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PLANT COMMUNITY STRUCTURE IN A FRESHWATER TIDAL WETLAND

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ABSTRACT. The vascular plant community in a freshwater tidal wetland on the lower Connecticut River was studied in 2000. The effects of abiotic conditions on density and species density of plants in 70 samples, each 0.25 m^2 in area, were characterized. Sixty species were recorded. The mean species density was highest in shallow water because the number of emergent species in the community was far greater than the number of submerged species, which occurred with higher frequency in deeper water. Plant density had a bimodal distribution because of the different responses of emergent and submerged plants to water depth and was lowest in shallow water, where physiological stress, physical disturbance, and possibly herbivory are suspected of being limiting. Ordination and regression analyses found that water depth and the amount of organic matter and nitrogen in the sediment had the greatest effect on wetland plant density, although other variables also were influential. Abundance of emergent and submerged species differed in their responses to ammonium and nitrate levels. Overall species density was most strongly correlated with water depth. Several plant associations, including associations of submerged and emergent species, were identified, based on shared affinities for environmental conditions.

Key Words: freshwater tidal marsh, New England flora, wetland plants, nutrients, SAV

The description of biological communities and the characterization of species' affinities for environmental conditions has a long tradition in aquatic plant ecology, stretching back many decades in both Europe (Jones 1955; Misra 1938; Pearsall 1920) and the United States (Denniston 1922; Moyle 1945). Much of this work has been done on the regional scale and has considered large numbers of communities—574 lakes in Northern Ireland (Heegaard et al. 2001), for example. This research has shown that water chemistry, often measured by conductivity or pH, frequently is related to the distribution of submerged species within a region (Jackson and Charles 1988; Moyle 1945; Seddon 1972).

However, the factors most important in determining community composition depend on the scale of examination (Allan et al. 1997), and different conditions may determine presence of species across a landscape and at smaller spatial scales. Macrophytes in lakes have been shown to occur at particular water depths because of light (Spence 1967) or disturbance (Keddy 1983). Disturbance regimes related to current velocity and flooding frequency often affect species' presence and abundance in lotic systems as well (Nilsson 1987). Biotic interactions among species able to reach a location and tolerate the abiotic conditions also influence community composition. Competition has been demonstrated in few aquatic plant communities (McCreary et al. 1983; Van et al. 1999; Wilson and Keddy 1986) but may play a role in sites with high productivity and low disturbance (Titus and Stephens 1983), and certainly herbivory and predation by invertebrates, waterfowl, and fish can have profound effects on aquatic plant communities (Jupp and Spence 1977; Mathiasson 1973).

Most attempts to relate the structure of plant communities to local conditions have focused on lakes (Fox 1992), while riverine systems, especially freshwater tidal wetlands, have been less well studied (Mitsch and Gosselink 1986; Odum et al. 1984), particularly in the Northeast. Furthermore, wetland studies often have focused on emergent species, aggregating submerged plants as minor members of associations dominated by the more obvious emergents (Auclair et al. 1973; Day et al. 1988), and less attention has been paid to differences that may exist between emergent and submerged plants as distinct components of wetland communities.

Plant communities in freshwater tidal wetlands are highly dynamic (Capers 2003b), and the occurrence of species depends to a large degree on their ability to colonize appropriate habitat after frequent small-scale disturbance events (Capers 2003a). Therefore, the deterministic effects of environmental conditions may be less strong in these communities. Nevertheless, an understanding of these effects is urgent because wetlands are environmentally valuable and rapidly disappearing. Half of the world's wetlands were lost during the 20th century, and freshwater habitats are being destroyed at a rate that likely exceeds the rate of destruction of tropical forests (Myers 1997). Freshwater tidal wetlands are particularly vulnerable to global climate change, including both sea level rise (Titus 1988) and atmospheric nitrogen deposition (Howarth 1998), but a full assessment of the threat faced by wetland communities cannot be made without an understanding of the environmental affinities of the plants that are their foundation.

In this study, we characterize the affinities of emergent and submerged vascular plants for abiotic conditions in a freshwater tidal wetland. Ordination was used to characterize the community, and linear regression then was used to determine how species density and the density of wetland plants correlated with abiotic variables.

SITE DESCRIPTION

Freshwater tidal wetlands represent a small proportion of wetlands in the northeastern United States. In Connecticut, 71,000 ha of wetlands exist (Metzler and Tiner 1992), and of this area, less than 10% is tidal. Of the tidal wetlands, only 678 ha are freshwater (Metzler and Tiner 1992). The Connecticut River drains an area of 2.9 million hectares. Its mean discharge rate is 566 cubic meters per second, comparable to major rivers such as the Delaware and the Hudson, and it provides nearly 70 percent of the freshwater input to Long Island Sound (Rozsa 2001). Tidal influence extends upriver 90 km north of Long Island Sound. On average, the river rises and falls 1.2 m at its mouth and 60 cm in Middletown, 50 km to the north. Freshwater tidal marshes, beginning about 12 km from the river's mouth, are particularly diverse, supporting more than 150 species of plants (Barrett 1989). The tidal marshes and adjacent riparian habitat form a nearly continuous ecosystem that has been declared a wetland of international importance under the Ramsar Convention (Anonymous 1994).

Whalebone Cove (41°25′N, 72°25′W) is 17.4 km north of the mouth of the river in the Hadlyme section of Lyme, Connecticut (Figure 1). This freshwater tidal wetland is 50 ha in area, intermediate in size among similar wetlands on the lower Connecticut River. Water rises and falls approximately 80 cm with each semidiurnal tide, and most of the wetland is submerged at high tide. Whalebone Cove is connected to the river by a channel 30 m wide, and small streams enter on the east and north. The cove occurs at the edge of the Southeast Hills and Coastal Plain climate regions (Brumbach 1965). The mean annual temperature in the area is 8–10°C. The last freezing temperature of the winter usually occurs around April 20, and the first freeze of the fall occurs about Oct. 10 (Brumbach 1965).

From Middletown to Long Island Sound, the Connecticut River runs through eroded and glacially scoured metamorphic rock dating from the Paleozoic (Lewis 2001). The lower Connecticut River valley was covered by glaciers until approximately 16,500 years before present (BP). After glacial retreat, the Connecticut River reestablished itself in its present bed by about 13,500 BP, cutting deeply into sediments deposited in postglacial lakes (Lewis 2001). With rising sea levels, the lower river valley was flooded and began to fill with sediment after about 9000 years

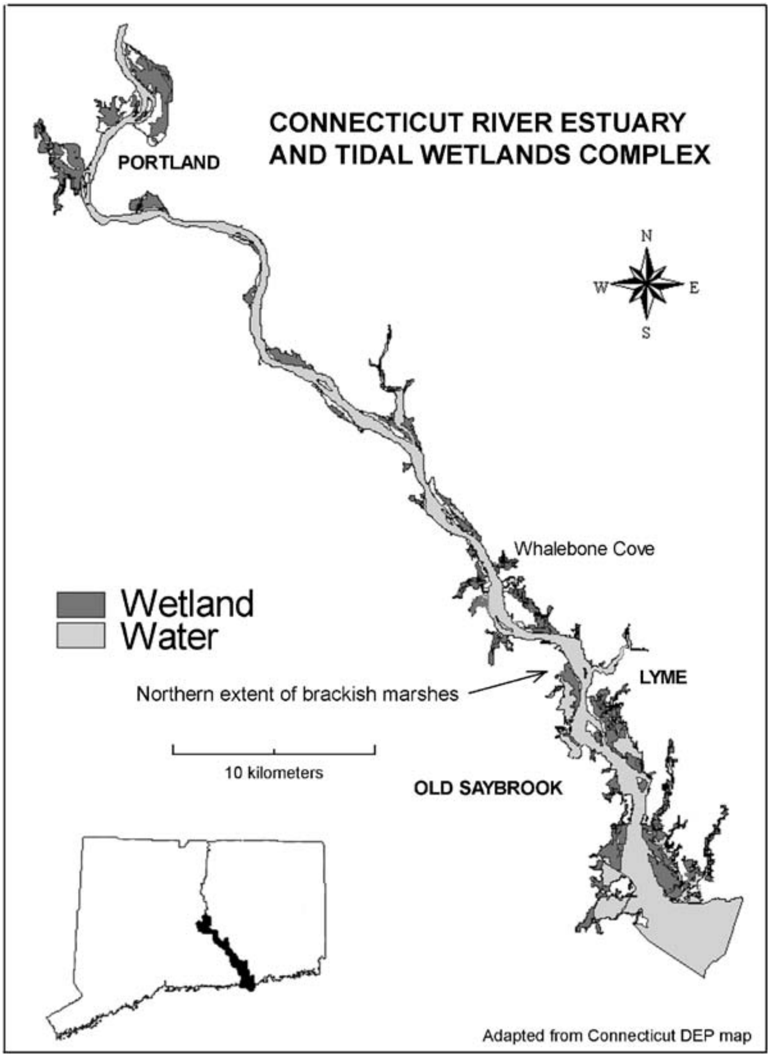

Figure 1. Map of the lower Connecticut River in Connecticut, showing the location of tidal wetlands recognized under the international Ramsar Convention, including Whalebone Cove, a 50 ha freshwater tidal wetland in Lyme, 17.4 km upriver from Long Island Sound. Salt marshes occupy only a small area at the mouth of the river, and brackish marshes extend upriver about 12 km.

bp. Because of the relatively rapid rise in sea level, tidal wetlands were unable to develop until about 3,000 years ago, when the rate of rise slowed to about 1 mm per year (Bloom and Stuiver 1963; Niering and Warren 1980). Not all wetlands developed at the same time, however. Radiocarbon dating indicates that the tidal wetlands farther upriver are younger than those at the mouth of the river and that the Whalebone Cove community developed 340 ± 100 years ago (R. Orson, Orson Environmental Consulting, Branford, Connecticut, unpubl. study).

In the area of Whalebone Cove, the bedrock is overlain by Hinckley gravelly sandy loam, an excessively drained soil that forms on glacial outwash, and by recent alluvial deposits (Crouch 1983). The wetland itself occurs on Westbrook mucky peat, low salt, sediment (Crouch 1983). This is a very poorly drained soil that forms in organic deposits 40–130 cm thick over loamy mineral deposits.

MATERIALS AND METHODS

Field sampling. Sampling locations were selected randomly, using an aerial photograph of Whalebone Cove on which a grid of north-south and east-west lines was drawn, dividing the wetland into 10 m × 10 m squares. Coordinates of the vertices of the lines, a 58 × 103 matrix, were selected at random as sampling locations. Sampling was done from a canoe, and locations were approached from locations in the wetland that could be positively identified on the aerial photograph, with distances from those points measured approximately, based on the number of paddle strokes. The point of this process was not to locate sampling locations precisely but to avoid bias in their selection.

We sampled a total of 70 locations, using a frame 0.5 m × 0.5 m, a size commonly used in surveys of marsh vegetation (e.g., Day et al. 1988). All stems actually rooted within the quadrat were identified to species and counted. Many wetland plants are clonal, and individual plants may produce multiple shoots along rhizomes in the sediment. However, except in the case of obviously clonal plants, such as *Carex stricta*, that produce multiple stems all closely connected to each other, no attempt was made to determine whether shoots of the same species were clones. The survey was not exhaustive but produced a representative sample of the vegetation and captured information on the plants occurring with the highest frequency, based on six years of research in this wetland (R. Capers, pers. obs.).

At each sampling location, a sample of the upper 3 cm of sediment was obtained, using a small scoop, for nutrient and particle size analysis, and temperature, conductivity, and pH of the water were measured with an Oyster meter, Model 341450-P (Extech Instruments Corp., Waltham, MA). Turbidity of the water was measured with an Orbeco-Hellige portable turbidimeter, Model 966 (Orbeco Analytical Systems Inc., Farmingdale, NY). We also measured water depth, recording the time of each measurement, so maximum depth could be calculated from river height data recorded every five minutes at a U.S. Geological Survey station in Old Lyme. After converting Old Lyme data from inches to centimeters, we used the following equation:

$$\text{Whalebone Depth} = (0.80 \times \text{Old Lyme Depth}) + 25$$

Measurements were made only on days when the river was not unusually high because of recent rains. In a number of cases, sampling locations had to be visited twice because there was no water over the location during the first visit; in these cases the location was marked with a stake to ensure it could be found again. No water measurements were made at one sampling location because it was above the high water level; elevation above high water at this site was estimated visually, based on the level of the nearest water. Water velocity was measured with a Global Water Flow Probe (Global Water Instrumentation Inc., Gold River, CA) during periods of maximum flow, at least two hours before or after high and low tides. All sediment samples were taken and water measurements made in July–August, 2000.

Sediment analyses. Sediment samples were analyzed for NH_4, NO_3, and PO_4 as well as organic matter and particle size. Before chemical analysis, sediment was air-dried for several days, then oven-dried at 30°C for 24 hours. Dried sediment samples were ground in a mortar and passed through a 2 mm screen. We determined PO_4 levels colorimetrically using a Lachat Automatic Ion Analyzer (Zellweger Analytics Inc., Lachat Instruments Division, Milwaukee, WI). In extraction, 2 g of the screened sediment was shaken for five minutes in 20 ml of Bray's solution No. 1 (0.025M hydrochloric acid and 0.03 M ammonium fluoride; Bogren and Hofer 2001; Bray and Kurz 1945). The extract then was filtered and frozen. Nitrogen extractions were done with 5 g samples of screened sediment and 25 ml of 2M potassium chloride as an extractant. Samples were shaken in KCl for one hour in the extractant, refrigerated overnight, then filtered. Extract was frozen until analyzed colorimetically for NO_3 and NH_4 (analysis conducted by Environmental Research Institute, Storrs, CT). While air-drying sediment before extraction inevitably results in oxidation of some ammonium to nitrate, all samples were treated identically so nutrient levels should be unbiased relative to each other.

Before analysis for organic content and particle size, sediment was air-dried, then dried in an oven for 24 hours at 100°C and passed through a 2 mm screen. Sediment was analyzed for organic matter by weighing out 20 g and firing it in a muffle furnace for six hours at 400°C. The percentage loss by weight then was calculated. Particle size was analyzed by treating approximately 12 g of sediment (20 g of sandy sediment) with hydrogen peroxide (Sheldrick and Wang 1993), then washing it through a 0.05 mm screen. Sediment washed through the screen and sediment left in the screen were dried separately at 60°C, then weighed to determine the sand and silt + clay proportions of the sediment.

Sample comparisons. Mean species density (number of species in 0.25 m^2 samples) was calculated, and the difference in density at different water depths was analyzed with ANOVA and a post-hoc least significant difference (LSD) test. Mean stem density (number of plants in samples) was compared between submerged sites and sites exposed at low tide, using a t-test. The mean stem density of submerged plants and emergent plants was compared along a gradient of water depth to determine if response to inundation differed. The tendency of environmental conditions to vary together was evaluated with correlation.

Ordination. To characterize the community in terms of important environmental gradients (Gauch 1982), we used ordination, limiting the analysis to the 16 species present in three or more samples to eliminate the effect of rare species. Ordination was performed first on the 16-species data set after eliminating samples from locations where no plants were recorded. This data set included information on plants at 62 locations as well as information on depth/elevation of sampling locations at high tide; strength of the water current (a value of 0 was entered for the single site above high water); water pH, temperature, conductivity, and turbidity; sand and silt + clay fractions of the sediment; sediment organic content, PO_4, NO_3, and NH_4 concentration; and the ratio of nitrogen ions to phosphate (NO_3+NH_4 : PO_4). Water pH, temperature, conductivity, and turbidity proved uninformative, probably because these conditions tend to vary with the time of day, so measured values likely reflected sampling time more than growing conditions for plants, and we were unable to control for this variation. Ultimately these variables were removed from the data set (and all other analyses), as was the silt + clay fraction because it was highly correlated with sand. Collinearity among variables can produce unstable solutions (ter Braak 1986).

Ordination was done with Canonical Correspondence Analysis (CCA), which uses species abundance data and environmental variables iteratively to arrange species on axes that represent linear combinations of the measured variables, choosing variables that will explain the maximum amount of variation in the data. PC-Ord for Windows (McCune and Mefford 1997) was used for the ordination. Data were centered and standardized to unit variance before the analysis.

Regression analysis. Regression was used to determine the effect of abiotic variables on plant density and species density of all plants and of emergent plants and submerged plants separately. In the regression analyses, plant density and species density first were regressed on environmental variables individually. The dependent variables then were regressed on the variables significant in simple linear regressions, and variables insignificant at a level of $\alpha = 0.05$ were removed sequentially until only significant variables remained. Plant density (stems per 0.25 m^2 samples) was square root transformed to reduce heteroscedasticity; nutrient values were natural log transformed, and the proportion of organic matter in the sediment was arcsine square root transformed.

RESULTS

Sixty species were recorded in the 70 samples (Table 1). These included 10 submerged species, one floating-leaved plant (*Nuphar variegata*), 16 emergent species that commonly occur in standing water, one mudflat species that often is found submerged (*Gratiola aurea*), and 32 that occur on wet soils. Only 11 species occurred in the 18 submerged locations (water depth $\geq$ 80 cm), compared to 55 species in the 51 intertidal locations (14–79 cm depth). At the single site above the high water level, 11 species were found, including three species that were found nowhere else (*Salix sericea*, *Galium* sp., and an unidentified leguminous vine). Three species were limited to submerged locations: *Vallisneria americana*, *Potamogeton perfoliatus*, and *Myriophyllum spicatum*.

Species density ranged from 0 to 7 in submerged locations and from 1 to 16 in intertidal sites. Mean species density across the community was 3.6 (SE = 0.33). Species density was highest in the most shallow water ($F = 13.154$, $p < 0.0001$; Figure 2), declining in deeper water.

Table 1. Plant species recorded in 70 samples in a freshwater tidal wetland in Lyme, Connecticut, in July–August 2000. Nomenclature follows Gleason and Cronquist (1991).

Species Names
Acorus calamus L.
Agrostis perennans (Walter) Tuck.
Alisma triviale Pursh
Amaranthus cannabinus (L.) Sauer
Aster sp.
Bidens connata Muhl.
Bidens frondosa L.
Calamogrostis canadensis (Michx.) P. Beauv.
Callitriche sp.
Cardamine pensylvanica Muhl.
Carex scoparia Schkuhr
Carex stricta Lam.
Carex sp.
Ceratophyllum demersum L.
Coptis trifolia var. *groenlandica* (Oeder) Fassett
Cornus amomum Mill.
Eleocharis palustris L.
Eleocharis sp.
Elodea nuttallii (Planch.) H. St. John
Equisetum arvense L.
Galium sp.
Grass, unidentified
Gratiola aurea Pursh
Helenium autumnale L.
Impatiens capensis Meerb.
Iris versicolor L.
Leersia oryzoides (L.) Sw.
Leguminous vine, unidentified
Ludwigia palustris (L.) Elliott
Myriophyllum spicatum L.
Najas flexilis (Willd.) Rostk. & Schmidt
Nuphar variegata Durand
Onoclea sensibilis L.
Orontium aquaticum L.
Oxalis stricta L.
Peltandra virginica (L.) Schott & Endl.
Pilea pumila (L.) A. Gray
Polygonum arifolium L.
Polygonum hydropiper L.
Polygonum punctatum Elliott
Polygonum sagittatum L.
Pontederia cordata L.
Potamogeton nodosus Poir.
Potamogeton perfoliatus L.
Potamogeton pusillus L.
Potamogeton spirillus Tuck.
Rosa palustris Marshall
Sagittaria graminea Michx.
Sagittaria latifolia Willd.
Sagittaria rigida Pursh
Sagittaria spatulata (J.G. Smith) Buchenau
Salix sericea Marshall
Scirpus fluviatilis (Torr.) A. Gray
Sedge, unidentified
Sparganium eurycarpum Engelm.
Thalictrum pubescens Pursh
Typha latifolia L.
Vallisneria americana L.
Viola sp.
Zizania aquatica L.

Although fewer species occurred in submerged sites, they were more widespread. Mean frequency for these species was 14.0%, compared with 4.3% for species found in intertidal locations, although the difference was not significant between the groups ($0.2 < p < 0.1$ in a Wilcoxon two-sample test). Of the 55 species recorded at 51 intertidal locations, 28 appeared in only one sample. The most widespread emergents were *Pontederia cordata* and *Sagittaria latifolia* (in 15 and 11 samples, respectively). The most frequently found submerged species

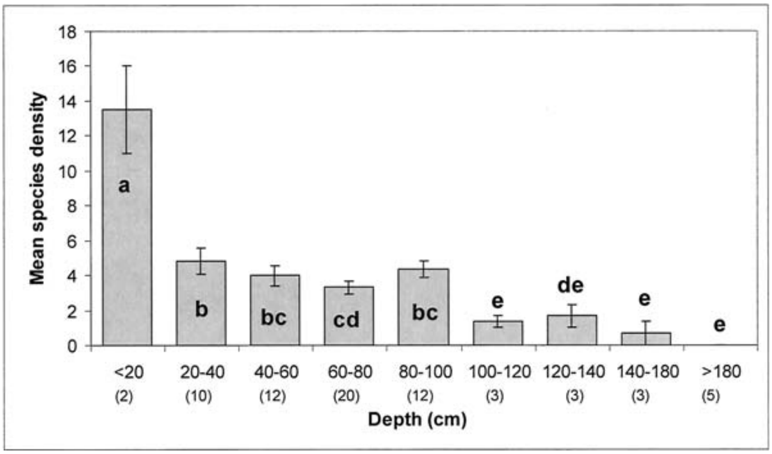

Figure 2. Distribution of the mean species density (± SE) of wetland plants in 0.25 m^2 samples is shown across a gradient of water depth. Mean species density declined with increasing depth in the studied freshwater tidal wetland in Connecticut. An ANOVA indicated that species density was significantly different among the depth classes ($p < 0.0001$), and letters in bars indicate significant differences among classes identified in a post-hoc LSD test ($\alpha = 0.05$). Numbers in parentheses under depth classes indicate the number of observations in each class.

were *Elodea nuttallii* (in 4 subtidal and 31 intertidal samples) and *Ceratophyllum demersum* (in 2 subtidal and 24 intertidal samples).

In addition to being more widespread, submerged species had higher average density. The mean number of stems at submerged sites was 45.9 ± 5.06 compared with 20.7 ± 5.15 at intertidal sites ($t = -3.486$, $p = 0.001$). Density ranged from 0 to 62 in submerged samples and from 5 to 153 in intertidal locations. Overall density of stems had a bimodal distribution (Figure 3) because emergent plant density peaked in shallow water (< 20 cm), while submerged plant density peaked at greater depth (80–100 cm).

The 16 most abundant species occurred in broadly overlapping ranges across the depth gradient (Figure 4). Among emergent plants, *Sparganium eurycarpum*, *Zizania aquatica*, and *Pontederia cordata* occurred in the deepest water, indicating the greatest tolerance of inundation, and *Pilea pumila* and *Onoclea sensibilis* were least tolerant. The submerged species occurring in the shallowest water, indicating greatest tolerance to exposure, were *Callitriche*, *Elodea nuttallii*, and *Ceratophyllum demersum*.

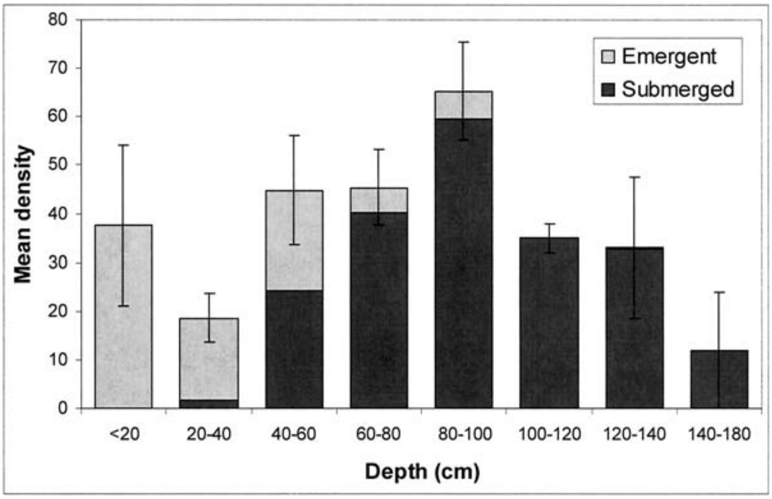

Figure 3. Distribution of stem density values is shown across a depth gradient. The mean density of wetland plants had a bimodal distribution because the abundance distributions of emergent and submerged plants overlapped but peaked at different depths. Error bars (± SE) are for means of total plant density at each depth.

Sampling locations ranged from 1 cm above high water to 320 cm below high water. Environmental conditions varied widely at the locations sampled (Table 2). Nutrient values were especially variable, reflecting a high degree of environmental heterogeneity at small spatial scales. The strength of the water current, water depth, and the proportion of sand in the sediment were correlated positively (Table 3), and ammonium levels were positively correlated with the amount of organic matter in the sediment.

Ordination. The CCA indicated that the variables most strongly correlated with Axis 1 were water depth, which determines the length of time that plants are exposed to water or saturated soil, and the percent of organic matter in the sediment, which was negatively correlated with the axis (Table 4; Figure 5). The percentage of sand in the sediment and nitrate levels also were highly correlated with Axis 1 (positively and negatively, respectively). The second axis separated species primarily according to their affinity for NH_4 (low on the axis) or for sandy sediment and flowing water (high on the axis; Table 4, Figure 5).

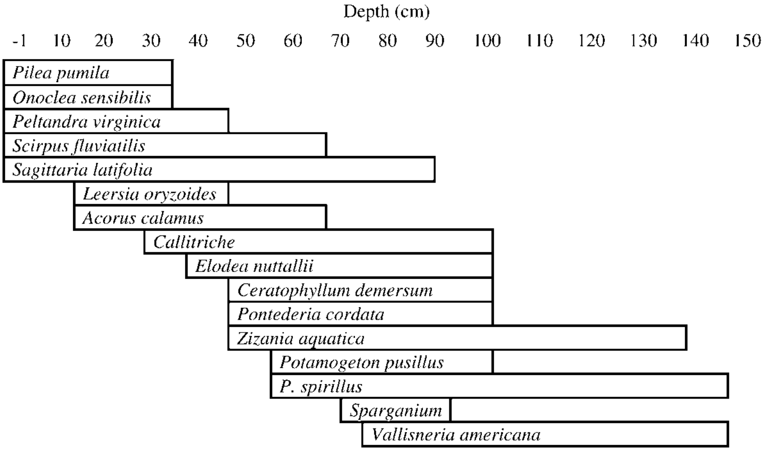

Figure 4. Water depths at which common species occurred in a freshwater tidal wetland are shown. Depth was measured from high tide, which would be at zero, with −1 indicating the single location above normal tidal flooding. Sampling locations below 80 cm were lower than the low tide level, so were always under water.

Vallisneria americana occurred alone in the deepest water and in areas with the strongest current and highest proportion of sand in the sediment. Several other species appeared in the ordination to be associated with each other because of shared affinities for abiotic conditions. *Potamogeton pusillus* and *P. spirillus* occurred with *Sparganium*

Table 2. Water and sediment conditions as measured in Whalebone Cove, a freshwater tidal wetland on the lower Connecticut River.

Conditions	Median	Mean	StdDev	Min	Max	N
Depth (cm)	71.0	85.0	62.47	−1.0	319.9	70
Turbidity (NTU)	3.6	4.8	4.15	0.6	22.0	67
pH	7.1	7.3	0.76	6.5	9.3	69
Temp (°C)	25.2	25.2	2.73	20.6	33.4	69
Conductivity (μS)	90.0	92.0	21.0	50.0	135.0	68
Current (cm/sec)	0	5.8	10.8	0	45.7	64
NH_4 (mg N/kg)	89.6	102.0	86.35	4.25	406.45	67
NO_3 (mg N/kg)	1.62	12.67	37.43	0.62	257.75	67
PO_4 (mg P/kg)	38.95	40.85	15.28	9.85	76.97	68
Organics (%)	3.1	3.2	1.90	0.4	10.9	68
Sand (%)	17.3	31.2	28.55	2.3	97.7	68
Silt + Clay (%)	82.7	68.8	28.55	2.3	97.7	68
NH_4+NO_3 (mg N/kg)	92.1	114.6	90.44	5.47	407.9	67
NH_4+NO_3 : PO_4	2.26	3.60	5.54	0.15	41.43	67

Table 3. Pearson correlation coefficients among water and sediment variables in Whalebone Cove are shown. The variables were used in an ordination of the wetland plants in the community. Several other variables were excluded from the analysis, primarily because of small-scale temporal variation that could not be addressed by the sampling protocol. Correlation coefficients significant after Dunn-Ŝidák correction are in boldface.

Variables	Depth	Current	NH_4	NO_3	PO_4	Organic (%)	Sand (%)	NH_4+ NO_3 : PO_4
Depth	1							
Current	**0.605**	1						
NH_4	−0.298	−0.374	1					
NO_3	−0.193	−0.118	−0.105	1				
PO_4	−0.174	−0.282	−0.142	0.295	1			
Organic (%)	**−0.553**	−0.192	**0.372**	0.140	−0.004	1		
Sand (%)	**0.659**	**0.587**	**−0.551**	−0.140	−0.223	**−0.638**	1	
NH_4+NO_3 : PO_4	−0.183	−0.181	**0.767**	0.038	**−0.392**	0.284	−0.326	1

eurycarpum and *Zizania aquatica* in moderately deep, running water where the sediment had low levels of organic matter and ammonium and a high sand fraction, while *Elodea nuttallii*, *Ceratophyllum demersum*, *Pontederia cordata*, and *Callitriche* occurred in moderately deep water with little or no current and where the sediment had low levels of organic matter and nitrate but high ammonium levels. Other emergent species were clustered less tightly in areas with more shallow water, where the sediment contained higher levels of organic matter and nitrate. These species also were separated on the third axis, which was correlated with phosphate levels (Table 4; Figure 5).

Eigenvalues for the first three axes of the CCA (Table 5) were statistically significant ($p = 0.01$ in a Monte Carlo permutation test), and all three axes were correlated with the environmental variables ($p = 0.01$

Table 4. Correlation of abiotic variables with axis scores in a canonical correspondence analysis of 16 wetland plant species and eight environmental variables.

Variables	Axis 1	Axis 2	Axis 3
Water depth	0.889	0.206	0.028
Organic (%)	−0.710	−0.258	−0.103
NO_3	−0.545	0.228	−0.349
Sand (%)	0.504	0.814	0.141
Current	0.120	0.738	0.041
NH_4	0.204	−0.679	0.006
PO_4	−0.279	0.028	0.668
NH_4+NO_3 : PO_4	0.023	−0.359	−0.232

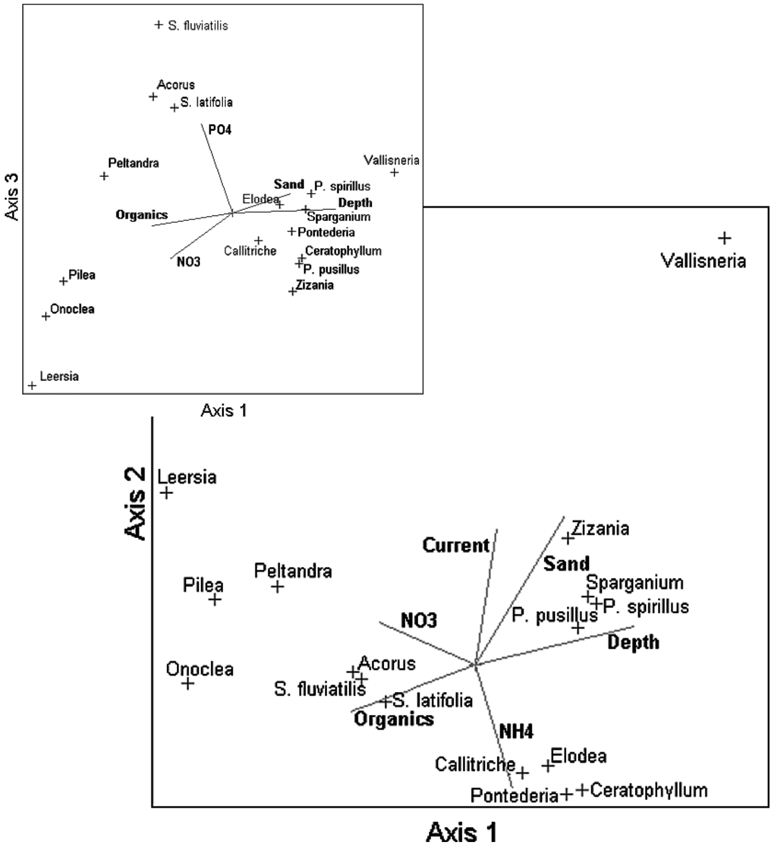

Figure 5. Biplot of canonical correspondence analysis involving the 16 most common species and eight environmental variables in a freshwater tidal wetland. Water depth, the amount of organic matter in the sediment and the nitrate levels in the sediment were most strongly correlated with the first axis, and ammonium levels, strength of the water current, and sediment texture were correlated most strongly with the second axis. Phosphate values were correlated with the gradient represented by the third axis (shown in inset).

for Axis 1 and $p = 0.02$ for Axes 2 and 3 in a Monte Carlo test of the likelihood that the correlations could have been generated by chance). However, the three axes explained only a modest amount of total variation, a cumulative total of 22.5%.

Regression analysis. In the reverse stepwise regression, water depth was the only variable with a significant linear relationship to total

Table 5. Results of a canonical correspondence analysis of a freshwater tidal wetland plant community in Connecticut. The data that were analyzed included the abundance of 16 species and eight environmental variables.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.713	0.532	0.385
Correlation coefficients	0.886	0.825	0.758
% of variance in data explained	9.8	7.3	5.3

species density in the 0.25 m^2 samples ($p < 0.0001$, $r^2 = 52$; Table 6A), reinforcing the finding of the ANOVA (Figure 2). Because the importance of depth might vary between submerged plants and others, species density of these groups was analyzed separately as well. Only sediment nitrate concentration explained a significant amount of the variability in submerged species density (species density declined as NO_3 levels rose; Table 6B), while depth alone was significant in the model for other plants (Table 6C).

Total plant density was most strongly influenced by the ratio of nitrogen ions to phosphate and by the concentration of NO_3 (Table 7A). Submerged plants' density declined as NO_3 rose and increased with NH_4 levels. In contrast, emergent plants' density increased with NO_3 and

Table 6. The best-fit multiple regression models characterizing total species density in 0.25 m^2 plots in terms of environmental variables are shown. Species number was square root transformed before analysis, and NO_3 was natural log transformed. The model for all species combined is shown in A, followed by the model limited to submerged species in B, and the model for other plants in C.

	Coefficients	t	F	*p*	r^2
A. All plants					
Intercept	2.465	22.674	—	< 0.0001	—
Depth	−0.009	−8.499	—	< 0.0001	—
Model	—	—	72.239	< 0.0001	0.515
B. Submerged plants					
Intercept	1.333	13.191	—	< 0.0001	—
NO_3	−0.226	−4.557	—	< 0.0001	—
Model	—	—	20.756	< 0.0001	0.242
C. Emergents and other wetland plants					
Intercept	0.793	2.416	—	0.0185	—
Depth	−0.005	−2.376	—	0.0205	—
Model	—	—	18.434	< 0.0001	0.366

Table 7. The best-fit multiple regression models characterizing the number of wetland plants in 0.25 m^2 plots in terms of environmental variables are shown. Plant density was square root transformed before analysis, nutrient levels were natural log transformed, and organic matter levels were arcsine square root transformed. The model for all species combined is shown in A, followed by the model limited to submerged species in B, and the model for emergents and other plants in C.

	Coefficients	t	F	*p*	r^2
A. All plants					
Intercept	5.331	11.788	—	< 0.0001	—
NH_4+NO_3 : PO_4	1.181	3.800	—	0.0003	—
NO_3	−0.498	−2.091	—	0.0405	—
Model	—	—	8.368	0.0006	0.207
B. Submerged plants					
Intercept	0.878	0.601	—	0.550	—
NO_3	−1.102	−4.238	—	< 0.0001	—
NH_4	1.108	3.369	—	0.0013	—
Model	—	—	15.602	< 0.0001	0.331
C. Emergents and other wetland plants					
Intercept	0.352	0.360	—	0.720	—
Organics	26.573	4.573	—	< 0.0001	—
NH_4	−0.792	−2.811	—	0.0066	—
NO_3	0.426	2.356	—	0.0216	—
Model	—	—	12.603	< 0.0001	0.375

declined with increasing NH_4 levels but was most strongly influenced by sediment organic matter (Table 7B, 7C).

DISCUSSION

Water depth, which determines how long plants are submerged, nitrogen levels, and the proportion of organic matter in the sediment had the greatest effect on where species occurred and how abundant they became in Whalebone Cove. Other factors affecting the plant community included water velocity, sediment texture, and phosphate levels. That water depth plays a role in determining species occurrence and density is obvious and has been shown repeatedly in studies of lakes (Lehmann et al. 1997; Pearsall 1920; Spence 1967) and marshes (Auclair et al. 1973; Day et al. 1988), although it rarely has been demonstrated quantitatively in freshwater tidal wetlands (Odum et al. 1984). What may be more interesting is the strong response of both the emergent and submerged components of the community to sediment nitrogen levels, showing that patchiness in the distribution of nutrients over small spatial scales can affect distribution of both emergent and submerged plants within a community.

Recent work has demonstrated that nutrients play key roles at the landscape scale, influencing whether the plants in a wetland are herbaceous or woody; vascular or nonvascular; competitors, ruderals, or stress tolerators (Bedford et al. 1999; Willby et al. 2001). Vascular herbaceous plants as a group are nitrogen limited (Bedford et al. 1999), and temperate marshes of North America, which are dominated by herbaceous plants, are generally nitrogen limited as a result. Fewer studies have considered the importance of nutrients on smaller spatial scales in wetlands, and they often have inferred the importance of nutrients based on conductivity, sediment texture, or the amount of organic matter in the sediment (Day et al. 1988; Lieffers 1984).

In the CCA, nitrate levels were strongly correlated with the first axis, and ammonium levels were strongly correlated with the second axis. Furthermore, results of regression analysis suggested that species density and plant density both were influenced by nitrogen levels. Density of emergents was strongly influenced by sediment organic matter as well. In Whalebone Cove, ammonium, nitrate, and the organic content in the sediment all were highest in the intertidal and reached their lowest levels in the deepest water, probably because strong current there prevents the accumulation of litter; few of the intertidal locations had any measurable current at all. For submerged species as a group, the peak in density may come where conditions represent the optimal balance between nutrient availability and the avoidance of stresses associated with exposure at low tide. For emergent plants, peak density may represent the optimal balance between nutrient availability and stresses associated with submergence.

Disturbance and herbivory were not considered in this analysis, but their influence often is great, especially in the intertidal, where plants are exposed to grazing by ducks, sediment erosion, and scouring by waves, ice, and tree trunks (Day et al. 1988; Keddy 2000; Niering and Warren 1980). Disturbance and herbivory may contribute to the bimodal distribution in plant density in Whalebone Cove. The density minimum occurs at a water depth of 20 to 40 cm, which is the same depth range in which Keddy (2000) found the maximum disturbance frequency on a sheltered lakeshore. It is known from previous work in this wetland that submerged plants have a largely ephemeral existence, and persistence at any location from one year to the next is very low (Capers 2003b). Submerged species persist at the community level only because they have high colonization rates, relying primarily on vegetative propagules

(Capers 2003a). This would presumably be less true of emergent plants, which root more firmly in the sediment. Experimental work is needed to quantify the role of disturbance and biotic interactions as well as their interactions with nutrients, water depth, and other environmental conditions in influencing plants' density and frequency.

Disturbance interferes with the deterministic effects of environmental conditions, and this is reflected in the low correlation between axes in the ordination and the measured environmental variables. This is not unusual in wetland ordinations (e.g., Walker and Wehrhahn 1971) and indicates only that there is much variation in the data (Gauch 1982; ter Braak 1986). Leck and Simpson (1995) reported similarly weak relationships between seed germination, seedling establishment, and vegetation cover even within species in a freshwater tidal wetland in New Jersey; over a 10-year period, performance of individual species was idiosyncratic, and no causes for fluctuations in abundance were apparent (Leck and Simpson 1995).

In spite of the variation, several plant associations were identified in Whalebone Cove:

1. Three submerged species, *Elodea nuttallii*, *Ceratophyllum demersum*, and *Callitriche*, commonly occurred with the emergent *Pontederia cordata* in areas with moderately deep water, silty sediment, no detectable current, and high ammonium levels;
2. The emergents *Zizania aquatica* and *Sparganium eurycarpum* occurred with the submerged *Potamogeton pusillus* and *P. spirillus* in areas with moderately deep water, stronger current, high sand content, and low ammonium levels;
3. Four emergent species, *Sagittaria latifolia*, *Scirpus fluviatilis*, *Acorus calamus*, and *Peltandra virginica*, occurred with overlapping ranges on a gradient of decreasing water depth and increasing amounts of organic matter and sediment nitrate.

Although emergent and submerged species can be distinguished from each other on the basis of their different responses to environmental variables, these associations show that the environmental affinities of some submerged and emergent species differ very little. In fact, much variation remains in the responses of individual species within both groups. This may be most clear among submerged species in regards to *Vallisneria americana*, which existed alone in the deepest water with strong current and sandy sediment.

The order of emergent species appearing on the gradient of increasing depth and declining organic matter in the ordination of Whalebone Cove was essentially the same as that outlined for freshwater wetlands in the Northeast by Nichols (1920), Metzler and Rozsa (1982), Odum et al. (1984), Barrett (1989), and Metzler and Tiner (1992). Barrett (1989), who prepared the most detailed analysis of species assemblages in freshwater tidal wetlands, found that the emergents *Zizania aquatica*, *Pontederia cordata*, and *Sparganium eurycarpum* occurred in the deepest water, as also was found in Whalebone Cove. In somewhat higher positions occurred *Peltandra virginica*, *Acorus calamus*, and *Scirpus fluviatilis*. Barrett found *P. virginica* in deeper water and *S. fluviatilis* in shallower water than the Whalebone Cove ordination indicated, but this is likely a result of small-scale variation captured by the particular samples taken in the different wetlands. Barrett reported that *Z. aquatica* occurred over the greatest range of depths, as was also found in Whalebone Cove.

The results of this study show that plants in freshwater tidal wetlands respond to variation in environmental conditions over small spatial scales and that the variables with the greatest influence differ somewhat between submerged and emergent species. Furthermore, the work shows that water depth and nitrogen levels affect abundance and species density of both submerged and emergent plants. This finding has particular relevance for conservation of freshwater tidal wetlands because of the threats posed by rising sea levels and increasing nitrogen availability (Titus 1988; Vitousek 1994). Human activity has increased the amount of nitrogen in rivers of the Northeast eight-fold compared to pristine waters, largely through atmospheric deposition and agricultural runoff (Howarth 1998). Environmental variables establish thresholds for many species in Whalebone Cove, but density and frequency do not generally respond linearly within species' tolerance ranges (R. Capers, unpubl. data). Therefore, predicting the response of individual species (and persistence of the community) to increasing water depth and nitrogen availability will not be straightforward. Experimental work is needed to determine the conditions required by individual species and the rate at which they adjust to changes in those conditions. Globally changing environmental conditions make the need for this research particularly urgent.

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