especially if change is being evaluated by resampling sites using different plots each time that the vegetation is monitored.

The region where this study was conducted (hereafter referred to as Jug Bay) has undergone modification over the past 250 years related to high rates of sedimentation originating in the upper watershed caused by forest clearing for tobacco farms and, more recently, to urban and suburban development, as well as from the construction of a railroad levee in the 1890s across the study marsh. Additionally, Jug Bay is located in a region characterized by high rates of relative sea level rise (RSLR) as a result of regional subsidence (Boon et al. 2010). Although the rate of RSLR in Jug Bay is not known, in the Chesapeake Bay, it ranges from 2.91 to 5.80 mmyear⁻¹ (Boon et al. 2010); in some areas, this rate is more than twice the estimated global average of 1.8 mmyear⁻¹ (Zervas 2001). This region of the Patuxent River has also experienced an increase in salinity spikes (readings over 0.5 ppt), particularly during summer and fall, which appear to be related to changes in river discharge in dry versus wet years (Whigham et al. 2009; Harris, personal communication). Finally, grazing by recently established resident Canada Geese (*Branta canadensis*) on the young shoots of wild rice (*Zizania aquatica*) over the past two decades had significantly reduced the prevalence of this important plant throughout the Jug Bay wetlands (Haramis and Kearns 2007).

Given the large number of factors that could influence vegetation patterns in tidal freshwater wetlands, the major goal of our study was to evaluate plant community dynamics over the past 25 to 45 years and to establish a baseline from which future changes could be evaluated. At a broad scale, we used aerial photographs to examine vegetation change over a span of almost four decades. At a fine scale, we evaluated species occurrences and vegetation change over the past two to three decades by monitoring plants in permanent plots and along transects established in different vegetation communities. Considering the highly dynamic nature of tidal freshwater wetlands, we expected that changes in vegetation would be caused by increases or decreases in the abundance of species that would most likely respond to four factors: salinity changes due to increased

intrusion of brackish water caused by RSLR; increased flooding caused by RSLR; the ability of wetlands to accrete vertically; and impacts from the invasion of non-native plants and by herbivorous animals.

Study Area

This study was conducted on the Patuxent River in the Jug Bay Wetlands Sanctuary (North 38°46'54"; West -76°42'30") in Anne Arundel County, Maryland. This shallow bay, a component of Maryland's Chesapeake Bay National Estuarine Research Reserve, is in the tidal fresh region of the estuary about 65 km upriver from the mouth. The study area encompassed about 85 ha of a 489-ha wetland complex (Fig. 1). The tidal wetlands consist of about 134 perennial and 11 annual emergent plant species (Swarth, unpublished data). Dominant species in the lowest level of the marsh (referred to hereafter as low marsh; Simpson et al. 1983) included *Nuphar lutea*, *Pontederia cordata*, and *Z. aquatica*.

Dominant species in the herb-dominated portion of high marsh habitats were *Leersia oryzoides*, *Hibiscus moscheutos*, *Peltandra virginica*, *Phragmites australis*, *Polygonum arifolium*, and *Typha* × *glauca*. The common species in high marsh and in swamp forest habitats dominated by trees or shrubs were *Acer rubrum*, *Bidens laevis*, *Cephalanthus occidentalis*, *Cornus amomum*, *Dioscorea villosa*, *Fraxinus profunda*, *Ilex verticillata*, and *Mikania scandens*. The species identified in the permanent plots and transects, along with their growth form and occurrence in the plant communities, are shown in the Appendix. The standard reference for species nomenclature is the US Department of Agriculture (USDA) (2011) Plants Database.

Semidiurnal tides at Jug Bay have an amplitude that averages about 0.75 m and salinity is generally <0.5 ppt. Water temperature varies from 0 to 35 °C and winter ice scour occurs in shallow areas. The sediments are high in organic matter and are composed of varicolored silts and clays with brown to dark gray lignitic silty clay. The study area is bisected by an 800-m-long levee built in the

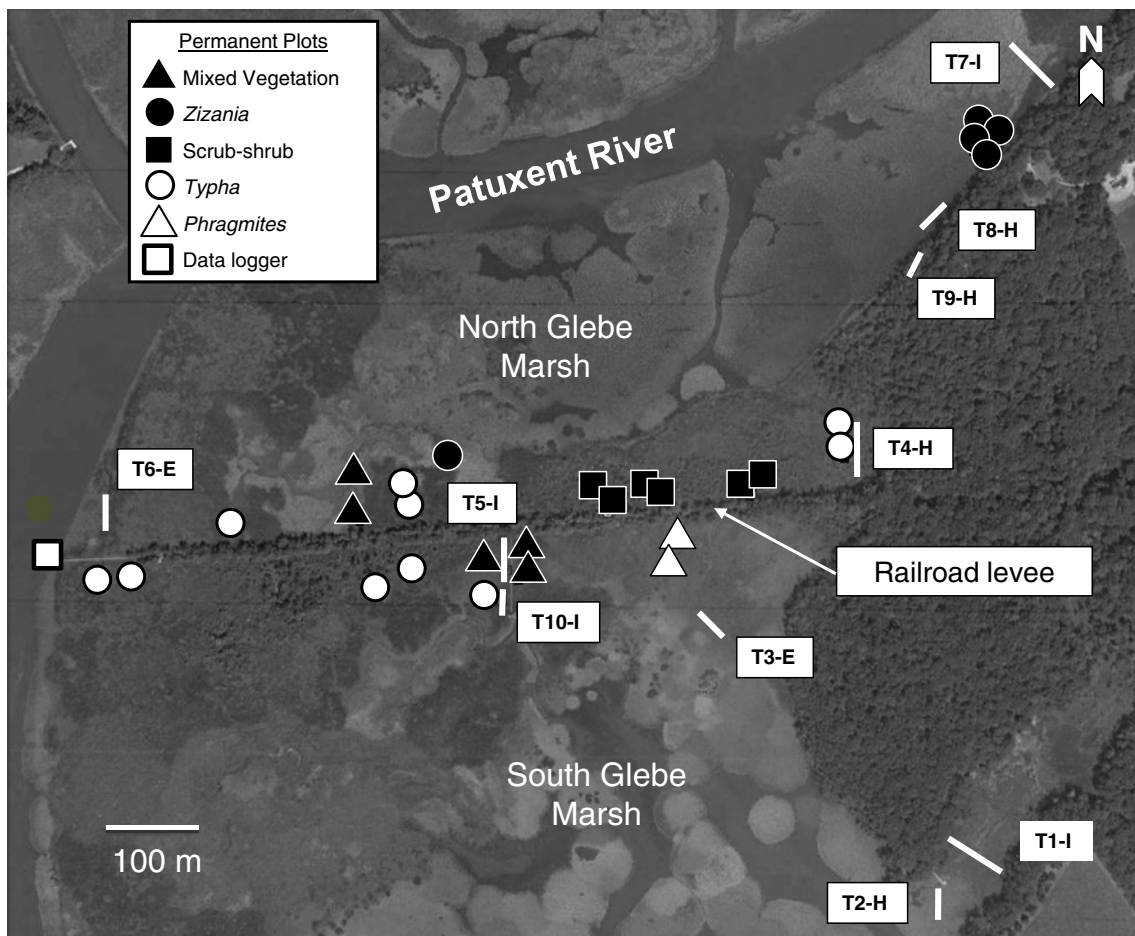


Fig. 1 Aerial photograph of the study area showing 28 permanent plots and 10 transects. For plant transects (white bars), *E* along community ecotone, *H* within homogenous community, *I* across inundation zone. For

further descriptions of transect communities, see Table 1. Aerial image from Google Earth; 29 August 2010

1890s for a short-lived railway line; the levee runs in an east–west orientation across the wetland and river (see Fig. 1). Levee construction caused localized sedimentation (Khan and Brush 1994) and its position has altered the hydrology and rates of wetland vertical accretion (Delgado et al., this volume). The wetland north of the levee is called North Glebe Marsh and that to the south is South Glebe Marsh.

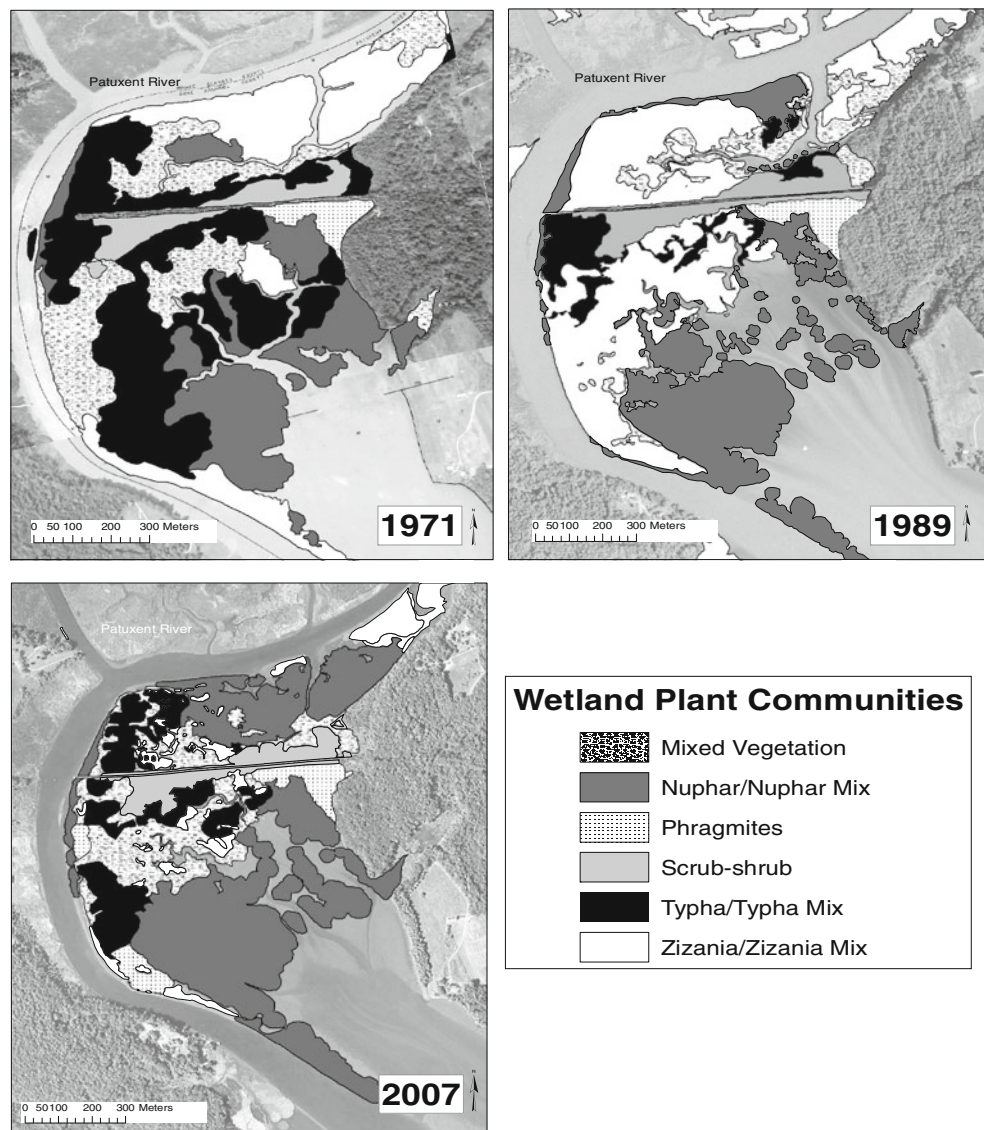
Methods

Broad-Scale Measurements

Plant communities were mapped and their coverage measured using aerial photographs taken during the growing season in

1971, 1989, and 2007 (Fig. 2). We identified six communities: *N. lutea*-dominated; *Typha*-dominated; mixed vegetation; *Z. aquatica*-dominated; *P. australis*-dominated; and scrub–shrub dominated by woody vegetation. *Nuphar*-, *Typha*-, and *Zizania*-dominated communities included monospecific stands. Areas that contained additional species were defined as *Nuphar* mix, *Typha* mix, and *Zizania* mix, and for purposes of aerial coverage calculations, we combined similar groups (for example, *Nuphar* with *Nuphar* mix). Aerial photographs were digitized at an average scale of 1:2,000 and then interpreted by delineating polygons representing the six communities. Individuals who had over 20 years of experience with Jug Bay plant communities reviewed results of the photographic interpretation. After a first review, a second or third round of polygon edits were made until the delineation

Fig. 2 Major wetland plant communities as determined from study area aerial photographs taken during the growing season in 1971, 1989, and 2007



best represented the different communities. All images were georeferenced to the Maryland State Plane NAD83 meters. The 1971 and 2007 photographs were provided by the Maryland Department of Natural Resources (<http://dnrweb.dnr.state.md.us/gis/data/data.asp>). The 1989 photograph was provided by Air Photographics, Inc. and was taken at 12.5 μm from imagery acquired at 12,000 ft elevation, 1:24,000 scale, by the Virginia Institute of Marine Science. Orthophotography for 2007 was obtained from the National Agriculture Imagery Program (NAIP). The NAIP true color image was collected at 1:40,000 scale and was scanned at 25 μm .

Changes in the coverage of plant communities over time were calculated using the equation for the intrinsic rate of natural population growth (Ricklefs 1990) that was used by Rice et al. (2000) in their studies, which included Jug Bay. In this equation:

$$N = N_0 e^{rt}$$

where the known terms of the equation were defined as follows: N is the total area of plant community at time 1, N_0 is the total area of plant community at time 0, e is a constant, 2.718281828, the base of the natural logarithm, and t is the difference in years between time 1 and time 0. This equation was then solved for r , the intrinsic rate of growth.

Fine-Scale Measurements

Permanent Plots

In 1988, 18 permanent 1×1-m plots were established in 3 communities: *Typha* (7 plots), scrub-shrub (6 plots), and *Z. aquatica* (5 plots). In 1997, two new communities were sampled: mixed vegetation community that was not clearly dominated by any single species (five plots) and *P. australis*-dominated community (two plots). Three more plots in *Typha*-dominated areas were also added in 1997. Permanent plots were not established in *Nuphar* communities. Eighteen plots were located in North Glebe Marsh and 10 were located in South Glebe Marsh (Fig. 1). Plots were located from 4 to 87 m (mean=30 m) from the upland edge of the wetland (high tide line) and were marked with tall PVC poles. We did not determine the specific identity of *Typha*, however, the taxon at Jug Bay appears to be *Typha* × *glauca*, a hybrid between *Typha angustifolia* and *Typha latifolia*.

Plots were monitored annually between July and September from 1988 to 1999 and again in 2010 for a total of 225 plot visits. In the plots, the percent cover of each species was estimated based on four cover categories: 0–10, 10–40, 40–70, and 70–100 %. For analytical purposes, the midpoint of each percent cover category was used. Importance values (IV) for each plant community for each year of sampling were calculated as the sum of the relative frequency and relative

cover divided by two. The variation in the seasonal timing of plot surveys did not impact our findings.

Species IVs for the permanent plots were analyzed with nonparametric, nonmetric multidimensional scaling (NMS) in PCOrd (McCune and Medford 2006). The ordination was run using a variety of scenarios in which we eliminated the combinations of plots and species that had a minimal number of data appearances. The final version of the ordination that was selected included all of the permanent plots and species that appeared more than three times ($n=53$). We analyzed the data using different numbers of iterations and the best fit to the data resulted from 500 iterations. Other features of NMS that were used included a comparison of the ordination using real data and random data. The results of the ordination using real data provided significantly more reduction in stress ($p<0.004$) for the first three axes. The starting coordinates for the ordination were random with a step length of 0.20 and the distance matrix that is part of the procedure was calculated using Sørensen's dissimilarity. The x -axis matrix was normalized. The stability was 0.9154 and was determined by comparing the standard deviation of the stress over the final 10 iterations. The ordination resulted in three axes, which accounted for 93.3 % of the variance. Two axes accounted for approximately the same amount of variance (31.2 and 31.8 %) and the third axis accounted for 23.3 %. For purposes of presentation and interpretation, we used the two axes that accounted for the highest percentages of the variance.

Line Transects

Ten line transects were established in 1994 (Fig. 1): five in North Glebe Marsh and five in South Glebe Marsh. Transect length ranged from 15 to 57 m (mean=30.3 m) and each was divided into 3 m intervals. Transects were placed in wetland areas where species composition could be assessed under different conditions. Four transects were placed within homogenous vegetation composed entirely of either a single species or a single community type; four transects were established perpendicular to inundation zones from low to high marsh; and two transects were placed parallel to and along the ecotone or boundary between two communities. Descriptions of the transects are provided in Table 1 and their locations are shown in Fig. 1.

Transect surveys were made in 1994 and 1995 and in 2007 and 2008; however, for the analysis, we used the 1994 and 2008 data to maximize the time interval between measurements. Data were collected in late July or early August. A meter tape was stretched along the transect, and the line-intercept method was used to measure the length of each individual plant leaf or stem that intercepted the transect line (Cox 1985). For species with multiple stems (clumps), such as *N. lutea*, *P. virginica*, *P. cordata*, and *Sagittaria latifolia*,

Table 1 Comparison of changes in plant communities based on transect data; 1994 to 2008

Transect number	Transect length (m)	Number of intervals	14-year comparison		Wilcoxon–Mann–Whitney test <i>p</i> value	Transect type
T1-I	57	19	Aug-94	Aug-08	0.243	Across inundation zones (low to high marsh)
T5-I	24	8	Aug-94	Aug-08	0.638	Across inundation zones (low to high marsh)
T7-I	36	12	Aug-94	Aug-08	0.685	Across inundation zones (low to high marsh)
T10-I	15	5	Aug-94	Aug-08	0.055*	Across inundation zones (low to high marsh)
T2-H	21	7	Aug-94	Aug-08	NV	Within homogeneous community (<i>Nuphar</i>)
T8-H	48	16	Aug-94	Aug-08	1.000	Within homogeneous community (<i>Nuphar</i>)
T4-H	24	8	Aug-94	Aug-08	1.000	Within homogeneous community (mixed vegetation)
T9-H	18	6	Aug-94	Aug-08	0.934	Within homogeneous community (swamp forest)
T3-E	42	14	Jun-94	Jun-08	0.625	Along community ecotones (<i>Nuphar</i> – <i>Phragmites</i>)
T6-E	18	6	Aug-94	Aug-08	0.110*	Along community ecotones (<i>Nuphar</i> – <i>Typha</i>)

Transects are organized by vegetation community. Intervals along transects were 3 m long. The Wilcoxon–Mann–Whitney test did not generate a *p* value for transect T2-H because only a single species (*N. lutea*) was located here.

NV no value; * represents a significant difference at $p < 0.1$

each clump was considered an individual plant. The total number of individual plant stems, leaves, or clumps was recorded for each species to estimate the density index. Transect cover data for each species were used to calculate IVs for each species following procedures in Cox (1985). A nonparametric Wilcoxon–Mann–Whitney test (signed rank test) was used to compare the transect IVs. This analysis tests for differences between pairs of observations, indicating changes in species composition and dominance. Statistical comparisons were performed using SAS 9.1® (Proc ANOVA).

Environmental Data

To determine trends in river discharge for the Patuxent River, data from 1978 to 2010 were obtained from the US Geological Survey (USGS 2011) gauge station at Bowie, MD, located about 20 km upriver from the study area and just upstream of the head of tide. Local water level data were obtained from a continuous water quality monitoring station (station RR) that used a YSI V2 sonde data logger located at the Jug Bay River Pier (National Oceanic and Atmospheric Administration (NOAA) 2012; see Fig. 1). Salinity data were obtained at the River Pier station (NOAA 2012) and from the long-term monitoring station at Jackson Landing (TF1.4) on the western edge of the study area (Chesapeake Bay Program 2011).

Results

The plant communities sampled varied from low marsh areas, comprised largely of a single species (for example,

N. lutea) to high marsh habitats that were dominated by *Typha* × *glaucua* and *P. virginica*, but also included as many as 22 other species. Most of the sites that were sampled have remained remarkably stable since the late 1980s. In contrast to the lack of any obvious directional change in vegetation at the fine scale, interpretation of aerial photographs over a period of approximately 37 years suggests dynamic shifts in the location and extent of some community types.

Broad-Scale Change

Aerial photographs spanning almost four decades revealed changes in the coverage and spatial distribution of plant communities (Fig. 2). For example, in 1971, *Typha* dominated a large area south of the railroad levee between the river on the west and areas dominated by *Nuphar*. By 1989, this area was dominated by *Z. aquatica*; however, by 2007, the same area had become dominated by *Phragmites*, *Typha*, and mixed vegetation. *Nuphar*-dominated areas expanded in both North Glebe Marsh and South Glebe Marsh over the four decades. *P. australis*, on the other hand, expanded only slightly in the area adjacent to the levee, but by 2007, new patches appeared on the edge of the river.

Of the six plant communities analyzed, two increased substantially in coverage, two were stable, and two fluctuated (Table 3). *Nuphar*-dominated areas expanded the most, increasing from 22 % coverage of the study area in 1971 to 49 % in 2008. The overall rate of annual change for *Nuphar*-dominated communities was 2.1 %, but the rate of change has increased from 1.3 % between 1971 and 1989 to 2.8 % between 1989 and 2007. *P. australis* only covered a small percentage of the study area in the earliest aerial photograph, but has expanded at an annual rate of 2.7 % between 1989

and 2007. The coverage of mixed vegetation and scrub-shrub communities also changed but, because the overall rates of population growth were closer to zero, we interpreted them to be stable. The *Typha*-dominated community declined sharply from 1971 to 1989, but increased between 1989 and 2007. *Zizania*-dominated vegetation increased between 1971 and 1989, but declined from 1989 to 2007.

Fine-Scale Change

A total of 70 species (including 4 species identified to genus only) and 1 hybrid were sampled in the plots and transects; 51 species occurred in the permanent plots and 62 species were identified along transects (see Appendix). Sixty species are perennials and 10 are annuals (source: USDA (2011) Plants Database). The variation in mean number of species per plot (all plots combined for each community) among years in the five communities assessed using permanent plots was as follows: scrub-shrub=20.5 (14–32 species); *Typha*=11.0 (6–16 species); mixed vegetation=7.3 (7–8 species); *Phragmites*=3.0 (2–4 species); and *Zizania*=2 (2 species). Total species richness within a community, based on the sum of all plots,

was 44 species in scrub-shrub; 22 species in *Typha*; 8 species in mixed vegetation; 6 species in *Phragmites*; and 2 species in *Zizania* communities. Whereas most year-to-year variation was caused by changes in the occurrence of annuals, the persistence of perennials also varied. Marked seasonal changes in species dominance was a feature of the study area, with annuals (especially the vine *Polygonum arifolium*) increasing in importance between June and August (Swarth and Delgado, unpublished data).

IVs for the dominant species in the permanent plots are shown in Fig. 3. The high species richness in the scrub-shrub community was reflected in low IVs for many species, where no single species had a mean IV >0.16. *Typha* × *glauca* (mean IV of 0.25) was essentially a codominant with *P. virginica* (mean IV of 0.23) in the *Typha* community. In the mixed vegetation community, *N. lutea* and *P. virginica* had combined IVs exceeding 0.82. In areas where these two species co-occurred, *Nuphar* was usually in low marsh areas that experienced slightly greater tidal inundation. *Zizania*-dominated and *Phragmites*-dominated communities both exhibited low species richness. Although areas dominated by *Phragmites*, with an IV of 0.70, often appeared to consist entirely of this

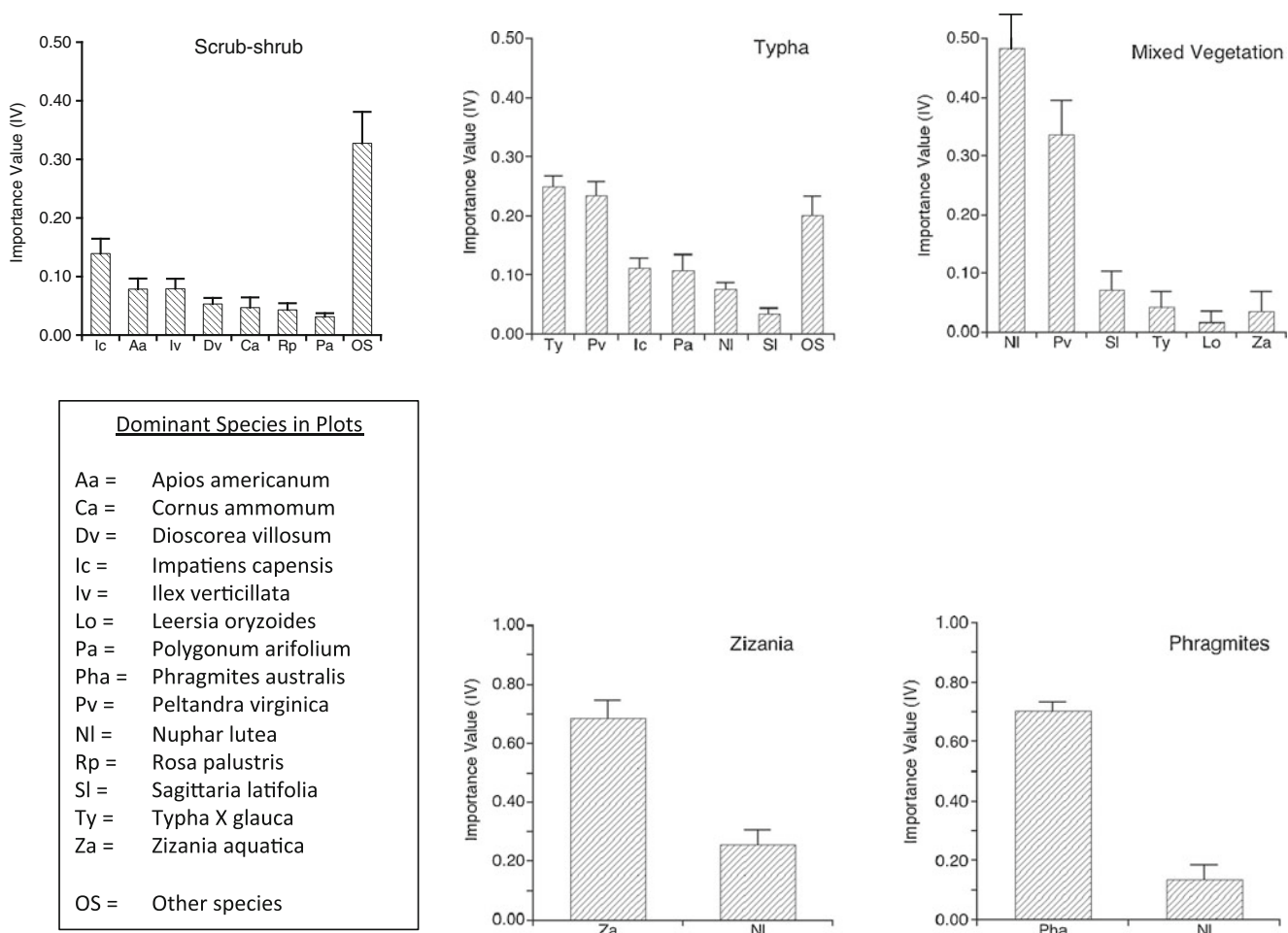


Fig. 3 Mean (±SE) IVs of dominant plants in permanent plots. IVs calculated from all years and all plots combined

species, a number of other species were present but with IVs mostly lower than 0.05. *N. lutea* occurred in all communities sampled and was among the most widely distributed and abundant species in the study area as indicated by high IVs in four of the five communities sampled (Fig. 3).

NMS ordination of IVs for the permanent plots (Fig. 4) showed that the communities were distinct from each other. We interpreted axis 1 to represent the relative positions of the communities within the tidal gradient. Scrub–shrub and *Phragmites* communities were located at the highest elevation within the tidal regime where they received less tidal flooding than communities at lower elevations (Swarth, personal observations). The *Zizania* community occurred in the lowest level within the tidal regime (as does the *Nuphar* community), whereas *Typha* and mixed vegetation communities were at intermediate locations. We interpreted axis 2 to be related to the diversity of species in each community. The scrub–shrub and *Typha* communities had the greatest number of species (44 and 22, respectively), but the other three communities had many fewer species (mixed vegetation=8, *Phragmites*=6, and *Zizania*=2). Although permanent plots were not established in the *Nuphar* community, we would expect data from such plots to cluster in the upper northwest quadrant of Fig. 4 because of the high degree of flooding and very low species richness characteristic of this community. For the *Typha* community, we connected the years (Fig. 4) to determine if there had been

any directional changes in species composition over the study period. The *Typha* example, which was typical of the other plant communities studied, demonstrated differences between years but no overall temporal trend in species composition.

Analysis of the transect data showed, as with the permanent plot data, an overall stability of plant communities through time. The number of species on transects varied from 1 (*N. lutea*) on T2-H to a high of 28 woody and herbaceous species along T1-I (Fig. 1). With the exception of two transects (T6-E and T10-I; Fig. 1), no significant trends in species composition and dominance were observed over the 14-year time period (Table 1). Transect T10-I, located across inundation zones, showed shifts in species dominance with an increase in the IVs of *N. lutea*, *P. virginica*, and *Typha* (Fig. 5). Also, three species not recorded along transects in 1994 were found in 2008 (*Impatiens capensis*, *Leerzia oryzoides*, and *S. latifolia*). While not present along transects in 1994, the three species were, however, present and often abundant in 1994 (Whigham and Swarth, personal observations). In contrast, in transect T6-E (located along a *Nuphar*/*Typha* community ecotone), the number of species decreased from 13 in 1994 to 9 in 2008. Also, along this transect, major changes in species dominance included a decrease in the IVs for *Acorus calamus* and *P. virginica* and an increase in the IV of *P. cordata* (Fig. 5). Even though differences were not significant, the transects located along homogenous communities composed of mixed vegetation (for example, T4-H; Fig. 1) or swamp forest (T-H9; Fig. 1) showed a higher number of species and more variability in species dominance during the 14-year study period than the homogenous transects that were dominated by a single species (e.g., *N. lutea*). Another indication of vegetation stability was shown on transect T3-E, which was dominated by *Phragmites* on one side and *Nuphar* on the other. *Phragmites* is widely recognized as an aggressive clonal species, but no significant movement by the leading edge of the *Phragmites* into the *Nuphar*, or vice versa, was observed over 14 years (Fig. 2).

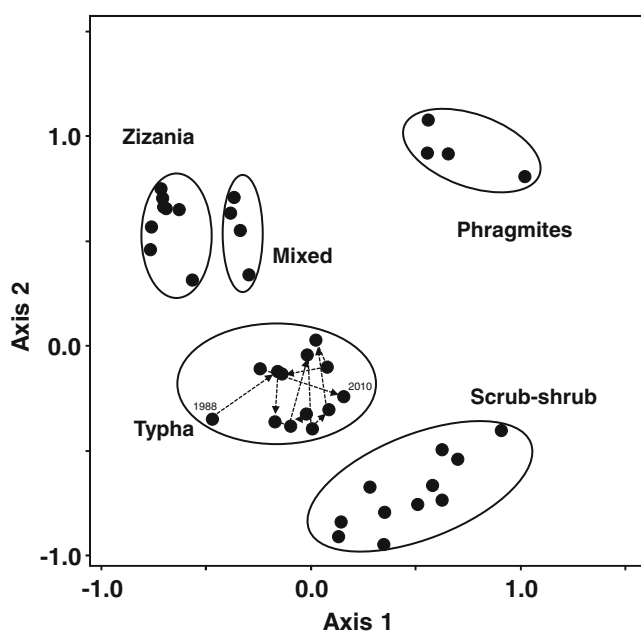


Fig. 4 NMS analysis of species IVs for the five plant communities monitored with permanent plots between 1988 and 2010. For the *Typha* community, which is representative of other communities, the years in which plots were sampled were connected consecutively from 1988 to 2010

River Discharge, Water Depth, and Salinity

We examined river discharge data (USGS 2011) into the Jug Bay area from the nontidal portion of the Patuxent River. Mean annual discharge ranged from 5 m³/s (1981) to 23 m³/s (2003), with a mean of 11 m³/s, but there was no trend ($r^2 < 0.01$) of either increasing or decreasing discharge rates between 1978 and 2009. Maximum discharge occurred in March and April, and minimum discharge occurred between July and October. Water depth in the main river channel measured at the River Pier station, ranged from 0.9 to 1.2 m (between 2003 and 2011) and averaged 1.1 m. Water depth did not show any increasing or decreasing trend nor any correlation with river

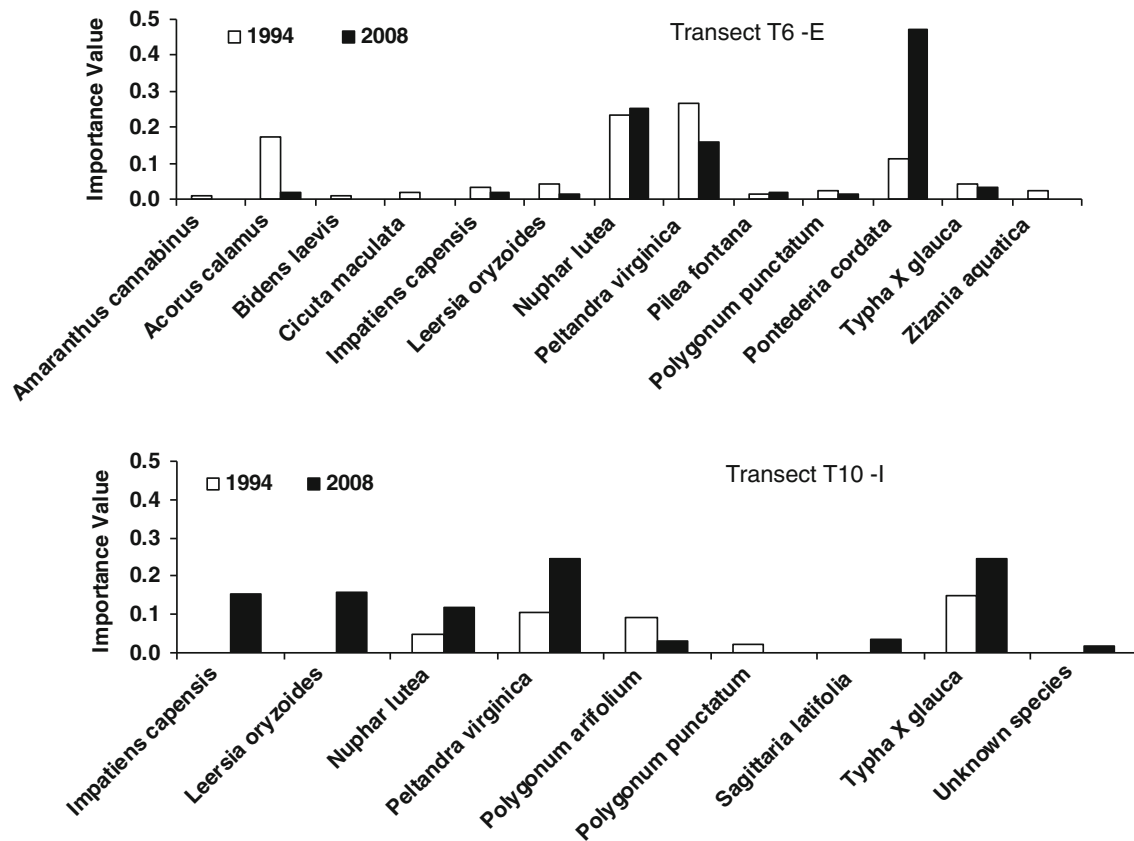


Fig. 5 Comparison of IVs measured in 1994 and 2008 for transects T6-E and T10-I

discharge, probably a result of the regular and strong tidal pulse from the estuary (Swarth, personal observation). Although water levels are not monitored within the wetlands, levels there are highly influenced by wind and regular tidal cycles.

Salinity readings exceeding 0.5 ppt were not recorded during monthly sampling between 1985 and 1994 (Chesapeake Bay Program 2011). However, based on continuous sampling between 1995 and 2010 (NOAA 2012), salinity spikes exceeding 0.5 ppt were recorded in 1995, 1998, 1999, 2002, 2005, 2007, 2008, and 2009, and the frequency of spikes appear to have increased between 2005 and 2009 (Table 2). These high salinity events lasted from several days to 3 months. The maximum salinity recorded was 2.4 ppt on 10 October 2007. That same year, about 3 % of all readings exceeded 1.0 ppt. Most events were between mid-July and October, although in 2009, high salinity occurred in late January. The seasonal timing of these events suggests that higher than normal salinity resulted from low riverine discharge, which reduced the dilution effect on estuarine waters, rather than from sea level rise. High salinity conditions did not generally persist throughout a 24-h period but varied with tide height; during high tide periods, salinity increased when estuarine waters mixed with fresh riverine water, but during low tide periods, salinity dropped to below 0.5 ppt.

Discussion

Temporal changes in the distribution of plant species in different types of wetlands have been examined by a number of researchers (e.g., Crain et al. 2004; Casey and Ewel 2006; Czerepko 2008; Smith et al. 2008; Stroh et al. 2008), including efforts to determine if plants are organized into distinct communities or if temporal changes occur at the level of individual species (Van der Valk 1981). Vegetation changes in tidal freshwater wetlands have also been investigated (e.g., Perry and Hershner 1999; Rice et al. 2000; Leck et al. 2009) but, to our knowledge, there have been no studies in which permanent plots or transects have been examined over a decade or more. Sediment cores have been used to study long-term changes in tidal freshwater wetlands in New Jersey (Orson et al. 1990, 1992), Chesapeake Bay (Khan and Brush 1994; Neubauer et al. 2002; Hilgartner and Brush 2006), and San Francisco Bay (Brown and Pasternack 2005). These studies have shown that most tidal freshwater wetlands formed in the past 300 to 1,500 years and vegetation dynamics have been strongly influenced by patterns of sediment deposition (Pasternack 2009). Analyses have demonstrated that many areas now dominated by emergent plant species were unvegetated open water or supported beds of

Table 2 Maximum salinity measurements and the duration of high salinity events for 1985 to 2010 at Jug Bay, Patuxent River, Maryland

Year	Maximum salinity (ppt)	Event duration
1985–1994	0.1	
1995	0.9	28 Aug–21 Sept
1996	0.4	
1997	0.0	
1998	0.6	21 Sept–8 Oct
1999	1.2	15 July–26 Aug
2000	0.1	
2001	0.0	
2002	1.3	13 Aug–17 Oct
2003	0.0	
2004	0.0	
2005	1.0	19 Sept–8 Oct
2006	0.0	
2007	2.4	28 July–26 Oct
2008	1.2	20–26 Oct
2009	1.0	30 Jan–4 Feb
2010	0.0	

Data courtesy of Chesapeake Bay Program, Maryland Department of Natural Resources (1985–1994); NOAA, National Estuarine Research Reserve, Centralized Data Management Office (1995–2010)

submersed aquatic plants and that many tidal freshwater wetlands similar to those at Jug Bay have only developed in the past two to three centuries (Pasternack 2009).

Broad-Scale Change

Vegetation changes in tidal freshwater wetlands have been shown to occur as a result of increased flooding related to rising sea levels (Orson et al. 1992), the intrusion of brackish water which initiates species replacements (Perry and Hershner 1999), increased eutrophication (Schuyler et al. 1993), herbivory by non-native animals (Haramis and Kearns 2007), and expansion of invasive plants species, such as *P. australis* (Rice et al. 2000). Other than conversion of tidal freshwater wetlands to oligohaline and brackish wetlands over long periods of time (Neubauer and Craft 2009), no previous studies have demonstrated any autogenic directional changes that might be characterized as succession from one type of vegetation to another such as low marsh to high marsh dominated by herbaceous species or the conversion of high marsh dominated by herbaceous species to high marsh habitats dominated by woody species (Leck et al. 2009).

Our analysis identified changes at the broad-scale but no distinct changes in vegetation based on fine-scale measurements. Interpretation of the differences between the two methods of assessment requires an understanding of the

events at Jug Bay and in the Patuxent River watershed over the past 300 to 400 years. Khan and Brush (1994) concluded that two events were responsible for the current physical settings upon which today's wetlands developed. In the 1700s and 1800s, much of the Jug Bay area was open water and water depth was sufficient to serve as a port for ocean-going ships. In the late 1800s, coincident with high rates of land clearing (forest removal) in the watershed, large amounts of sediment were deposited in Jug Bay (0.64 cm year⁻¹; Khan and Brush 1994) at the same time that fill material was placed in the wetland for the railroad levee (Fig. 1). High rates of sedimentation coincident with the construction of the levee would have altered the patterns of tidal flows and most likely resulted in the accumulation of sediment in areas adjacent to the levee, resulting in the establishment of the high marsh habitats that are now dominated by scrub-shrub vegetation on both sides of the railroad levee (Fig. 2). In addition, the high rates of sedimentation certainly decreased the mean water depth throughout Jug Bay to the point where emergent plants were able to expand, resulting in the matrix of vegetation that is present today. Similar patterns and processes of the conversion of open water areas to habitats dominated by tidal freshwater vegetation have been documented by Pasternack and Brush (2001) in another tidal freshwater estuarine area in the upper Chesapeake Bay. The main causes of sedimentation at Jug Bay are no longer extensive forest removal. For the past 115 years, the vertical accretion in North and South Glebe Marshes has been largely influenced by the railroad levee (Delgado et al., this volume).

The aerial photographs provide evidence of changes since the 1970s in the distribution and extent of some of the plant communities analyzed, whereas other communities remained almost constant (Fig. 2). The scrub-shrub communities in the North and South Glebe Marshes have not expanded. The *Phragmites*-dominated community has expanded at the broad scale (Fig. 2), but there have been no changes in species composition at the fine scale (Fig. 3; Table 3). To our knowledge, there have not been any long-term plant-monitoring studies in tidal freshwater habitats dominated by trees and shrubs, even though these species-rich habitats have been described previously (Rheinhardt 1992; Leck et al. 2009). Scrub-shrub and swamp forests (globally rare habitats) are located at the upper end of the tidal zone and experience lower sedimentation rates than low marsh areas. Additionally, the hummocky topography (Rheinhardt 1992) and shading from trees and shrubs creates few opportunities for seedlings of woody species to become established. If current environmental conditions persist, the species composition and physical characteristics of shrub-dominated and tree-dominated habitats would not change much over the next decades. However, under predicted accelerated rates of RSLR throughout the Chesapeake Bay

Table 3 Changes in plant community coverage (based on aerial photographs; see Fig. 2) at the Jug Bay Glebe Marsh during three periods (1971–1989; 1989–2007; and 1971–2007)

Plant community	Aerial coverage (ha)			Proportion of marsh (%)			Intrinsic rate of growth (%) ^a			
	1971	1989	2007	1971	1989	2007	1971–1989	1989–2007	1971–2007	Trend
<i>Nuphar</i>	19.9	25.2	42.3	22	32	49	1.3	2.8	2.1	Increasing
<i>Phragmites</i>	2.1	2.2	4.3	2	3	5	0.3	2.7	1.5	Increasing
Mixed vegetation	17.2	6.7	14.4	19	9	17	-5.2	4.3	-0.5	Stable
Scrub–shrub	4.3	5.6	5.4	5	7	6	1.5	-0.2	0.6	Stable
<i>Typha</i>	29.4	5.8	11.7	32	7	14	-9.0	3.9	-2.5	Fluctuating
<i>Zizania</i>	18.1	32.7	8.0	20	42	9	3.3	-7.8	-2.3	Fluctuating
Total coverage (ha)	91.0	78.1	85.3							

^a The intrinsic rate of growth is a measure of the annual change in community size

(Boon et al. 2010), the stability of these communities might be at risk.

According to Rice et al. (2000), *Phragmites* has been present in Jug Bay since at least 1938. At that time, four *Phragmites* stands covered only 2.5 % (about 6 ha) of the greater Jug Bay marsh area (Rice et al. 2000). By 1971, these stands had doubled in size to about 12 ha and one additional stand appeared. The four stands continued to expand between 1971 and 1985, but declined from 1985 to 1994 after the aerial application of herbicides in some parts of Jug Bay (Kearns, personal communication). The stand adjacent to the southeast side of the railroad levee in our study area (Fig. 2) has expanded little since 1938 (see Rice et al. 2000) and has remained almost constant in size for the past four decades. An interesting aspect of that particular *Phragmites* stand is that it contains a number of other species, although (except for *Nuphar*) their IVs were quite low. The species composition of areas dominated by *Phragmites* would probably remain relatively stable over time because of competition and shading by this tall plant (Meyerson et al. 2000). One of the authors (Whigham) has observed the site for more than 30 years and has noticed that the height and density of *Phragmites* has decreased and other species have become established. The same changes have not occurred in other stands of *Phragmites* at Jug Bay, except where herbicides have allowed the establishment of *P. virginica* and other species. One possible explanation for the changes in species diversity is that surface elevation has increased and the site is less frequently flooded during high tides, potentially resulting in more frequent aerobic conditions in the surface sediments allowing the establishment of seedlings of other species. Furthermore, because of its location distant from the main river channel, the water that reaches the site may be lower in nutrients due to nutrient uptake by wetland vegetation that separates this *Phragmites* stand from the river. Whigham and Simpson (1978) found that nutrients were assimilated as tidal waters flowed from

the tidal creeks to high marsh areas. The combination of less frequent flooding and lower nutrient inputs would result in nutrient limitations and reduced growth (i.e., shorter and less dense ramets) of *Phragmites*, which would allow more sunlight to reach the wetland surface and subsequently a higher probability that other species could become established. Our ideas remain to be tested, but if correct, the long-term directional changes in the coverage of *Phragmites* are likely to occur in some parts of Jug Bay.

The reasons for decadal variations in the extent of *Nuphar*-dominated areas are unknown but a few factors could contribute to the dynamics of this long-lived species. The expansion we noted in South Glebe Marsh is probably caused by positive marsh elevation change rates, which convert deep areas devoid of *Nuphar* to shallower areas where this species can spread or become established. In contrast, the expansion of *Nuphar* in North Glebe Marsh is not due to colonization of bare mudflats, but rather to a shift from a *Typha*-dominated community in 1989 to one dominated by *Nuphar* by 2007 (Fig. 2). North Glebe Marsh is not gaining elevation (Delgado et al., this volume). As a result, areas that were formerly shallow may have increased in depth, causing the observed shift from *Typha* to *Nuphar*. As *Nuphar* expands in coverage as a result of clonal propagation, the leaves and stems trap more sediment.

Causes for contraction of *Nuphar* from 1971 to 1989 in South Glebe Marsh could be due to herbivory by the water lily beetle (*Galercuella nymphaeae*). Herbivory by this beetle can reduce leaf longevity and can lead to the complete loss of the canopy (Kouki 1993). Beetle herbivory occurs during the growing season when water and substrate temperatures are high and the metabolically active rhizomes and roots of *Nuphar* have a high oxygen demand. In *T. angustifolia*, the loss of the leaves results in the elimination of gas exchange with belowground structures, conditions that resulted in substantial death of belowground biomass (Jordan

and Whigham 1988). If this process also occurs with *Nuphar*, the loss of the emergent leaves over consecutive years could potentially result in death of rhizomes and a decrease in the aerial extent of *Nuphar* clones. Wind fetch across the open waters of Jug Bay and ice scour could also create unfavorable conditions for the establishment of rooted macrophytes such as *Nuphar* (see also Heinle and Flemer 1976), although prolonged ice cover has diminished in recent years (Swarth, personal observation).

Striking changes also occurred with the *Typha* community, which comprised 29 % of the wetland in 1971, but declined to only 6 % of the wetland by 1989, an annual loss rate of 9 %. Most of this loss occurred in South Glebe Marsh. Mammalian herbivory could have played a role in reducing *Typha* abundance. *Typha* is a favorite food of muskrats (*Ondatra zibethicus*), rodents that are common in the Jug Bay area (Swarth, personal observation). When muskrat populations are high, they can create “eat outs” by devouring large areas of the marsh (Lynch et al. 1947; Connors et al. 2000). Fortunately, nutria (*Myocastor coypus*) are not established in this area (Swarth, personal observation).

Z. aquatica is an annual grass that occurred in the tidal freshwater portion of the Patuxent River (Scofield 1905) from White's Landing (13.5 km downriver from our study area) to Leon (1.0 km above our study area). The abundance of this species typically fluctuates annually, owing to seed production, seed predation, changes in optimal germination and establishment conditions, levels of herbivory, and possibly water quality. The interannual variability in coverage and extent of this annual plant across the wetland would generally be greater than that of perennials (Leck et al. 2009), which persist over the nongrowing season as a rhizome or rootstock in the sediment. In the past three decades, the abundance of *Zizania* in Patuxent River tidal freshwater wetlands (Fig. 2) has varied tremendously in response to grazing by resident Canada Geese and other herbivores (Haramis and Kearns 2007). Although we do not know which factors were most responsible for the spatial changes in *Zizania*-dominated areas at Jug Bay, clearly, goose herbivory has been important. *Zizania* expanded significantly from 2007 to near historic coverage (pre-1970s) by 2011, after a 10-year restoration program using three methods: a special early season hunt targeting the geese; wire mesh fencing to protect wild rice seedlings from geese grazing in early summer; and collecting and casting seeds in spring (Kearns, personal observation).

The lack of temporal change in the mixed vegetation sites may be due to the presence of a relatively high proportion of annuals (three of eight species) that exhibit dynamic population changes (Leck et al. 2009). Leck and Simpson (1995) studied changes in the seed bank and extant vegetation over a 10-year period in a Delaware River tidal freshwater wetland. Similar to our results, they found that there was little

variation in the abundance of the perennial species; however, most of the annuals varied from year to year with no clear relationship between their presence in the seed bank and emergence and/or establishment in the spring.

Fine-Scale Change

At the fine scale, the lack of evidence of directional change in any of the plant communities examined may be due to at least two factors. Several of the communities described above are dominated by long-lived clonal species that are able to persist over long periods of time because of their location within the tidal regime or because of their ability to dominate sites. *Nuphar*-dominated habitats typically occur in the lower portion of the intertidal zone where few other species can grow because they do not tolerate long periods of inundation. Few other species are able to coexist in *Phragmites*-dominated areas because it is a clonal species with long-lived rhizomes that form dense stands of tall ramets that shade other species. In a separate study of *Phragmites*-dominated stands in brackish wetlands in the Chesapeake Bay, one of the authors (Whigham) has compared vegetation in patches that have been dominated by *Phragmites* for more than four decades with sites that have been colonized more recently. In recently colonized sites, there were no other species present or the few species that coexisted with *Phragmites* were small in stature and clearly were declining in size and abundance. Sites that had been dominated by *Phragmites* for more than four decades almost always had no other species and if other species were present, they were only found at the margins of the *Phragmites* stand. In addition, stands of *Phragmites* shade the understory and develop thick litter layers, resulting in few opportunities for the establishment of seedlings of the annual species that are common in tidal freshwater wetlands.

The lack of directional change in the other communities (i.e., *Typha*-dominated, mixed vegetation, and scrub–shrub) is most likely due to the presence of long-lived species and the development of hummock–hollow microtopographic conditions. *Typha* is also a long-lived clonal species but it does not grow as high as *Phragmites* (McCormick and Somes 1982), which likely allows enough light penetration for other species, especially annuals, to co-occur. The leading dominant in the mixed vegetation, *P. virginica*, is also a long-lived perennial but it does not spread clonally and areas that it dominates typically develop a hummock–hollow topography which results in a high species diversity at the community level (e.g., Stribling et al. 2007). Similarly, a hummock–hollow topography develops in the scrub–shrub-dominated areas and the dominant woody species are long-lived and do not spread clonally, resulting in opportunities for annual species as well as other species to persist on the hummocks and in the hollows (Rheinhardt 1992). The

persistence of the hummock–hollow microtopographic condition in parts of the wetland that are not dominated by clonal species may be the key physical feature that allows for the persistence of a diverse plant community that changes little, if at all, over time.

Future Changes

The increase in flooding duration owing to RSLR and the eventual intrusion of brackish water into tidal freshwater wetlands will cause fundamental changes to several of these plant communities unless species are able to adapt or to move to higher elevations in the landscape (Neubauer and Craft 2009). The two NOAA tide gauges nearest to the study site (Solomon's Island and Annapolis, MD) showed RSLR rates between 3.41 and 3.44 mm year⁻¹, respectively. Whereas salinity readings over 0.5 ppt are still uncommon at Jug Bay, these events may be increasing. Many tidal freshwater wetlands plant species do not tolerate salinity above 2 ppt and some are also sensitive to increased inundation (Baldwin et al. 2001). Our field sampling did not find *Spartina cynosuroides*, a dominant oligohaline marsh indicator in the Patuxent River as described by Sharpe and Baldwin (2009).

The long-term fate of these wetlands remains unknown. Certainly, rising salinity and increasing inundation will favor species that are better adapted to these conditions (for example,

S. cynosuroides) and will cause declines in salt-intolerant species, such as *Zizania*. Given that this tidal freshwater wetland currently removes 31 % of total nitrogen (via denitrification and burial) from the Patuxent River watershed (Boynton et al. 2008), changes to the plant communities could have a major impact on water quality in this river.

Eventually, the tidal freshwater wetlands at Jug Bay will likely be converted to brackish wetlands. In the short term, changes in plant species abundance and distribution will be triggered more by variable rates of sedimentation, by herbivores, such as the water lily beetle, the emerald ash borer (*Agrilus planipennis*), muskrats, and Canada Geese, and by the gradual spread of the non-native haplotype of *P. australis*. The most probable long-term changes will be the replacement of species that are intolerant of brackish water and increasing water depth with species that are progressively more tolerant of these conditions.

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Appendix

Wetland plant species identified and measured in study area permanent plots and transects

Scientific name	Common name	Annual (A) or perennial (P)	Growth form	Community
<i>Acer rubrum</i>	Red maple	P	W	SS
<i>Acorus calamus</i>	Sweet flag	P	H	MV
<i>Alisma subcordatum</i>	American water plantain	P	H	MV
<i>Alnus serrulata</i>	Hazel alder	P	W	SS
<i>Amaranthus cannabinus</i>	Tidal marsh amaranth	P	H	MV, T
<i>Apios americana</i>	Groundnut	P	V	SS
<i>Bidens laevis</i>	Smooth beggartick	A	H	MV
<i>Boehmeria cylindrica</i>	Smallspike false nettle	P	H	SS
<i>Carex</i> sp.	Sedge	P	H	MV, SS
<i>Cephalanthus occidentalis</i>	Buttonbush	P	W	SS
<i>Cicuta maculata</i>	Spotted water hemlock	P	H	MV, SS
<i>Clethra alnifolia</i>	Coastal sweet pepperbush	P	W	SS
<i>Cornus ammomum</i>	Silky dogwood	P	W	SS
<i>Cornus sericea</i>	Redosier dogwood	P	W	SS
<i>Cuscuta gronovii</i>	Dodder	P	V	MV, SS, T
<i>Decodon verticillatus</i>	Swamp loosestrife	P	W	SS
<i>Dioscorea villosa</i>	Wild yam	P	V	SS

(continued)

Scientific name	Common name	Annual (A) or perennial (P)	Growth form	Community
<i>Echinochloa walteri</i>	Walter's millet	A	H	MV
<i>Fagus grandifolia</i>	American beech	P	W	SS
<i>Fraxinus profunda</i>	Pumpkin ash	P	W	SS
<i>Galium aparine</i>	Sticky willy	A	H	MV
<i>Geum canadense</i>	White avens	P	H	SS
<i>Hibiscus moscheutos</i>	Crimson-eyed rosemallow	P	H	MV, SS, T
<i>Ilex verticillata</i>	Winterberry	P	W	SS
<i>Impatiens capensis</i>	Jewelweed	A	H	MV, SS, T
<i>Itea virginica</i>	Virginia sweetspire	P	W	SS
<i>Justicia americana</i>	American water-willow	P	H	SS
<i>Leersia oryzoides</i>	Rice cutgrass	P	H	MV, Ph
<i>Ligusticum canadense</i>	Canadian licorice root	P	H	SS
<i>Lilium superbum</i>	Turk's cap lily	P	H	SS
<i>Lindera benzoin</i>	Spicebush	P	W	SS
<i>Lobelia cardinalis</i>	Cardinal flower	P	H	MV, SS
<i>Lonicera japonica</i>	Japanese honeysuckle	P	V	SS
<i>Ludwigia palustris</i>	Marsh seedbox	P	H	MV, SS
<i>Lycopus sp.</i>	Horehound	P	H	SS
<i>Mentha spicata</i>	Spearmint	P	H	SS
<i>Mikania scandens</i>	Climbing hempvine	P	V	MV, SS, T
<i>Murdannia keisak</i>	Wartremoving herb	P	H	MV
<i>Nuphar lutea</i>	Spatterdock	P	H	MV, N, Ph, T, Z
<i>Osmunda cinnamomea</i>	Cinnamon fern	P	H	SS
<i>Parthenocissus quinquefolia</i>	Virginia creeper	P	V	SS
<i>Peltandra virginica</i>	Arrow arum	P	H	MV, Ph, T
<i>Phragmites australis</i>	Common reed	P	H	Ph
<i>Pilea fontana</i>	Lesser clearweed	A	H	MV, T
<i>Pilea pumila</i>	Clearweed	A	H	MV, T
<i>Polygonum arifolium</i>	Halberdleaf tearthumb	A	V	MV, Ph, SS, T
<i>Polygonum hydropiper</i>	Marshpepper knotweed	A	H	MV
<i>Polygonum punctatum</i>	Dotted smartweed	A	H	MV, T
<i>Polygonum sagittatum</i>	Arrowleaf tearthumb	A	V	MV
<i>Pontedaria cordata</i>	Pickernelweed	P	H	MV, T
<i>Ranunculus abortivus</i>	Littleleaf buttercup	P	H	SS
<i>Rosa palustris</i>	Swamp rose	P	W	SS
<i>Rubus sp.</i>	Blackberry	P	W	SS
<i>Sagittaria latifolia</i>	Arrowhead	P	H	MV, Ph, T
<i>Sambucus canadensis</i>	American black elderberry	P	W	SS
<i>Schoenoplectus fluviatilis</i>	River bulrush	P	H	MV
<i>Schoenoplectus tabernaemontani</i>	Softstem bulrush	P	H	MV
<i>Sium suave</i>	Hemlock waterparsnip	P	H	MV, SS
<i>Smilax rotundifolia</i>	Greenbrier	P	H, W	SS
<i>Solidago sp.</i>	Goldenrod	P	H	MV
<i>Sparganium americanum</i>	American bur-reed	P	H	MV, SS
<i>Symphotrichum puniceum</i>	Purple stemmed aster	P	H	SS
<i>Symplocarpus foetidus</i>	Skunk cabbage	P	H	SS
<i>Thalictrum pubescens</i>	King of the meadow	P	H	SS
<i>Thelypteris palustris</i>	Eastern marsh fern	P	H	SS
<i>Toxicodendron radicans</i>	Poison ivy	P	V, W	SS

(continued)

Scientific name	Common name	Annual (A) or perennial (P)	Growth form	Community
<i>Typha</i> × <i>glauca</i>	Cattail hybrid	P	H	MV, T
<i>Vaccinium corymbosum</i>	Highbush blueberry	P	W	SS
<i>Viburnum dentatum</i>	Southern arrow-wood	P	W	SS
<i>Viola cucullata</i>	Swamp violet	P	H	SS
<i>Zizania aquatica</i>	Wild rice	A	H	MV, T, Z

The reference for species nomenclature is the USDA (2011) Plants Database

Wetland plant community codes: MV mixed vegetation, N *Nuphar*, Ph *Phragmites*, SS scrub-shrub, T *Typha*, Z *Zizania*. Growth form codes: H herbaceous, V vine, W woody

References

- Anderson, R.R., R.G. Brown, and R.D. Rappleye. 1968. Water quality and plant distribution along the upper Patuxent River, Maryland. *Chesapeake Science* 9: 145–156.
- Baden III, J., W.T. Batson, and R. Salter. 1975. Factors affecting the distribution of vegetation of abandoned rice fields, Georgetown, Co., South Carolina. *Castanea* 40: 171–184.
- Baldwin, A.H., M.S. Egnotovich, and E. Clarke. 2001. Hydrologic change and vegetation of tidal freshwater marshes: Field, greenhouse, and seed bank experiments. *Wetlands* 21: 519–531.
- Barendregt, A., P. Gloer, and F. Saris. 2009. Ecological consequences of a change in tidal amplitude in tidal freshwater wetlands. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 185–196. Leiden: Backhuys.
- Boesch, D.F. (ed.). 2008. *Global Warming and the Free State: Comprehensive Assessment of Climate Change Impacts on Maryland. Report of the Scientific and Technical Working Group of the Maryland Commission on Climate Change*. Cambridge: University of Maryland Center for Environmental Science.
- Boon, J.D., J.M. Brubaker, and D.R. Forrest. 2010. Chesapeake Bay Land Subsidence and Sea Level Change: An Evaluation of Past and Present Trends and Future Outlook. Report to the U.S. Army Corps of Engineers Norfolk District, VA. Special Report No. 425. Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Boynton, W.R., J. Hagy, J. Cornwell, W.M. Kemp, S. Greene, M. Owens, J. Baker, and R. Larsen. 2008. Nutrient budgets and management actions in the Patuxent River estuary, Maryland. *Estuaries and Coasts* 31: 623–651.
- Brinson, M.B., H.D. Bradshaw, and M.N. Jones. 1985. Transitions in forested wetlands along gradients of salinity and hydroperiod. *Journal of the Elisah Mitchell Scientific Society* 101: 76–84.
- Brown, K.J., and G.B. Pasternack. 2005. A paleoenvironmental reconstruction to aid in the restoration of floodplain and wetland habitats on an upper deltaic plain, California, USA. *Environmental Conservation* 32: 1–14.
- Casey, W.P., and K.C. Ewel. 2006. Patterns of succession in forested depressional wetlands in north Florida, USA. *Wetlands* 26: 147–160.
- Chesapeake Bay Program. 2011. CBP Water Quality Database (1984–present). http://www.chesapeakebay.net/data_waterquality.aspx. Accessed December 2011.
- Connors, L.M., E. Kiviat, P.M. Groffman, and R.S. Ostfeld. 2000. Muskrat (*Ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. *American Midland Naturalist* 143: 53–63.
- Cox, G.W. 1985. *Laboratory Manual of General Ecology*, 5th ed. Dubuque: Brown.
- Crain, C.M., B.R. Silliman, S.L. Bertness, and M.D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85: 2539–2549.
- Czerepko, J. 2008. A long-term study of successional dynamics in the forest wetlands. *Forest Ecology and Management* 255: 630–642.
- Field, R.T., and K.R. Philip. 2000. Vegetation changes in the freshwater tidal marsh of the Delaware estuary. *Wetlands Ecology and Management* 8: 79–88.
- Haramis, G.M., and G.D. Kearns. 2007. Herbivory by resident geese: The loss and recovery of wild rice along the tidal Patuxent River, Maryland. *Journal of Wildlife Management* 71: 788–794.
- Heinle, D.R., and D.A. Flemer. 1976. Flows of materials between poorly flooded tidal marshes and an estuary. *Marine Biology* 35: 359–373.
- Higinbotham, C.B., M. Alber, and A.G. Chalmers. 2004. Analysis of tidal marsh vegetation patterns in two Georgia estuaries using aerial photography and GIS. *Estuaries* 27: 670–683.
- Hilgartner, W.B., and G.S. Brush. 2006. Prehistoric habitat stability and post-settlement habitat change in a Chesapeake Bay freshwater tidal wetland, USA. *The Holocene* 16: 479–494.
- Jordan, T.E., and D.F. Whigham. 1988. The importance of standing dead shoots of the narrow leaved cattail—*Typha angustifolia*. *Aquatic Botany* 29: 310–319.
- Khan, H., and G. Brush. 1994. Nutrient and metal accumulation in a freshwater tidal marsh. *Estuaries* 17: 345–360.
- Kouki, J. 1993. Herbivory modifies the production of different leaf types in yellow water-lily, *Nuphar lutea* (Nymphaeaceae). *Functional Ecology* 7: 21–26.
- Krauss, K.W., and J.A. Duberstein. 2010. Sapflow and water use of freshwater wetland trees exposed to saltwater incursion in a tidally influenced South Carolina watershed. *Canadian Journal of Forest Research* 40: 525–535.
- Leck, M.A., and C.M. Crain. 2009. Northeastern North America case studies—New Jersey and New England. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D.F. Whigham, and A.H. Baldwin, 145–156. Leiden: Backhuys.
- Leck, M.A., and R.L. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *American Journal of Botany* 82: 1547–1557.
- Leck, M.A., A.H. Baldwin, V.T. Parker, L. Schile, and D.F. Whigham. 2009. Plant communities of tidal freshwater wetland of the continental USA and southeastern Canada. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D.F. Whigham, and A.H. Baldwin, 41–58. Leiden: Backhuys.
- Lynch, J.J., T. O'Neal, and D.W. Lay. 1947. Management significance of damage by geese and muskrats to gulf coast marshes. *Journal of Wildlife Management* 11: 50–76.
- McCormick, J., and H.A. Somes Jr. 1982. *The Coastal Wetlands of Maryland*. Chevy Chase: Jack McCormick & Associates, Inc.

- McCune, B., and M.J. Medford. 2006. PC-ORD. Multivariate analysis of ecological data, version 5.18. MJM software. Oregon: Glenden Beach.
- Meyerson, L.A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management* 8: 89–103.
- Neubauer, S.C., and C. Craft. 2009. Global change and tidal freshwater wetlands: Scenarios and impacts. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 353–366. Leiden: Backhuys.
- Neubauer, S.C., I.C. Anderson, J.A. Constantine, and S.A. Kuehl. 2002. Sediment deposition and accretion in a mid-Atlantic (U.S.A.) tidal freshwater marsh. *Estuarine Coastal and Shelf Science* 54: 713–727.
- National Oceanic and Atmospheric Administration (NOAA). 2012. Office of Ocean and Coastal Resource Management, National Estuarine Research Reserve System-wide Monitoring Program. Centralized Data Management Office, Baruch Marine Field Lab, University of South Carolina. <http://cdmo.baruch.sc.edu>. Accessed December 2011.
- Odum, W.E., T.J. Smith, J.K. Hoover, and C.C. McIvor. 1984. *The Ecology of Tidal Freshwater Marshes of the United States East Coast: A Community Profile*. Washington: U.S. Fish and Wildlife Service, FWS/OBS-83/17.
- Odum, W.E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecology and Systematics* 19: 147–176.
- Orson, R.A., R.L. Simpson, and R.E. Good. 1990. Rates of sediment accumulation in a tidal freshwater marsh. *Journal of Sedimentary Petrology* 60: 859–869.
- Orson, R.A., R.L. Simpson, and R.E. Good. 1992. The paleoecological development of a late Holocene, tidal freshwater marsh of the upper Delaware River Estuary. *Estuaries* 15: 130–146.
- Pasternack, G.B. 2009. Hydrogeomorphology and sedimentation in tidal freshwater wetlands. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 31–41. Leiden: Backhuys.
- Pasternack, G.B., and G.S. Brush. 1998. Sedimentation cycles in a river-mouth tidal freshwater marsh. *Estuaries* 21: 407–415.
- Pasternack, G.B., W.B. Hilgartner, and G.S. Brush. 2000. Biogeomorphology of an upper Chesapeake Bay river-mouth tidal freshwater marsh. *Wetlands* 20: 520–537.
- Pasternack, G.B., and G.S. Brush. 2001. Seasonal variations in sedimentation and organic content in five plant associations on a Chesapeake Bay tidal freshwater marsh. *Estuarine, Coastal and Shelf Science* 53: 93–106.
- Pasternack, G.B., and G.S. Brush. 2002. Biogeomorphic controls on sedimentation and substrate on a vegetated tidal freshwater delta in upper Chesapeake Bay. *Geomorphology* 43: 293–311.
- Perry, J.E., and C.H. Hershner. 1999. Temporal changes in the vegetation pattern in a tidal freshwater marsh. *Wetlands* 19: 90–99.
- Perry, J.E., D.M. Bilkovic, K.J. Havens, and C.H. Hershner. 2009. Tidal freshwater wetlands of the mid-Atlantic and southeastern United States. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 157–166. Leiden: Backhuys.
- Rheinhardt, R.D. 1992. Multivariate analysis of vegetation patterns in tidal freshwater swamps of lower Chesapeake Bay, USA. *Bulletin of the Torrey Botanical Club* 119: 193–208.
- Rice, D., J. Rooth, and J.C. Stevenson. 2000. Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. *Wetlands* 20: 280–299.
- Ricklefs, R.E. 1990. *Ecology*. New York: W.H. Freeman.
- Salter, R., and J. Baden. 1994. A twenty-year comparison of vegetation of three abandoned rice fields, Georgetown County, South Carolina. *Castanea* 59: 69–77.
- Scavia, D., J.C. Field, D.F. Boesch, R.W. Buddemeier, V. Burkett, D.R. Cayan, M. Fogarty, M.A. Harwell, R.W. Howarth, C. Mason, D.J. Reed, T.C. Royer, A.H. Sallenger, and J.G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25: 149–164.
- Schuyler, A.E., A.B. Anderson, and V.J. Kolaga. 1993. Plant zonation changes in the tidal portion of the Delaware River. *Proceedings of the Academy of Natural Sciences of Philadelphia* 144: 263–266.
- Scofield, C.S. 1905. The salt water limits of wild rice. US Department of Agriculture, Bureau of Plant Industry Bulletin No. 72.
- Sharpe, P.J., and A.H. Baldwin. 2009. Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. *Wetlands* 29: 225–235.
- Simpson, R.L., R.E. Good, M.A. Leck, and D.F. Whigham. 1983. The ecology of freshwater tidal wetlands. *BioScience* 34: 255–259.
- Smith, S.M., M. Hanley, and K.T. Killingbeck. 2008. Development of vegetation in dune slack wetlands of Cape Cod National Seashore (Massachusetts, USA). *Plant Ecology* 194: 243–256.
- Stribling, J.M., J.C. Cornwell, and O.A. Glahn. 2007. Microtopography in tidal marshes: Ecosystem engineering by vegetation? *Estuaries and Coasts* 30: 1007–1015.
- Stroh, C.L., D. De Steven, and G.R. Guntenspergen. 2008. Effect of climate fluctuations on long-term vegetation dynamics in Carolina Bay wetlands. *Wetlands* 28: 17–27.
- US Department of Agriculture (USDA). 2011. Plants database. <http://www.plants.usda.gov>. Accessed December 2011.
- US Geological Survey (USGS). 2011. USGS real-time water data for the nation. <http://waterdata.usgs.gov/usa/nwis/uv?01594440>. Accessed December 2011.
- Van den Bergh, E., A. Garniel, R.K.A. Morris, and A. Barendregt. 2009. Conservation of tidal freshwater wetlands in Europe. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 241–252. Leiden: Backhuys.
- Van der Valk, A.G. 1981. Succession in wetlands: A Gleasonian approach. *Ecology* 62: 688–696.
- Whigham, D.F., and R.L. Simpson. 1978. Nitrogen and phosphorus movement in a freshwater tidal wetland receiving sewage effluent. Proceedings of Coastal Zone '78 Symposium on Technological, Environmental, Socioeconomic, and Regulatory Aspects of Coastal Zone Management, Vol. III, American Society of Civil Engineering, New York, pp. 2189–2203.
- Whigham, D.F., A.H. Baldwin, and C.W. Swarth. 2009. Conservation of tidal freshwater wetlands in North America. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 267–270. Leiden: Backhuys.
- Zervas, C. 2001. Sea level variation of the United States, 1854–1999. Center for Operational Oceanographic Products and Services, National Ocean Service, National Oceanic and Atmospheric Administration, US Department of Commerce, Silver Spring, MD. NOAA Technical Report NOS CO-OPS 36, 66 pp.
- Zonneveld, I.S., and A. Barendregt. 2009. Human activities in European tidal freshwater wetlands. In *Tidal Freshwater Wetlands*, ed. A. Barendregt, D. Whigham, and A. Baldwin, 11–20. Leiden: Backhuys.