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BIOGEOMORPHOLOGY OF AN UPPER CHESAPEAKE BAY RIVER-MOUTH TIDAL FRESHWATER MARSH

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Abstract: Field mapping and monitoring of vegetation, sedimentation patterns, substrate characteristics, and geomorphology in the Bush River tributary to upper Chesapeake Bay has been conducted since 1991 to ascertain the process-morphology dynamics in a tidal freshwater marsh. Nine plant associations from 5 distinct marsh habitats were identified by clustering species abundance measurements from 115 quadrats throughout an 84-hectare area. High spatial variability in physical habitat conditions such as summer-average sediment deposition, summer-average organic content, and surface-sediment grain size distributions were explainable using combinations of independent variables, including elevation, plant distributions, and distances to the tidal inlet and an adjacent stream. Sedimentation and vegetation were both observed to show a predictable response to disturbance by animal activity.

Key Words: tidal freshwater wetlands; plant species distributions, geomorphology, hydrology, sedimentation, Chesapeake Bay

INTRODUCTION

Tidal freshwater marshes exist where watershed-derived sediment accumulates at the upstream boundary of an estuary (Orson et al. 1992, Pasternack and Brush 1998). The plant community structure of tidal freshwater marshes has been studied and compared with that of salt marshes (Good et al. 1978, Doumlele 1981, Simpson et al. 1983, Odum et al 1984, Odum 1988, Mitch and Gosselink 1993). Whereas salt marsh zones are strongly delineated by the presence or absence of species such as *Spartina alterniflora, Spartina patens,* and *Distichlis spicata* in response to duration of exposure to salt water (Davis 1910, Miller and Egler 1950, Smart and Barko 1978), tidal freshwater marshes consist of a gradient of ''plant associations'' (i.e., groups of species commonly found together) whose species composition and abundance shift in response to a combination of physical and biotic stresses (Odum et al. 1984, Parker and Leck 1985, Orson et al. 1992, Leck and Simpson 1995). For example, studies of Hamilton Marsh near Trenton, New Jersey, USA report significant zonation of seed, seedling, and mature plant densities, although individuals of some species occurred across several zones (Simpson et al. 1983, Parker and Leck 1985, Leck and Simpson 1987, Leck and Simpson 1994).

In contrast to plant community structure, little is known about processes contributing to formation and evolution of tidal freshwater marshes. Descriptions of physical conditions (e.g., Odum 1988, Orson et al. 1990, Orson et al. 1992), measurements of marsh channels (Myrick and Leopold 1963, Garofalo 1980), reconstructions of paleoecological and sedimentary conditions (Orson et al. 1990, Orson et al. 1992, Khan and Brush 1994, Hilgartner 1995), and sedimentation process studies (Serodes and Troude 1984, Pasternack and Brush 1998) have been conducted, but have not yielded predictive models of marsh function. In contrast, the hydrologic, sedimentary, and geomorphic dynamics of salt marshes have been thoroughly investigated (e.g., Redfield 1972, Stumpf 1983, Clark and Patterson 1985, Gardner et al. 1989, Stoddart et al. 1989, Childers and Day 1990, Swenson and Sasser 1992, Nydick et al. 1995, Haltiner et al. 1997).

The overall objective of this study was to use a combination of field monitoring and statistical analyses to ascertain the process-morphology interrelations in a tidal freshwater marsh, with particular attention to the role of plant associations in these dynamics. From a geomorphic perspective, landscape evolution results from interplay between transport processes and landform morphology. As changes are made to any one process or landform trait, there follows a mutual adjustment of all other processes and the landform itself (Leopold et al. 1964). As a result, there is a quantifiable balance between process and morphology. From a wetlands perspective, processes in marshes and the characteristics used to describe marsh morphology must include both biotic and abiotic elements, but the underlying concept of a balance between process and morphology is likely valid. An important consequence of such a balance is that there is no unidirectional cause-effect relationship between abiotic and biotic conditions in this view. Rather, each influences the other at the same time. This study aims to eludicate this dynamic interplay for the case of a tidal freshwater system.

Plant associations in intertidal marshes occur along an environmental gradient (Davis 1910, Miller and Egler 1950, Odum et al 1984, Mitsch and Gosselink 1993). Some studies have used elevation as a surrogate for this gradient and assessed plant community variability within and between elevation "bins" (e.g., Zedler 1977, Orson et al. 1992). Other studies have used ordination schemes (e.g., Curtis 1959, Gemborys and Hodgkins 1971, Robertson 1987) or a type of direct gradient analysis called "weighted averages" (e.g., Carter et al. 1988, Wentworth et al. 1988, Scott et al. 1989) to create indices that quantify transitions in species composition. We propose that the environmental gradient in a tidal freshwater marsh may be numerically approximated using an approach similar to "weighted averages" but using a tidal freshwater marsh-specific indexing scheme. This theoretical development provides a quantitative means for relating plants to physico-chemical parameters and thus facilitates study of marsh geomorphology and ultimately marsh restoration. Once quantified using the environmental gradient function, plant associations were combined with substrate characteristics, sedimentation rates, and marsh geomorphology to assess the spatial predictability of habitat conditions and sediment dynamics in tidal freshwater marshes.

STUDY LOCATION

The Otter Point Creek (OPC) component of Chesapeake Bay-MD National Estuarine Research Reserve is a 138.7-ha river-mouth tidal freshwater wetland at the head of Bush River in upper Chesapeake Bay (Figure 1). OPC consists of a 54.4-ha riparian forest, a 84-ha marsh, a 0.3-ha upland forest island, and an expansive subtidal front. An additional 3.8 ha of marsh and 1.4 ha of riparian forest are present in HaHa Branch

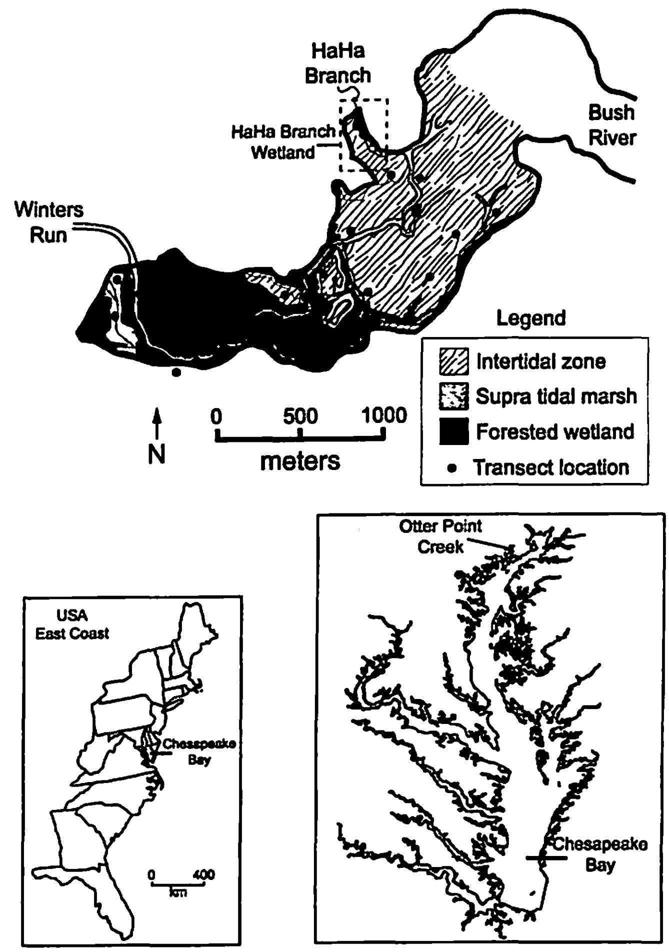

Figure 1. Map of OPC delta at the head of Bush River in upper Chesapeake Bay showing random locations of vegetation transects. Dot diameter equals transect length (50 m).

Wetland (HBW) at the mouth of a small basin adjacent to OPC. Water flow is primarily controlled by astronomical tides and meteorological forcing in the marsh areas and by runoff from the 150-km² Winters Run basin in the riparian forest. A detailed site description is available in Pasternack (1998).

Seasonal cycles of sedimentation and erosion in HBW were reported by Pasternack and Brush (1998). Two distinct sedimentation regimes were found. From late November to mid-March, deposition was found to be low (or even negative), with little variability between locations. From mid-March to late November, deposition varied by as much as 2.5 orders of magnitude between locations. This spatial variability was attributed to differences in plant community structure and dynamics based on the results of nonparametric statistical tests.

MATERIALS AND METHODS

To meet the study objective, plant associations in OPC had to be determined and their relationship to geomorphic conditions assessed. Vegetation was surveyed at a large number of locations within OPC to achieve the first need. Because assessment of geomorphic variables required regular sampling, monitoring, and laboratory analyses, fewer sites could be used. Also, independent monitoring sites from an ecologically equivalent marsh were needed to test the applicability of the habitat index algorithm developed using OPC vegetation data. Given these constraints, the second need was met by monitoring marsh vegetation, biweekly sedimentation, surface-sediment characteristics, and marsh geomorphology in adjacent HBW. Specific procedures are described below.

Vegetation Sampling in Both Wetlands

Herbaceous vegetation in the intertidal and supratidal marshes at OPC was surveyed in 1991–1992 in 115 1-m^2 quadrats at 5-m intervals along randomly located, 50-m-long belt transects (Figure 1). Percent cover of herbaceous plants and saplings was determined by counting leaf cover for each species within each square decimeter of a 1-m^2 quadrat (Mueller-Dombois and Ellenberg 1974). With different layers in the vegetation, total cover could exceed 100%. Relative percent cover was calculated by dividing the percent cover for each species by the total percent cover of all plants in a quadrat. No trees were observed in or near any of the quadrats. All vegetation data are reported in Hilgartner (1995), available upon request. Taxonomy follows Fernald (1970), except *Microstegium vimineum* from Hitchcock and Chase (1950) and *Phragmites australis* from Tiner and Burke (1995).

Twenty-three monitoring sites were uniformly distributed along 2 transverse and 2 longitudinal transects randomly located in HBW (Figure 2). Vegetation within a 1-m^2 quadrat at each site was assessed at the beginning of the study in July 1995 and once again in late summer 1996 using the same procedure described for OPC.

HBW Biweekly Sediment Sampling

Several methods for monitoring sedimentation exist (e.g., Serodes and Troude 1984, Reed 1989, Boumans and Day 1993), but few can handle highly variable deposition rates and yield samples for analysis. The approach and data used here were reported by Pasternack and Brush (1998) in a complimentary study of sedimentation cycles. Lightweight 1.22-m × 2.5-cm-diameter rods were sunk into the ground and capped with detachable 20 × 20 cm ceramic tiles flush with the marsh surface. The detachment mechanism for a tile involved gluing a 5-cm-long acrylic tube with a 2.5-cm inner diameter to a tile's underside. The ceram-

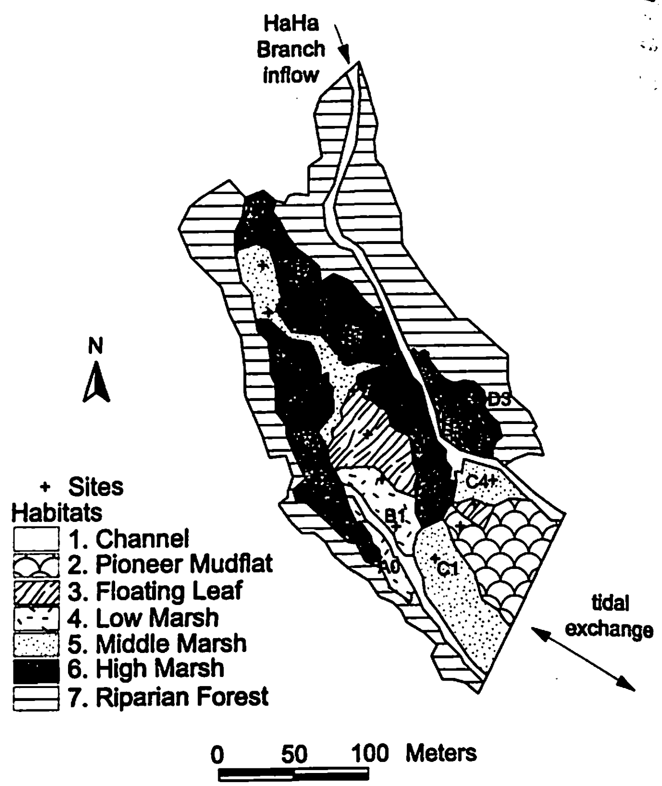

Figure 2. Map of HBW showing tidal freshwater wetland habitats and study sites (+).

ic tile/acrylic tube assembly dropped over the anchor rod.

Biweekly sedimentation and erosion were monitored from July 1995 to March 1997 at the same 23 sites where vegetation was surveyed. Accumulated sediments were scraped into pre-washed, pre-weighed glass jars biweekly during low tide. Procedures for obtaining net sedimentation and organic content were described by Pasternack and Brush (1998). Dry weights per tile were annualized (g cm^{-2} yr^{-1}) to facilitate comparison with other studies. Organic content is reported as percent loss-on-ignition.

HBW Surface Sediment Characterization

Surface samples from the 23 sites were collected to measure bulk density and determine grain-size distributions. Wet bulk density samples were collected by coring the marsh surface with a 26-ml acrylic tube. Samples were transferred to pre-weighed bags and weighed. Sample weight divided by 26 yielded the bulk density in g ml^{-1}.

Surface samples for grain-size analysis were collected with a hand shovel, transferred to bags, and stored in a refrigerator at 4° C. When collecting samples with the shovel, care was taken to sample only the top 3 cm of the soil profile. The grain-size distribution of each sample was determined using the method of Folk (1974), with the additional step of removing organics by adding 30% H_2O_2 to a sample (e.g., Black 1965), stirring for 20–30 minutes in a fume hood until degassing slowed, and leaving the solution to react completely over 24 hours.

HBW Geomorphic Characterization

Field surveys with Global Positioning System units were used to locate sites and delineate boundaries in HBW. The State Plane Zone 1900 coordinates (m) and the NAVD88 vertical elevations (m) for each site were obtained by field surveying carried out by the Geodetic Measurements Section personnel from nearby United States Army Aberdeen Proving Ground using a survey-grade Trimble• real time kinematic Global Positioning System approach (vertical precision of ±1–3 cm). HBW habitats (as defined by statistical procedure discussed below) were delineated by walking along boundaries with a hand-held MC-GPS• differential Global Positioning System unit (horizontal precision of ±1 m after post-processing).

A Geographical Information System (GIS) of HBW constructed with Arc/Info• (Environmental Systems Research Institute, Inc. (Redlands, California)) was used to calculate geomorphic parameters. The base layer was an April 1994 color infrared digital orthophoto (1.2-m resolution) obtained from the Maryland Department of Natural Resources. Distance to the nearest marsh channel (m), distance to the HaHa Branch stream (m), and distance to the tidal inlet (m) were calculated using the GIS. The Thiessen polygon method (Bedient and Huber 1992) was used to delineate the area within each habitat represented by each sampling station. Because there were only 23 sites within a 4-ha area, advanced geostatistics and GIS analysis procedures were unwarranted. GIS modeling would be premature given the current lack of understanding of the physical processes in tidal freshwater marshes.

STATISTICAL ANALYSES

Three statistical procedures were used in this study. First, multivariate cluster analysis was used to determine how plant species and their abundance were organized at OPC. This step yielded the categorization required for the weighted averages approach (Whittaker 1978). Second, an ordination algorithm was developed to transform vegetation data from an environmental gradient into an index of gradient position. Third, the significance of the derived index in relation to the geomorphology of HBW was tested.

Cluster Analysis

Cluster analysis is an individual-oriented multivariate technique for grouping individuals based on shared characteristics. The primary benefit of cluster analysis is that it does not require normally distributed or pre-conditioned data (Brown 1998). Other methods such as factor analysis, canonical correlation analysis, analysis of variance, and multiple discriminant analysis could not be used with this data set because the data do not fit their assumptions. Cluster analysis has been used to assess the community structure of many wetland types (Mitsch and Gosselink 1993), notably salt marshes (Kortekaas et al. 1976, Zedler 1977). In the analysis by Zedler (1977), only presence or absence was considered, which is appropriate for salt marshes. However, several investigators have shown that abundance must be used in characterizing tidal freshwater marshes (Parker and Leck 1985, Leck and Simpson 1987, Leck and Simpson 1994).

To ascertain the OPC plant associations, quadrats were clustered based on species' relative percent covers. A hierarchical "single linkage" algorithm was used (Hair et al. 1992). In this algorithm, a nearest neighbor criterion was applied to quadrat data to form clusters based on the Euclidean distance between quadrats in n-variable space, where each variable is a species' relative percent cover (0–100) and n is the number of species in the analysis.

Many plant species typically occur in only a few quadrats and in low absolute percent covers. The occurrence of species i in a low abundance in just a few quadrats would result in a cluster of a few points in that i^{th} dimension. Such a mathematical construct would have no ecological meaning. Misclassifications of this type were discussed by Zedler (1977). As a result, an analysis was performed to determine which observed species should be used as variables in clustering. This analysis involved assessing the probability distribution of the maximum percent cover of each species observed in the marsh. When the distribution is plotted cumulatively, a significant change in the slope of the function, if present at all, indicates a delineation between (high percent cover) dominant and (low percent cover) uncommon species. This method delineates plant associations by dominant species and is consistent with known distributions of species in coastal marshes in general (Chabreck 1972) and tidal freshwater marshes in particular (Simpson et al 1983, Odum et al. 1984). Even though the approach delineates by dominants, the structure of resulting associations can be analyzed to determine which uncommon species are indicative of associations.

Once the matrix of absolute percent covers for OPC marsh quadrats was reduced to dominant species and the relative percent covers of these species calculated, Statistica® v.98 by StatSoft (Tulsa, Oklahoma) was used for clustering. After quadrats were clustered, the complete matrix of species abundance for each quadrat was restored, thereby incorporating uncommon species into objective clusters. Cluster-average relative percent cover of each species was calculated by summing a species' absolute percent cover from all quadrats in a cluster and dividing by the sum of the total percent cover for all species in that cluster.

Parameterization of the Environmental Gradient

Because a tidal freshwater marsh plant association is characterized by a set of species and their abundance, there is no direct means for quantitatively relating it to individual physical variables such as elevation and substrate. To overcome this problem, we hypothesized that the environmental gradient in tidal freshwater marsh plant associations could be numerically approximated using an ordination scheme. This approach is a type of direct gradient analysis (Whittaker 1978), and it has been used in the past to create indices that quantify wetland-upland transitions (Carter et al. 1988, Wentworth et al. 1988, Scott et al. 1989).

The best choice for a mathematical function to approximate an environmental gradient based on plant associations is a linear function. First, many mathematical functions are transformable into linear functions and vice versa, so using a linear function can capture the dynamics inherent in the widest array of non-linear processes. Second, deviations from linearity and their statistical significances are quantifiable. Third, the local slope of a line is independent of values on the line, so the definition of the scale of the function is irrelevant.

Starting with a linear function for the environmental gradient in a tidal freshwater marsh, plant associations must be positioned relative to one another along the gradient line. The relative positions of plant associations must be assumed initially, but the marsh ecology literature provides strong evidence for what those positions should be. For example, Odum et al. (1984) documented and illustrated the relative positions of individual plant species with respect to open water, low marsh, high marsh, and wooded swamp habitats. If the postulated relative positions are wrong, then geomorphic data such as elevation will not show quantitative trends with respect to the hypothesized plant gradient. Unlike relative positions, the actual position values are irrelevant, except that some agreed-upon scale must be chosen. Such ordinations are frequently adopted in science. The scale proposed here is to assign each plant association that exists at a different gradient position a number beginning with 1 = open water, 2 = pioneer mudflat, and ascending through 3, 4, 5, etc. as needed (e.g., Table 1). Note that two or more plant associations may occur at the same gradient position, which means that they conform to the same physical and chemical milieu but are different in terms of their plant species composition because of community dynamics such as competition, predation, and reproduction strategies.

Given a linear environmental gradient and the relative positions of plant associations, the position of individual plant species must be determined. A species occurring in only one association shows no distribution along the gradient, by definition, and thus takes on the position value assigned to its association. However, many species likely show a distribution among associations, as has been shown for other systems (Curtis 1959, Gemborys and Hodgkins 1971). For such a species, its distribution is obtained by dividing its cluster-average relative abundance in each association by the sum of cluster-average relative abundance for all associations:

$$DPDV_{ia} = \left(\frac{c_a}{T}\right)_i \tag{1}$$

where $DPDV_{ia}$ is the discrete probability density value for species i in plant association a, c_a is the percent cover of species i in plant association a, and T is the total percent cover for species i in all plant associations. Because the positions of plant associations along the environmental gradient have been numerically approximated, it is possible to quantitatively assess the distribution of $DPDV_{ih}$ for each plant species. For example, is the distribution normal, uniform, exponential, etc.? Also, mean, standard deviation, or other relevant distribution parameters may be determined. This information provides insight into the ecology of individual species and marsh species overall. For example, uniformly distributed species have the widest tolerance to environmental conditions and are not useful for delineating marsh zones.

Given the distribution of a plant species in the numerical terms of equation (1), the expected or preferred position of a species is given by the mean of its distribution:

$$PP_i = \sum_{a=1}^{a_{max}} (a \cdot DPDV_{ia}) \tag{2}$$

where PP_i is the preferred position for species i, a is the gradient position value, and a_{max} is the position value assigned to the plant association at the top of the environmental gradient.

Once a database of expected gradient positions of all plant species is generated, it is possible to quantify

Table 1. The distribution of habitats along the hypothesized environmental gradient at Otter Point Creek. Habitats may have multiple plant associations, which are indicated by the presence of the dominant species named below.

Habitat	Gradient Position	Plant Associations
Subtidal front	1	none
Pioneer mudflat	2	none
Floating leaf	3	*Nuphar advena*
Low marsh	4	*Peltandra virginica*
	4	*Zizania aquatica*
Middle marsh	5	*Leersia oryzoides-Eleocharis ambigens*
	5	*Typha angustifolia*
High marsh	6	*Acorus calamus*
Shrub marsh	7	*Polygonum sagittatum*
	7	*Typha latifolia*
	7	Levee/Shrub

the gradient position of any actual marsh site. To do this, the observed relative percent cover of each species in a quadrat is multiplied by the corresponding PP_i, and then the values for all species are summed, yielding the "habitat index." Rounding this to the nearest whole number gives the "designated habitat type," which can be a useful simplification.

Test of the Significance of the Habitat Index

If the habitat index and the underlying hypothesized linear environmental gradient are indicative of real processes, then they should demonstrate strong relations with marsh structure and function. To test this, habitat indices were calculated for HBW sites and correlated with elevation. If a strong relation exists between the constructed variable (habitat index) and the independent variable (elevation), then the proposed environmental gradient theory is validated.

Once the basic validity of the habitat index for this system was tested, the habitat index was used with other variables to explore functional relationships in HBW. Stepwise multiple regression and associated statistical tests were performed with Statistica v. 98 to determine which variables control the spatial distribution of sedimentation rate, bulk density, organic content, and grain-size parameters. In each analysis, a forward stepwise scheme was used, with all orderings of variables examined. Independent variables were checked for statistical significance with respect to their predictability of the dependent variable, including potential redundancy where independent variables were themselves interrelated. When independent variables were standardized before regression, resulting parameters showed the relative contribution of each. The F-value and resulting p-value were used as an overall F test of the relationship between the dependent variable and independent variables (Lindeman et al. 1980). The Durbin-Watson statistic was used to check the assumption that the data consist of a random sample of independent observations (Brown 1998). The probability distribution of residuals was checked to test the normality assumption inherent in multiple regression analysis. Any data points whose residuals were more than 2 standard deviations from their expected values were identified.

RESULTS

Cluster Analysis

Sixty-eight plant taxa were recorded in 115 quadrats at OPC, and of those, 58 were identified. The 10 unidentified species were uncommon and only encountered a few times. The cumulative distribution function of the maximum percent cover of plant species was found to have a factor of 10 slope break at 35% (Figure 3). The only other significant slope breaks occurred at the tails of the distribution, which means they are of no use for delineating dominant from uncommon species. The fifteen species with a maximum percent cover of 35% or greater were used for clustering the OPC marsh vegetation. Those species were *Acorus calamus, Amphicarpa bracteata, Carex scoparia, Eleocharis ambigens, Impatiens capensis, Leersia oryzoides, Lysimachia nummularia, Nuphar advena, Peltandra virginica, Polygonum arifolium, Polygonum sagittatum, Saururus cernuus, Typha angustifolia, Typha latifolia,* and *Zizania aquatica.*

The hierarchical cluster diagram showed distinct groupings of quadrats (Figure 4). Quadrats with identical species composition and abundance had linkage distances equal to zero, so no lines are shown. Comparing the diagram to raw data, the basis for a cluster was the presence of a high abundance species, as expected. In the few cases when a quadrat had nearly equal cover of 2 or more dominant species, the algorithm did a poor job of grouping it. This problem was

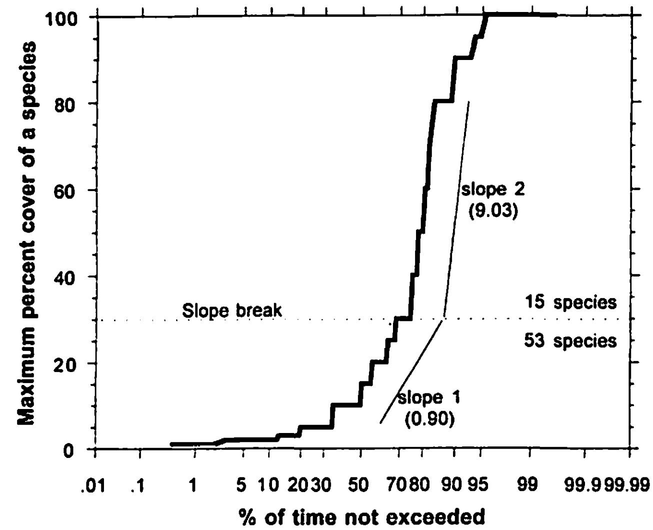

Figure 3. Cumulative distribution function of the maximum percent cover of each species among all vegetation quadrats showing an order of magnitude slope break at 35%, above which only 15 out of 68 species were present.

resolved by looking at the full array of species present in such a quadrat and placing it in the appropriate cluster manually. For example, quadrat 45 had 30% *Polygonum arifolium,* 30% *Carex scoparia,* 24% *Peltandra virginia,* 12% *Typha angustifolia,* and 4% *Nuphar advena.* This unusual mix of low and high marsh species resulted from a quadrat overlapping a levee and a channel, with some dry levee species and some flooded channel species. Looking at the whole array of species present in that quadrat revealed that a tree sapling (*Fraxinus pennsylvanica*) was present along with several other flood-intolerant species in very low abundance. These facts suggested that the quadrat be placed into a cluster with others representative of levees and not in one dominated by *Typha angustifolia,* where it was placed by the cluster analysis.

Nine plant associations were identified based on the cluster analysis (Figure 5). Seven associations included a single dominant species together with several low abundance taxa. For example, cluster 1 had *Nuphar advena* comprising 88 relative percent cover and the next closest species 4.17. Two associations showed lesser dominance by a single species. Cluster 5 was composed of *Leersia oryzoides* (37.63) and *Eleocharis*

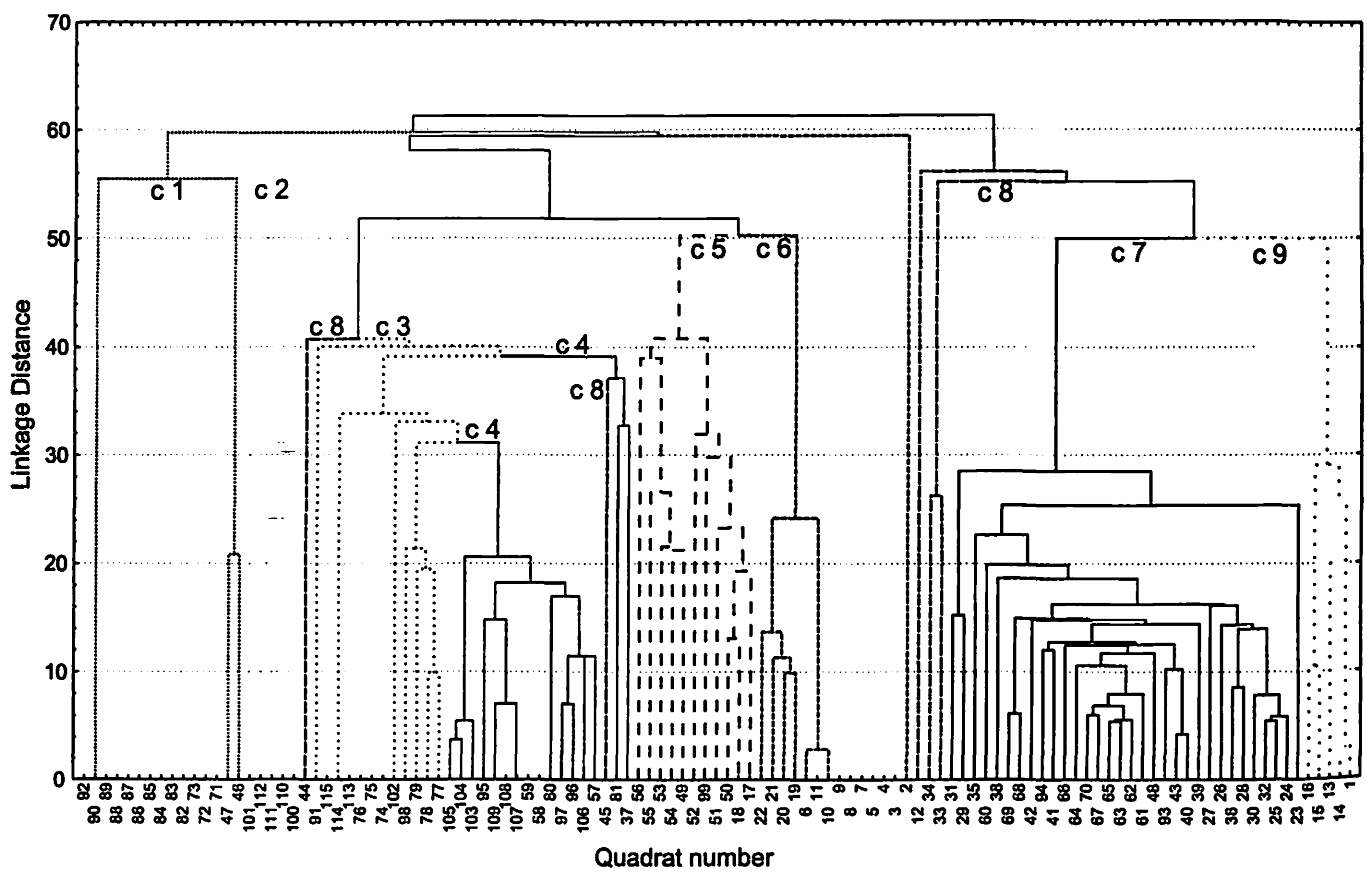

Figure 4. Hierarchical cluster diagram showing commonalities among 115 Otter Point Creek marsh quadrats based on the observed abundance of 15 dominant species. Dash-dot pattern and shading indicate which quadrats (1–115) fall in which clusters (1–9 as described in text).

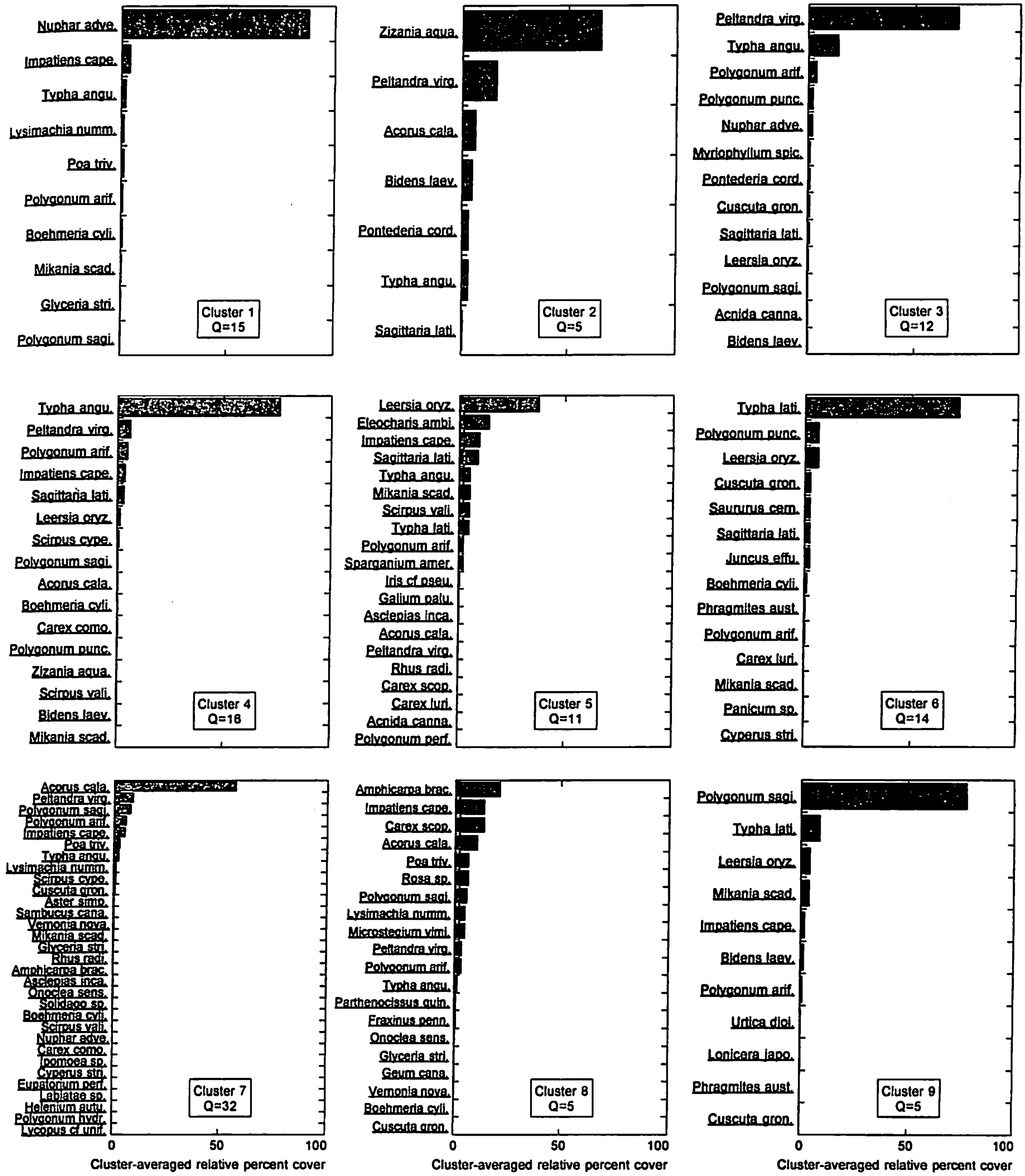

Figure 5. Species distributions for each plant association. Q is the number of quadrats available to characterize each cluster after a randomized field survey.

ambigens (14.21), with secondary species including *Impatiens capensis* (9.75) and *Sagittaria latifolia* (9.06). Cluster 8 had *Amphicarpa bracteata* (21.10) associated with comparable abundance of *Impatiens capensis* (13.80), *Carex scoparia* (13.80), and *Acorus calamus* (10.55). Based on species dominance observed in each cluster, the plant associations may be called 1. *Nuphar advena*, 2. *Zizania aquatica*, 3. *Peltandra virginicia*, 4. *Typha angustifolia*, 5. *Leersia oryzoides—Eleocharis ambigens*, 6. *Typha latifolia*, 7. *Acorus calamus*, 8. Levee/shrub, and 9. *Polygonum sagittatum*.

Environmental Gradient

The relative position of plant associations along the tidal freshwater marsh environmental gradient in OPC was assessed by comparing cluster analysis results to past research on tidal freshwater marshes. For example, it is widely recognized (and easy to see in the field) that the *Nuphar advena* association (cluster 1) is the most flood-tolerant. Consequently, it was put at the bottom of the gradient. The *Zizania aquatica* (cluster 2) and *Peltandra virginica* (cluster 3) associations are often characterized as "low marsh" indicators, so these were grouped together and placed at the next position. Similarly, the *Typha angustifolia* (cluster 4) and *Leersia oryzoides—Eleocharis ambigens* (cluster 5) associations were grouped and placed at the next higher position along the gradient. The *Acorus calamus* (cluster 7) association is less frequently flooded, so it was put at the second highest position. Finally, the remaining three associations were grouped at the highest position because cluster 8 represents levees, while clusters 6 and 9 were entirely composed of sites from the supratidal area at the upstream end of OPC (Figure 1).

Commonly in wetland science, names of marsh zones are simplified from species names to gradient-oriented terms, such as "high marsh." The groupings of plant associations along the environmental gradient suggested that each be considered a marsh habitat and termed appropriately. The terminology chosen here along with the corresponding gradient position number is given in Table 1. Even though little to no vegetation is present in the subtidal front and intertidal pioneer mudflats in OPC, these regions have geomorphic significance and are included for completeness. The above assignment of plant associations to gradient positions may seem somewhat arbitrary to those not familiar with tidal freshwater marshes, but the independent HBW data presented below objectively test the existence of a gradient.

Equation (1) was used to calculate the distribution of each plant species (Table 2). Strong habitat preferences were evident for most species (Figure 6). Twenty-seven of 58 taxa (46.6%) were restricted to 1 of 5 habitats. Only 4 species (7%) *Boehmerica cylindrica, Glyceria striata, Impatiens capensis*, and *Polygonum arifolium* had all *DPDV* values less than 0.5. While some studies have reported individuals of many species in many habitats, OPC data shows that almost all (93%) of river-mouth tidal freshwater marsh plant species sampled occurred primarily in a single habitat (i.e., one $DPDV > 0.5$). Presence in other habitats may occur, but when the full array of species found at a location is considered, the small abundance of a few widespread species are outweighed by the great abundance of habitat-specific species.

Equation (2) was used to calculate species' preferred positions along the environmental gradient at OPC (Table 2). The 27 species without distributions (i.e., one DPDV = 1) were perfect indicators of their respective habitats. Of the remaining 31 species, 21 (68%) had their highest *DPDV* in their preferred position, when the position was rounded to the nearest whole number for comparison. The 10 species whose preferred positions were inconsistent with their maximum *DPDV* had polymodal distributions. For example, the distribution of *Boehmerica cylindrica*, an uncommon but widely distributed species, was 0.00–0.00–0.30–0.00–0.19–0.05–0.46. On average, this species indicated a habitat of 5.38, which is between middle marsh and high marsh. While the average was not a strong indicator of habitat in this case, it must be remembered that the habitat index for a site is the sum of all species' preferred positions, with each weighted by its observed relative abundance. Consequently, the impact of a few polymodal species, especially uncommon ones, will be minimal for the majority of actual field sites. Sites dominated by polymodal species may not be accurately characterized by equation (2).

Characterization of Environmental Gradient at HBW

Once underlying distributions of species' populations among different habitats at OPC were determined, they were used along with observed species' abundance to characterize HBW study sites (Table 3). Out of the 23 locations surveyed in HBW, 13 were found to be high marsh, 4 were middle marsh, 2 were low marsh, 3 were floating leaf habitat, and 1 was a pioneer mudflat (Figure 2). The pioneer mudflat at station C2 had a few stalks of *Peltandra virginica* colonizing in the adjacent quadrat, so the relative percent cover for that species was high even though its absolute percent cover was low.

The elevations at HBW averaged −2 cm and ranged from −27 to 25 cm. Remarkably, the 5 habitats span a mere 52 cm vertical range. A strong relationship between habitat index and elevation ($r^2 = 0.83$) was found (Figure 7). Compared to their standard errors, the terms in the polynomial model are significant above the 99.8% confidence level. The strong correlation and high significances of model parameters validate the environmental gradient algorithm.

Because sedimentation occurred in seasonal cycles that coincided with the seasonal cycle of plant growth, sedimentation should only relate to the habitat index characterizing plant associations when plants were present, which was during summer. Summer-average (June–September) HBW sedimentation rates ranged from 0.01 to 22.5 g cm^{-2} yr^{-1} (Figure 8). Divided by the bulk density of surface sediment at each site, these quantities yield vertical accretion rates of 0.15–23.8 cm yr^{-1}, which are high for emergent marshes, although these data exclude erosional winter periods that lower the long-term average.

Sedimentation from July through November 1995 was plotted as a function of station habitat index to see if the habitat index alone revealed important sediment dynamics. A strong exponential decay was evident (Figure 9a). Lower rates of sedimentation in the high marsh than in the low marsh have been observed elsewhere, but the degree to which the species-based habitat index can predict the gradient in sedimentation over a wide range of habitats shows the close relationship between sediment dynamics and species abundance.

Stepwise multiple regression showed which variables controlled the spatial distribution of summer-average sedimentation rates. Elevation (m), distance to tidal inlet (m), habitat index, distance to the HaHa Branch stream (m), and distance to nearest tidal channel (m) were included as independent variables. Because elevation explains 83% of the variability in habitat index, statistical redundancy between these variables was checked. The logarithm of summer-average sedimentation rate was used as the dependent variable, as the data span 3–4 orders of magnitude. Of the independent variables, elevation, habitat index, and inlet distance were statistically significant above the 99% confidence level (Table 4). Sedimentation rate was found to decrease with increasing elevation, habitat index, and inlet distance (Figure 10a). These variables explained 92% of the spatial variability in summer sedimentation, with nearly equal roles for topography and plant association (Table 4). Hydraulics and sediment transport, as indicated by distance from tidal inlet, played a lesser role. The three statistical tests described in the methods showed the multivariate relationship to be statistically significant and in accordance with the key assumptions of the analysis methodology (Table 5).

Identical analyses were performed for bulk density, summer-average organic content, and parameters of grain-size distributions. Spatial variations in bulk density were random. For the logarithm of summer-average organic content, elevation and distance to tidal inlet were statistically significant ($p < 0.01$), while habitat index ($p = 0.073$) was not significant (Table 4). Organic content increased with elevation and distance from tidal inlet (Figure 10b). These two explained 90% of the spatial variability, with elevation accounting for the majority (Table 4). Again, statistical tests indicate that the analysis is statistically significant and in accordance with key assumptions. The residual for site B7 was greater than 2 standard deviations from the expected value, so the conditions at that site will be discussed further below.

Two grain-size parameters were studied to assess transport processes. Percent clay was selected to indicate extremes in energy conditions; a low % clay indicated a high energy regime capable of transporting sand, while a high % clay indicated a low energy regime. Percent silt was analyzed to capture the influence of moderate energy events related to wind-enhanced high tides. Tables 4 and 5 summarize the results. Only one variable, distance to HaHa Branch stream, controlled the variation in clay (Figure 10c). Meanwhile, % silt decreased with increasing distance to HaHa Branch and habitat index; it increased with inlet distance (Figure 10d). These results indicate that the primary source of sand for the marsh is the adjacent stream, and some of that sand may be redistributed around the front of the system to the tidal inlet leading to the marsh interior. Interestingly, the main stand of *Phragmites australis* occurred where there was the second lowest % clay (21.03%) and second highest % sand (40%). Residuals were within 2 standard deviations of expected values, except those for sites C2 and D3. C2 received less clay and more sand than expected from its distance to HaHa Branch. C2 was the pioneer mudflat site, and it received sand that was tidally transported around the front of the system. The source of that sand was most likely sand splay deposits where HaHa Branch makes a 90-degree turn to the east. D3 was relatively close to the stream, but it was a high marsh site protected behind the stream's natural levee, so it only received tidally transported fine sediment. Because sand availability is governed by the relative magnitude of streamflow from the HaHa Branch basin, sand distribution is independent of *in situ* marsh biogeomorphology. Meanwhile, silt is readily available and transportable, so its distribution is affected by local hydraulic processes and biotic factors.

Table 2. Tidal freshwater plant species' population distributions among habitats. The mean of a distribution is the species' preferred position.

Species (Latin Name)	Discrete Probability Density Values					Species Preferred Position
	FL[a]	LM[a]	MM[a]	HM[a]	SM[a]	
Acnida cannabina L.	0.00	0.78	0.22	0.00	0.00	4.22
Acorus calamus L.	0.00	0.09	0.01	0.76	0.14	5.95
Amphicarpa bracteata L.	0.00	0.00	0.00	0.02	0.98	6.98
Asclepias incarnata L.	0.00	0.00	0.68	0.32	0.00	5.32
Aster simplex Willd.	0.00	0.00	0.00	1.00	0.00	6.00
Bidens laevis L.	0.00	0.74	0.04	0.00	0.21	4.69
Boehmeria cylindrica L.	0.30	0.00	0.19	0.05	0.46	5.38
Carex comosa Boott	0.00	0.00	0.84	0.16	0.00	5.16
Carex lurida Wahlenb.	0.00	0.00	0.33	0.00	0.67	6.35
Carex scoparia Schkuhr	0.00	0.00	0.01	0.00	0.99	6.98
Cuscuta gronovii Willd.	0.00	0.21	0.00	0.16	0.62	6.19
Cyperus strigosus L.	0.00	0.00	0.00	0.35	0.65	6.65
Eleocharis ambigens Fern.	0.00	0.00	1.00	0.00	0.00	5.00
Eupatorium perfoliatum L.	0.00	0.00	0.00	1.00	0.00	6.00
Fraxinus pennsylvanica Marsh.	0.00	0.00	0.00	0.00	1.00	7.00
Galium palustre L.	0.00	0.00	1.00	0.00	0.00	5.00
Geum canadense Jacq.	0.00	0.00	0.00	0.00	1.00	7.00
Glyceria striata Lam.	0.31	0.00	0.00	0.29	0.40	5.48
Helenium autumnale L.	0.00	0.00	0.00	1.00	0.00	6.00
Impatiens capensis Meerb.	0.11	0.00	0.35	0.14	0.40	5.73
Ipomoea sp. L.	0.00	0.00	0.00	1.00	0.00	6.00
Iris cf *pseudacorus* L.	0.00	0.00	1.00	0.00	0.00	5.00
Juncus effusus L.	0.00	0.00	0.00	0.00	1.00	7.00
Labiatae sp. L.	0.00	0.00	0.00	1.00	0.00	6.00
Leersia oryzoides Willd.	0.00	0.02	0.92	0.00	0.06	5.10
Lonicera japonica Thunb.	0.00	0.00	0.00	0.00	1.00	7.00
Lycopus cf *uniflorus* Michx.	0.00	0.00	0.00	1.00	0.00	6.00
Lysimachia nummularia L.	0.18	0.00	0.00	0.18	0.64	6.09
Mikania scandens L.	0.04	0.00	0.52	0.04	0.40	5.75
Microstegium vimineum Trin.	0.00	0.00	0.00	0.00	1.00	7.00
Myriophyllum spicatum L.	0.00	1.00	0.00	0.00	0.00	4.00
Nuphar advena Ait.	0.97	0.02	0.00	0.00	0.00	3.03
Onoclea sensibilis L.	0.00	0.00	0.00	0.32	0.68	6.68
Panicum sp. L.	0.00	0.00	0.00	0.00	1.00	7.00
Parthenocissus quinquefolia L.	0.00	0.00	0.00	0.00	1.00	7.00
Peltandra viginica L.	0.00	0.82	0.06	0.09	0.03	4.33
Phragmites autralis Trin.	0.00	0.00	0.00	0.00	1.00	7.00
Poa trivialis L.	0.13	0.00	0.00	0.28	0.59	6.21
Polygonum arifolium L.	0.04	0.17	0.32	0.25	0.22	5.44
Polygonum hydropiperoides Michx.	0.00	0.00	0.00	1.00	0.00	6.00
Polygonum perfoliatum L.	0.00	0.00	1.00	0.00	0.00	5.00
Polygonum punctatum Ell.	0.00	0.26	0.04	0.00	0.70	6.13
Polygonum sagittatum L.	0.00	0.01	0.01	0.08	0.90	6.87
Pontederia cordata L.	0.00	1.00	0.00	0.00	0.00	4.00
Rhus radicans L.	0.00	0.00	0.53	0.47	0.00	5.47
Rosa sp. L.	0.00	0.00	0.00	0.00	1.00	7.00
Sagittaria latifolia Willd.	0.00	0.11	0.73	0.00	0.16	5.22
Sambucus canadensis L.	0.00	0.00	0.00	1.00	0.00	6.00
Saururus cernuus L.	0.00	0.00	0.00	0.00	1.00	7.00
Scirpus cyperinus L.	0.00	0.00	0.40	0.60	0.00	5.60
Scirpus validus Vahl.	0.00	0.00	0.98	0.02	0.00	5.02
Solidago sp. L.	0.00	0.00	0.00	1.00	0.00	6.00

Table 2. Continued.

Species (Latin Name)	Discrete Probability Density Values FL[a]	LM[a]	MM[a]	HM[a]	SM[a]	Species Preferred Position
Sparganium americanum Nutt.	0.00	0.00	1.00	0.00	0.00	5.00
Typha angustifolia L.	0.02	0.16	0.78	0.03	0.02	4.85
Typha latifolia L.	0.00	0.00	0.06	0.00	0.94	6.88
Urtica dioica L.	0.00	0.00	0.00	0.00	1.00	7.00
Vernonia novaboracensis L.	0.00	0.00	0.00	0.59	0.41	6.41
Zizania aquatica L.	0.00	1.00	0.00	0.00	0.00	4.00

[a] FL = floating leaf, LM = low marsh, MM = middle marsh, HM = high marsh, SM = shrub marsh.

Biogeomorphic Feedbacks

Because HBW has an uneven distribution of habitats, Figure 9a is preferentially influenced by the few points from the pioneer mudflat and floating leaf habitats. Nevertheless, the habitat index shows important biogeomorphic feedback processes that are not evident when deposition is plotted against elevation. For example, the vicinity of site A6 was disturbed by beaver activity in autumn 1995. The activity consisted of plant uprooting, surface mixing, and channel maintenance. According to Figure 9a, the resulting decrease in elevation, increase in flooding depth and duration, and increase in sediment accumulation should cause a switch from middle to low marsh. In late spring 1996, such a transformation was evident in the high percent cover of *Peltandra virginica* and *Orontium aquaticum*.

Another interesting habitat dynamic was illustrated by site B7. B7 received four to seven times less sediment than expected from its habitat index and elevation. B7 is far from the beaver channel network that directs flow inland beyond station A6 (Figure 2). It may be that, by the time flood waters reach B7, all but the finest suspended sediments have already settled out, leaving the site incapable of accreting under normal conditions. Thus, B7 has physically stabilized to the point where species interactions should be the driving mechanism for succession in that vicinity.

To test the robustness of the statistical relationships, random data were generated and put through the habitat index algorithm. Number of species (0–10), species composition (1–36), and species abundance (0–100) were chosen using uniform distributions. Sedimentation rates were randomly generated from a log normal distribution ($\mu = -0.495$, $\sigma = 0.826$). Distribution parameters were obtained from the real data sets. No trend was evident for the random data (Figure 9b). Furthermore, the random assignment of species was incapable of generating floating leaf habitats because the probability was only 0.0028. The random data test demonstrates that plant distributions at HBW were not governed by stochastic processes, and the observed relationships were not an artifact of the habitat index algorithm itself.

DISCUSSION

Tidal freshwater marsh plant associations at OPC show a distinct zonation. This zonation stems partly from the high abundance of rhizomatous plant species. *Nuphar advena* and *Peltandra virginica* are dominant perennials in lower elevation habitats, while *Typha angustifolia, Typha latifolia, Acorus calamus,* and *Leersia oryzoides* are dominant perennials at higher elevations. All of these species are known to occur widely in Atlantic coast tidal freshwater marshes (Simpson et al. 1983). Meanwhile, dominant annual species include *Zizania aquatica, Eleocharis ambigens,* and *Polygonum sagittatum,* with *Impatiens capensis* and *Polygo-*

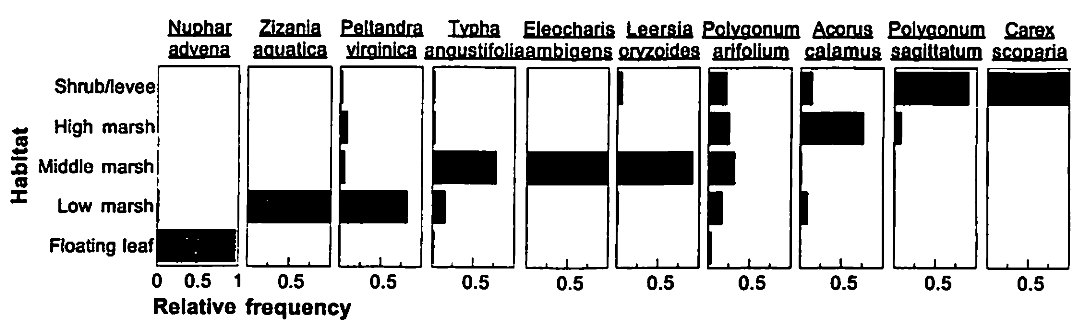

Figure 6. Habitat distributions of some key tidal freshwater marsh species at OPC.

Table 3. Relative percent cover and station habitat index for the 1995 vegetation survey at HaHa Branch Wetland.

Species	Relative Percent Cover at Each Station											
	A0	A1	A2	A3	A4	A5	A6	A7	A8	B1	B2	B3
Acorus calamus	76.04	61.01	71.32	79.65	67.11	36.63	28.57	32.20	31.95			
Bidens laevis							1.90	0.34				
Boehmeria cylindrica									3.76			
Carex A								1.36				
Cuscuta gronovii						27.47						
Eleocharis ambigens									11.28			
Galium palustre									1.88			
Impatiens capensis	22.81				3.36				1.13			
Juncus effusus								10.17				
Leersia oryzoides							0.48	32.20			3.19	2.06
Microstegium vimineum									37.59			
Mikania scandens								1.69				
Nuphar advena												97.94
Orontium aquaticum L.					10.07		4.76					
Panicum sp.									3.76			
Peltandra virginica		9.43	4.41	0.88	6.71	1.83	26.19	16.95	5.64	100	95.74	
Phragmites australis				17.70								
Polygonum arifolium		10.69	8.09	1.77	6.71	34.07	38.10	5.08	3.01			
Typha angustifolia	1.15	18.87	16.18		6.04							
Unknown C											1.06	
HABITAT INDEX:	5.89	5.54	5.66	6.12	5.54	5.81	5.21	5.49	6.13	4.33	4.34	3.07
HABITAT TYPE:	6	6	6	6	6	6	5	5	6	4	4	3

Species	Relative Percent Cover at Each Station										
	B4	B5	B6	B7	C1	C2	C3	C4	D1	D2	D3
Acnida cannabina									1.29		
Acorus calamus		61.22	47.26	32.47				9.05	61.29	33.56	50
Bidens laevis			1.00								
Boehmeria cylindrica				5.19						16.78	
Carex A								0.90			
Cicuta maculata L.				0.87							
Cuscuta gronovii								1.36			
Galium palustre			4.98	1.30							
Helenium autumnale			3.98								
Impatiens capensis								22.62	9.68	28.52	
Juncus effusus	4.27										
Leersia oryzoides		17.01	24.88					44.34			
Microstegium vimineum				34.63							
Nuphar advena	85.47						94.83				
Orontium aquaticum				0.87							
Peltandra viginica	8.55	17.01	7.46	9.52	13.04	93.02	5.17	6.79	14.84	1.01	
Phragmites australis		3.40									
Polygonum arifolium	1.71	1.36	5.47	2.60				12.67		3.36	50
Polygonum sagittatum			1.49	1.73					12.90	16.78	
Pontenderia cordata								0.90			
Sagittaria latifolia								0.90			
Scirpus cyperinus			2.49								
Typha angustifolia					86.96	6.98		0.45			
Unknown A			1.00								
Unknown B				10.82							
HABITAT INDEX:	3.35	5.56	5.55	6.23	4.78	2.00	3.10	5.33	5.78	5.91	5.70
HABITAT TYPE:	3	6	6	6	5	2	3	5	6	6	6

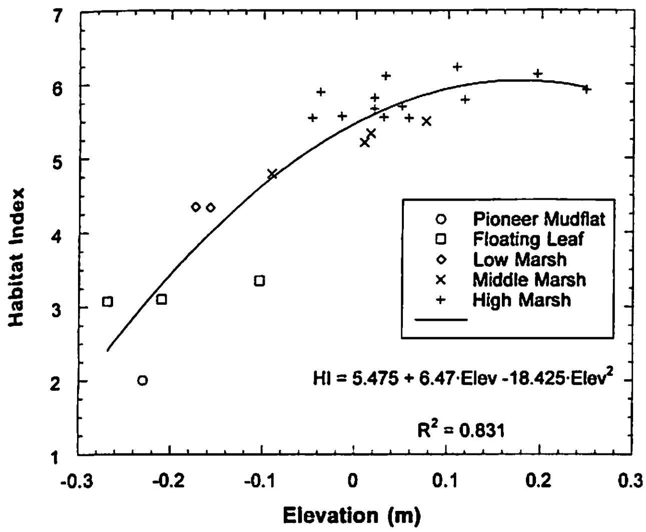

Figure 7. Regression between an index parameterizing plant associations and elevation, showing that the two a strongly related.

num arifolium as important sub-dominants (Figure 5). Compared with salt marshes, the results from OPC confirm that the simple division into low and high marsh does not adequately characterize the structure of this ecosystem. Several more distinct zones occur (Table 1), and each contains more species than reported for salt marsh zones.

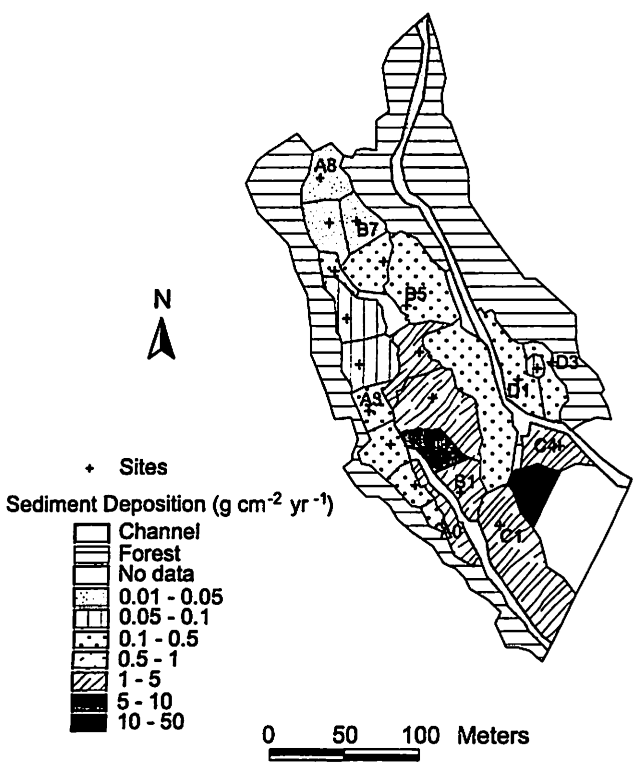

Figure 8. Map of summer-average sedimentation at HBW on a half-logarithm scale.

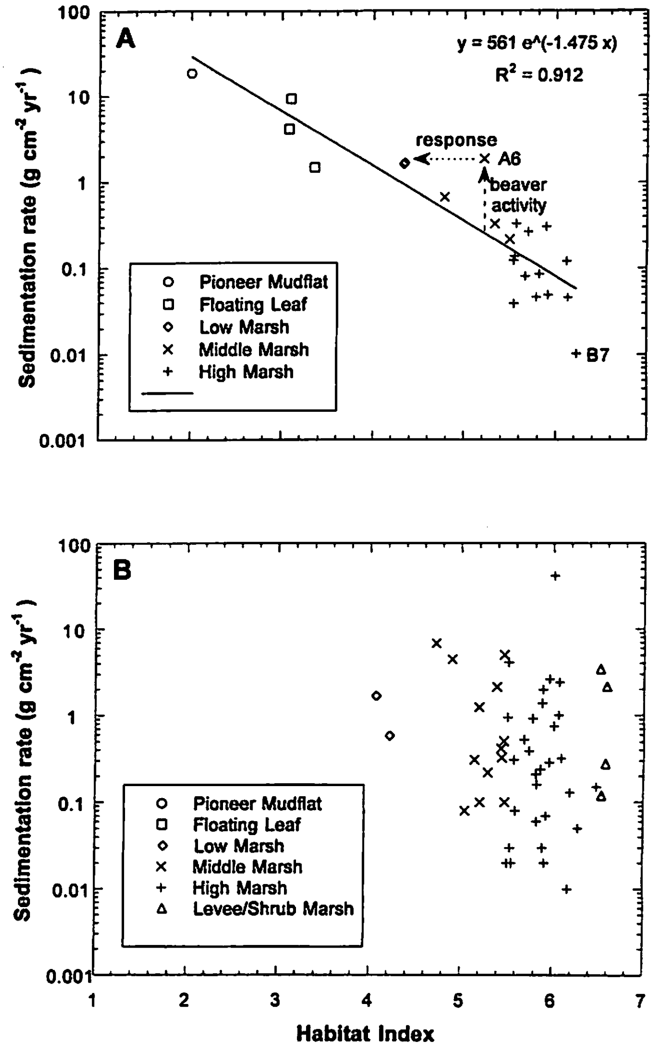

Figure 9. Relationship between plant association and July through November 1995 sedimentation for a) real data from HBW and b) randomly generated data.

Vegetation data from a series of Chesapeake Bay tidal freshwater marshes distributed along the axis of the estuary show a similar community structure as OPC. At Jug Bay Wetland in the Upper Patuxent River, Maryland, *Nuphar advena, Peltandra virginica, Zizania aquatica,* and *Pontederia cordata* dominate the lower elevation habitats, while *Typha angustifolia* and *Typha latifolia* dominate the high marsh (Khan and Brush 1994). At Sweet Hall Marsh in Pamunkey River, Virginia, *Peltandra virginica* and *Leersia oryzoides* have the highest biomass (Doumlele 1981).

In contrast to those of Chesapeake Bay, tidal freshwater marshes of the Delaware River have more annual species occurring in higher relative percentages that vary from year to year (Leck and Simpson 1987, Leck and Simpson 1994). Species such as *Bidens laevis, Ambrosia trifida,* and *Zizania aquatica* occur in significantly higher abundances along the Delaware

Table 4. Fraction of the explainable variability in each dependent variable that is attributed to each independent variable. P-value in parenthesis.

Independent Variable	Dependent Variable: Sedimentation Rate	Organic Content	Percent Clay	Percent Silt
Elevation	0.43 (0.001)	0.71 (0.0001)		
Habitat index	0.37 (0.004)			0.35 (0.008)
Distance from tidal inlet	0.20 (0.007)	0.29 (0.007)		0.26 (0.040)
Distance to nearest tidal channel				
Distance to HaHa Branch stream			1.0 (0.0001)	0.39 (0.002)
Total variability explained	92%	90%	69%	54%

River. However, the dominant perennials observed at Otter Point Creek are present and important vegetation components in the Delaware marshes. For example, at Hamilton Marsh, *Acorus calamus* and *Peltandra virginica* occur with frequencies of 59 and 76, respectively (Leck and Simpson 1995). Given the similarities among tidal freshwater marshes throughout Chesapeake Bay and along the Delaware River, the habitat index derived by combining plant species distributions and abundance in a simple algorithm to characterize the plant association at any location within a marsh would be very useful for fine scale comparative studies in any of these systems. Application to the Delaware River system in particular could help to further elu-

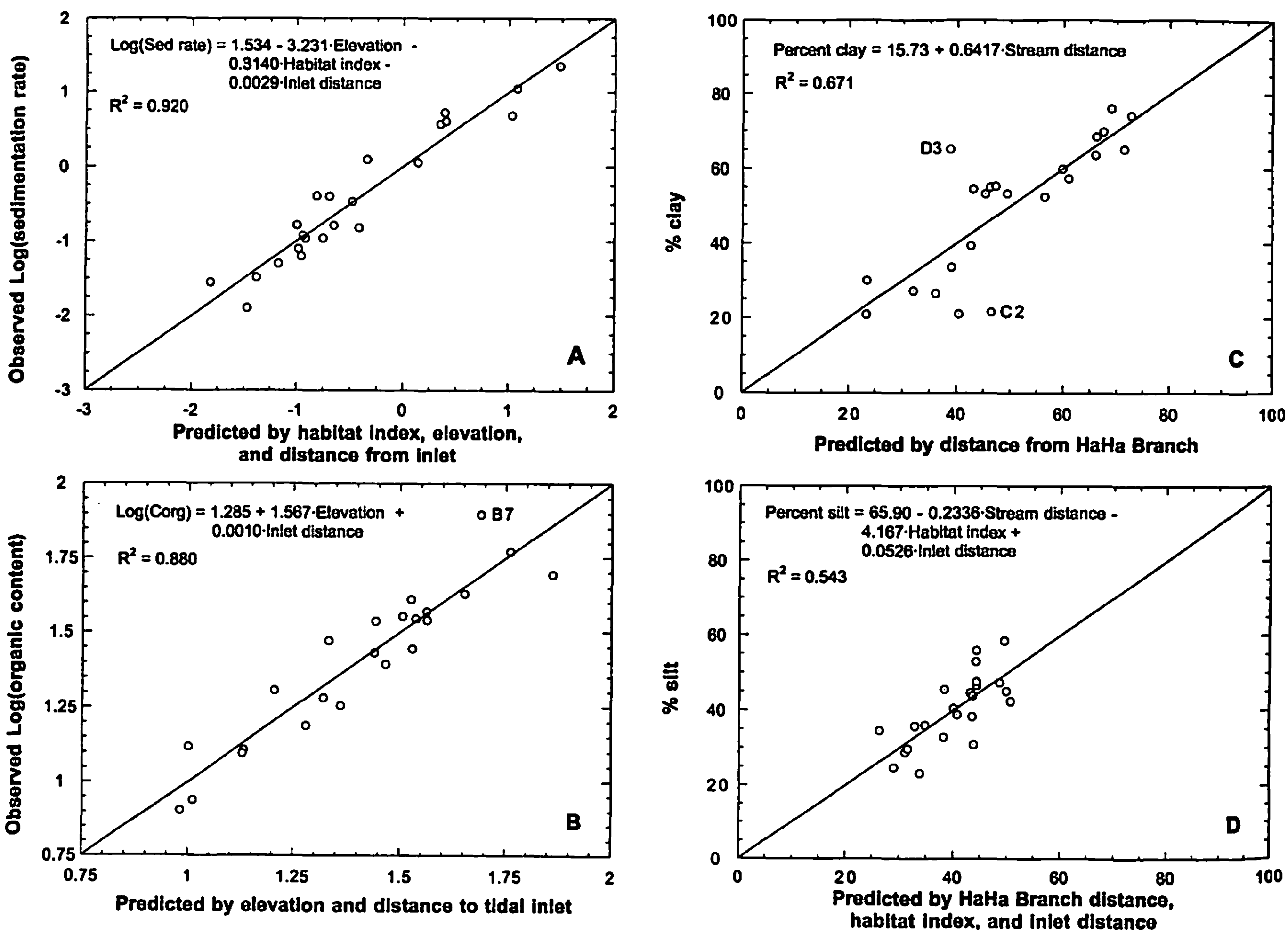

Figure 10. Predicted versus observed plots with one-to-one lines for reference are shown for a) Log(summer-average sedimentation), b) Log(organic content), c) percent clay, and d) percent silt. No regression lines are shown, but their equations are given.

Table 5. Values for statistical parameters that test the outcome of the multiple regression for each dependent variable.

Statistical Parameter	Dependent Variable			
	Sedimentation Rate	Organic Content	Percent Clay	Percent Silt
F test of correlation	$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.01$
Durbin-Watson serial r^2	0.04	0.23	0.01	0.03
# of residuals > 2 st.dev	0	1	2	0

cidate marsh ecology there including the relative roles of perennials and annuals.

The habitat index was directly related to elevation and is less costly to obtain in the field than traditional topographic surveying. As a result, it could serve as a tool for preliminary wetland assessment. Multivariate analyses showed that when the habitat index was combined with geomorphic variables, it was highly predictive of the spatial distribution of substrate characteristics, except bulk density, which was randomly distributed in this system. Further application of the habitat index might reveal such abiotic-biotic relations where good monitoring data exist, such as for Sweet Hall Marsh and the Delaware marshes.

The habitat index was also useful for predicting the consequences of disturbance, such as animal activity, on the composition of plant species. Beavers (*Castor canadensis* Kuhl) and muskrats (*Ondatra zibethicus* L.) are the primary wildlife observed to affect marsh zonation at OPC, whereas nutria (*Myocastor coypus* Molina) dominate other systems. Unlike nutria, the animals at OPC do not cause widespread damage to the plants. Animal activities were observed to be important at the local scale, but it is not yet clear what role the localized changes play in overall wetland evolution. A comparison of data from sites with and without animal activity is underway at this time.

Beyond the habitat index, this study shows how geomorphology relates to habitat conditions. As expected, elevation was the most important physical variable impacting summer-average sedimentation and organic content, but it was not the only variable. Both plant association and distance from the tidal inlet were significant factors, and these have not been accounted for in wetland creation/restoration efforts. Also, the further away a site was from the HaHa Branch stream, the less sand was present. Sand is an important substrate constituent for some species. For example, the main stand of *Phragmites australis* in the marsh occurs on a sand deposit fed by seasonal overbank flooding of the stream. The only other stand is much smaller and occurs where a ditch carries polluted storm water (and sand) into the marsh from the adjacent street. Thus, stream-marsh interactions impact the evolution of marsh conditions.

Another notable finding was the lack of significance of distance from nearest channel within the marsh. Stoddart et al. (1989) reported that the major creek and third-order tributaries in a salt marsh strongly influenced sedimentation, while first- and second-order creeks did not. The entire channel network in HBW was created and is maintained by animals. These channels are ~30 × 30 cm in cross-section and are too small to form levees or impact the distribution of sediment. The observed role of animals in building and maintaining channels casts doubt on efforts by theoretical hydrologists to relate the hydraulic geometry of marsh channels to flow measurements such as tidal prism or bankfull discharge where wildlife is present.

Finally, the structure of a tidal freshwater marsh results from a dynamic interdependence among abiotic and biotic processes. Elevation is not an *a priori* constant but rather a variable that changes through time as a function of sedimentation, which is in turn a function of plant association, distance to tidal inlet, distance to stream, elevation, and animal activity. At HBW, elevation only spans a 52-cm range, while sedimentation rate varies over 2.5 orders of magnitude. During the growing season, species composition at a location depends on elevation, which is the result of past deposition. During summer and autumn, the resulting plant association controls sedimentation, which changes elevation. Disturbing one of these conditions causes a cascade of changes to the others. These changes feed back into the initial condition to which the disturbance was applied, as predicted by modern geomorphic theory. Consequently, efforts to create marshes with predictable plant associations and wildlife habitats cannot rely solely on constructing an elevational gradient.

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