

**NUTRIENT RETENTION AND VEGETATION DYNAMICS
IN RESTORED FRESHWATER WETLANDS
ON THE MARYLAND COASTAL PLAIN**

FINAL REPORT

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EXECUTIVE SUMMARY

Objectives

We studied twelve wetlands that were restored in agricultural watersheds on the Maryland Coastal Plain. The objectives of the study were to investigate the effects of the wetlands on watershed discharges of nutrients and sediments, to evaluate vegetation development in the wetlands, and to compare patterns of vegetation succession among different wetlands, hydrologic zones, and soil types.

Study Wetlands

The 0.4 - 7.3 ha wetlands were restored to control agricultural runoff and provide wildlife habitat. They were restored at different times ranging from about 1-30 years before the beginning of the study. The wetland restorations occurred in areas that originally were wetlands that had been converted to non-wetland agriculture by ditching and drainage. To restore the wetlands, a thin layer of soil was removed to create a shallow depression and an earthen dam. Then top soil was returned to the surface, and wetland vegetation was established by natural succession. Water levels in the wetlands are controlled with stand-pipe drains installed in the dams. Water enters and leaves the wetlands mostly as surface flow during times of high runoff. Most of the wetlands are underlain by a clay aquiclude within 0.5 m of the soil surface.

Water Quality Effects

To investigate effects on water quality, we first compared the concentrations of materials in water entering and leaving the wetlands. Concentrations of dissolved inorganic forms of nitrogen (N) and phosphorus (P) were compared at 7 wetlands and, at 4 of those wetlands, concentrations of particulate and organic forms of N, P, and carbon (C) were also compared. Samples of flowing water were taken at several times throughout the year.

Concentrations of materials varied among different sampling times and wetlands. Usually concentrations of total suspended solids and dissolved N, P, and organic C were higher in inflowing water than in outflowing water. However, there were no systematic differences between inflowing and outflowing concentrations for particulate organic N, P, and C, nor for particulate bound phosphate and ammonium.

From the concentration data, we estimated the percentage of inflowing nutrient trapped, assuming that the amount of water entering was equal to the amount leaving. This is a conservative estimate of nutrient trapping because actually more water enters than leaves due to evaporation within the wetland. By this conservative estimate, about 50% of the dissolved phosphate, 70% of the dissolved nitrate, 45% of the total suspended solids, and 30-40% of the dissolved organic N, P, and C that entered the wetlands was trapped during the year that this study was conducted. There was no clear evidence of trapping of dissolved or particulate ammonium, particulate phosphate, or particulate organic N, P, and C. It is surprising that our restored wetlands can act as depositional environments, trapping total suspended solids (TSS), and yet be poor traps for particulate nutrients. Perhaps particle deposition is counter-balanced by export of nutrient-rich particulate organic matter produced by wetland macrophytes, periphyton, benthic algae, and phytoplankton.

Nutrient Mass Balance

To improve our estimates of nutrient trapping in the wetlands, we developed automated sampling systems that continuously monitor water flow in and out of the wetlands and pump samples of inflowing and outflowing water in volumes proportional to flow rate. The first wetland equipped for automated sampling has been monitored for two

full years, including a dry year (May 1995-May 1996) and a wet year (May 1996-May 1997). Water flow through the wetland was very episodic, depending almost entirely on storm events. Most of the flow occurred within a day of a storm event. During major flow events, the amounts of daily inflow and outflow often approached and sometimes exceeded the total volume of standing water in the wetland.

Comparing the annual flow-weighted mean concentrations in inflowing and outflowing water revealed differences in the wetland function during the wet and dry years. During the dry year, the annual flow-weighted mean concentrations of total phosphate and total organic P were significantly higher in inflow than in outflow, and the magnitude of the difference suggested that the wetland trapped more than half of the inflowing P. During the wet year, P concentrations were about the same in inflow and outflow. Patterns of N concentration also suggested greater trapping of N during the dry year than during the wet year. However, the difference between inflow and outflow concentrations was statistically significant only for NO_3 in the wet year. Organic C concentrations were significantly higher in inflowing water than in outflowing water in both years, although the difference was greatest in the wet year. TSS concentrations also suggested trapping of TSS in the wetland in both years, but the differences between inflow and outflow concentrations were not statistically significant.

Based on the annual flow-weighted mean concentrations and annual water flow we calculated what percentages of the inflowing materials were trapped in the wetland in the wet and dry years and over the whole two-year period. During the dry year, 49% of the total N and 69% of the total P entering the wetland was trapped, but during the wet year there was essentially no trapping of total N and total P. Although 49% of the NO_3 influx was trapped during the wet year this was offset by a slight net loss of total organic nitrogen (TON) resulting in no net trapping of total N. About half of the total organic carbon (TOC) influx was trapped in both years. There appeared to be a net trapping of TSS, but due to the extreme variability among weekly fluxes the apparent trapping was not statistically significant. Over the whole two-year period, trapping of NO_3 , total N, TOC, and all forms of P was statistically significant; and 23% of the total N influx and 39% of the total P influx was trapped. The difference between wet and dry years suggests that N and P trapping depends on water residence time within the wetland.

Vegetation Dynamics in Restored Wetlands

Permanent plots were established during the first year of the study to evaluate temporal changes in vegetation and to measure the biomass and nutrient characteristics of the vegetation. The percent cover of all species was determined in permanent plots in three vegetation zones. The outer vegetation zone, called the temporary zone, was flooded for the shortest period of time. The inner zone, where the water was deepest and where few emergent plants grow, is called the submerged zone. Between the temporary and submerged zones is a zone, the emergent zone, that is characterized by a dominance of emergent wetland plants and variable water levels. We sampled the three zones at approximately the same time each year for three years. Biomass in permanent plots that were adjacent to the plots used to measure vegetation cover were harvested in the autumn each year. The harvested biomass was analyzed to determine concentrations of nitrogen (N), phosphorus (P), carbon (C), calcium (Ca), sodium (Na), potassium (K), and magnesium (Mg).

There was significant variability in biomass among the 12 wetlands and significant annual differences within and among wetlands. Annual variation in vegetation dynamics was primarily due to differences in hydrologic conditions over the three years of the study. Differences among wetlands were not related to time since restoration. When data for all sites were combined, annual differences in biomass and most measurements of nutrients (concentrations and standing stocks) did not, however, differ significantly. These results suggest that biomass resources do not vary from year to year at the landscape level, even

though biomass varies from year to year in individual wetlands and among wetlands in any given year. These results further suggest that organisms that move around the landscape (e.g., birds and some mammals) will be able to locate patches (i.e., wetlands) with differing types of vegetation and different levels of resources (i.e., seeds and other plant parts used for feeding, nesting, resting, etc.)

Within wetlands, the pattern of biomass distribution was similar. The highest levels of biomass were found in the outermost temporary zone and the lowest levels were in the innermost submersed zone. This pattern varied little between wetlands and years. In contrast, nutrient concentrations in plant biomass increased from the outer temporary zone to the innermost submersed zone resulting in few differences in nutrient standing crops across zones when concentration and biomass data were combined.

Results demonstrate that some measurements of restoration success (e.g., biomass production) are likely to be highly variable among sites and across years. Other ecosystem parameters (e.g., nutrient concentrations of biomass) are much more constant spatially and temporally indicating that nutrient cycling processes in vegetation are established quickly following restoration.

The dynamic nature of the wetland vegetation was also demonstrated by changes in vegetation cover and species. Seventy-two species were identified in the permanent plots during the three years in which the 9 wetlands restored by the Chesapeake Wildlife Heritage were sampled. *Echinochloa crusgalli*, *Eleocharis obtusa* and *Ludwigia palustris* were the only species that occurred in permanent plots at all sites in each of the three years. Forty-four percent of the species were present at only one site during the three years, 19 species occurred in only one permanent plot during the three years and 4 species were recorded in only two plots. Yearly differences in hydrologic conditions appear to have a particularly strong influence on vegetation dynamics. Species characteristic of drawdown conditions (*Bidens polylepis*, *Cyperus erythrorhizos*, *Eclipta alba*, *Fimbristylis autumnalis*, *Hypericum mutilum*) were more abundant during the driest year (1995). Other species (*Polygonum punctatum*, *Scirpus mucronatus*) were more abundant during wetter years.

Future Research Needs

1. Our initial results suggested that the restored wetlands trap dissolved forms of N and P but not particulate forms. However, our automated sampling could not distinguish particulate forms from dissolved forms because the samples are preserved with acid during the week-long period of sample accumulation. Future automated monitoring should include separate analysis of particulate and dissolved N and P in samples without preservative added.
2. Mass balance studies of several different wetlands are needed to test the generality of our findings. Differences among wetlands may reveal factors that influence the efficiency of nutrient trapping. Because water retention is likely to be an important factor, nutrient trapping in wetlands with different retention times should be compared.
3. Future studies should investigate the mechanisms of nutrient trapping in the wetland including denitrification and accumulation of nutrients in deposited sediments. Knowledge of the factors that control nutrient trapping could then be synthesized in simulation models which would aid in designing wetland restoration to optimize nutrient trapping.
4. The potential benefits of wetland restoration should be extrapolated to larger spatial scales using knowledge of the nutrient trapping processes and geographic information on agriculture and hydrology. Future research should be aimed at developing methods to map sites for future wetland restoration and to predict the benefits of restoration.

5. We did not detect any directional changes in vegetation succession indicating that the vegetation and biomass characteristics of these small restored wetlands are likely to remain dynamic in response to annual variations in hydrologic conditions. These findings need to be evaluated at additional sites and for longer periods of time.
6. At the landscape level, our results suggest that restored wetlands increase plant biodiversity. Vegetation in additional restored wetlands need to be examined to provide a more detailed evaluation of plant species biodiversity than was possible in this project.
7. *Scirpus mucronatus* is apparently an uncommon species in the region but it was both abundant and common in several of the restored wetlands. The potential of the restored wetlands to attract rare and threatened plant species needs to be evaluated in more detail.

Management Implications

1. Nutrient and sediment discharges may be significantly reduced by restoration of wetlands in agricultural watersheds where water discharge is mainly surface runoff. Averaging over wet and dry years, restored wetlands covering about one tenth of the watershed area could trap about one quarter of the N and one third of the P discharged from upstream.
2. The most effective trapping is likely to be achieved by wetland designs that maximize water retention time in the wetland.
3. Wetland restoration should be accompanied by assessment of the effects of restoration because more research is needed to discover the mechanisms of nutrient trapping and to test the generality of our findings over large spatial scales and long time scales.
4. One of the most important objectives of the Chesapeake Bay Program is to improve water quality by controlling non-point runoff from agricultural landscapes. Two primary approaches are currently being used to control non-point runoff from agricultural fields (best management practices, restoration of riparian buffers). Results of this study suggest that wetland restoration may provide an additional approach to control non-point runoff, especially runoff from agricultural fields that have been ditched to remove surface water. Restored wetlands clearly have the potential to retain nutrients and sediments discharges from agricultural landscapes. Information from this study can be used in combination with spatial data that can be analyzed using geographic information systems (i.e., topography, land-use, soils maps) to develop management strategies for specific farms and watersheds.

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WATER QUALITY EFFECTS

**Thomas E. Jordan, Dennis F. Whigham, Kirsten Hofmockel,
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Introduction

Anthropogenic sources of nitrogen (N) and phosphorus (P) to Chesapeake Bay are thought to be responsible for major changes in ecosystem structure and function. Increased N and P loading (Taft et al. 1980, Officer et al. 1984, Conley and Malone 1992) have led to excessive phytoplankton production causing depletion of dissolved oxygen and declines in submersed aquatic vegetation (Malone et al. 1986, Boynton et al. 1982, Gallegos et al. 1992, Kemp et al. 1983). The sources of N and P inputs to Chesapeake Bay (hereafter referred to as the Bay) are numerous as it receives runoff from approximately 50 rivers which drain its 178,000 km² watershed. Many point sources of pollution (e.g., sewage plant effluents) have been identified and actions taken to reduce nutrients and toxins in discharges. Atmospheric inputs of N and P, from within and outside of the watershed, are also significant (Jordan and Weller 1996). One of the main sources of N inputs to the Bay is non-point source runoff, primarily from croplands (Jordan et al. 1997a, b). Large amounts of P also enter the Bay from croplands but most of the P loading to the Bay is associated with suspended sediments (Jordan et al. 1997a, b) which can have numerous sources.

Several initiatives are underway to restore the ecological health of the Bay. A goal of the Chesapeake Bay Program, the largest coordinated restoration effort in the United States, is to reduce nutrient inputs to the Bay by 40% by the year 2000. Toward this goal a variety of initiatives and approaches are being used to reduce non-point sources of N and P. For example, farmers are encouraged to use less fertilizer and pesticides and to adopt practices that reduce soil erosion. Also, incentives for restoring riparian forests have been implemented because both wetland and non-wetland riparian forests are known to improve water quality by removing N, P, and sediments (Pinay and Decamps 1988, Lowrance et al. 1995). However, restoration of riparian forests is often less attractive to farmers than restoration of emergent wetlands, in part because emergent wetlands provide the added benefit of attracting wild waterfowl. Recent research has shown that constructed or restored herbaceous wetlands can also be used to remove sediments and nutrients from non-point sources including agricultural discharges (e.g., Fleischer et al. 1994, Mitsch 1994, Raisin and Mitchell 1995, Whigham 1995). Wetlands may act as filters, removing particulate material, or as sinks, accumulating nutrients, or as transformers, converting nutrients to different forms, including gaseous forms of N and C (Richardson 1989). Thus, restoration of wetlands in agricultural watersheds may reduce nutrient discharges.

In this chapter, adapted from Jordan et al. (1999), we report results of a study to examine the potential to restore emergent wetlands in agricultural fields as an effective means for reducing N and P runoff to the Bay. The project takes place on the Delmarva peninsula on the Eastern Shore of the Bay (Fig. 1), a very flat landscape that has a high percentage of the land in agriculture, primarily corn (maize) and soybeans (soya). Soils throughout the study area typically have a high clay content and an impermeable clay layer near the soil surface. For crops to be successfully grown in these soils, excess water is removed from fields to avoid waterlogging. Most fields in the study area contain a network of connected drainage channels, created by plowing and ditching, that discharge water into wetlands, streams, riparian forests, or directly into the Bay. The drainage networks effectively convert non-point runoff into point source pollution. Ditches that are at the lowest topographic position within an agricultural field are typically in areas that were once wetland habitat. Wetlands restored in such areas were the subject of our study.

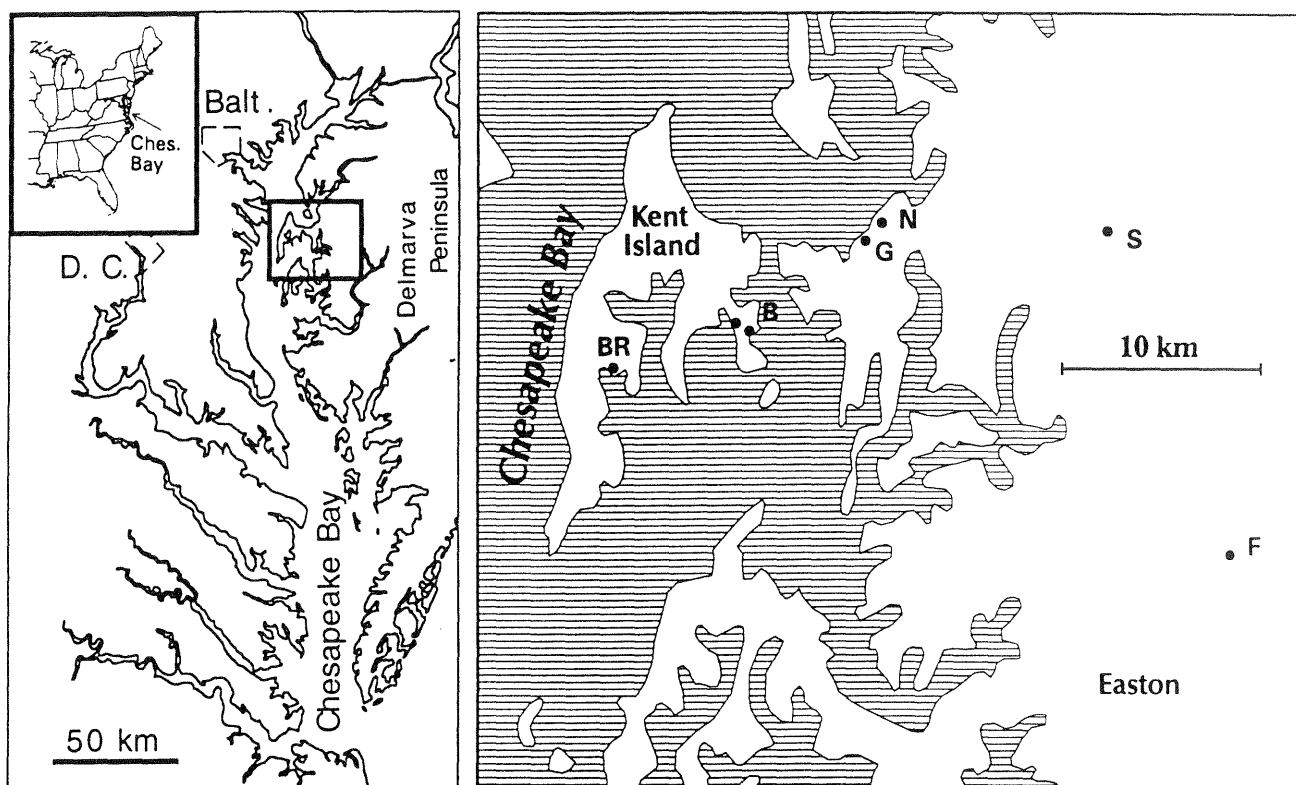


Fig. 1. Inset: Location of Chesapeake Bay on the east coast of the United States. Left: Chesapeake Bay and the cities of Baltimore and Washington, D. C. The box outlines the area of the study wetlands on Kent Island and the Delmarva Peninsula. Right: Locations of the study wetlands on Kent Island and the Delmarva Peninsula near the town of Easton. The different wetlands are Braun (BR), Barnstable (B, two wetlands), Gerber (G), Nesbit (N), Sultenfuss (S), and Foster (F).

Study Sites

The wetlands we studied occur in watersheds dominated by croplands (Table 1). The wetlands were restored by the Chesapeake Wildlife Heritage as part of their program to provide wildlife habitat and improve the quality of runoff water from agricultural fields. The restored wetlands were created 1-8 years before this study began. During restoration, a thin layer of soil was removed to create a shallow depression. Some of the excavated soil was used to create a dam to retain water. After excavation, top soil was returned to the surface and wetland vegetation was established by natural succession. Water levels in the wetland are controlled with stand-pipe drains installed in the dams.

Table 1. Date of restoration of the study wetlands, areas (ha) of the wetlands and their watersheds, percentages of cropland in each watershed, and the ratio of watershed:wetland area. Note: the term watershed here refers to the land draining into the wetland not including the wetland itself.

Name	Wetland		Watershed		Area Ratio
	Date Restored	Area (ha)	Area (ha)	% Cropland	
Barnstable 1	1986	1.3	14	85	11
Barnstable 10	July, 1992	3.7	19	70	5.1
Braun	Sept., 1992	2.3	12	80	5.2
Foster	Oct., 1993	0.49	4.4	60	8.8
Gerber	July, 1990	0.41	3.6	30	9.0
Nesbit	July, 1989	0.39	10	95	25
Sultenfuss	Nov., 1992	1.4	19	95	16

Water enters and leaves all but one of the wetlands almost entirely as surface flow that is mostly restricted to times of high runoff associated with heavy rain. All the wetlands, except the Nesbit site, are underlain by an impermeable layer of clay within 0.5 m of the soil surface. We concluded that the clay layer blocks water infiltration because we found that clay sampled from beneath inundated areas appears to be dry. Water levels in the wetlands typically remain close to the tops of the standpipes during late fall, winter, and spring. When the wetlands were full, water depths were generally less than 0.5 m and nowhere more than 1 m. In summer, evapotranspiration lowers the water levels, thus exposing most of the sediment that is submerged the rest of the year. Occasionally, rain storms partly refill the wetland during the summer.

A variety of emergent and submerged macrophytes colonized the wetlands soon after restoration. At the time of our study, 40 macrophyte species were found in the wetlands. Each of the 7 wetlands had a different combination of macrophytes, but *Eleocharis obtusa* was the most dominant species in 3 wetlands and the second most dominant in one of the wetlands (Table 2). *Echinochloa crusgalli* was among the top 3 dominant in 3 of the wetlands; and *Ludwigia palustris*, *Potamogeton diversifolius*, and *Panicum virgatum* were among the top 3 dominants in 2 of the wetlands. None of the 7 wetlands had a completely unique assortment of species comprising the three most dominant (Table 2).

Table 2. The three most dominant macrophyte species in the wetlands in 1994 based on importance values ([relative frequency+relative cover]/2) in permanent plots (see chapter 4).

Wetland	Most Dominant Macrophyte Species		
	First	Second	Third
Barnstable 1	<i>Eleocharis obtusa</i>	<i>Ludwigia palustris</i>	<i>Scirpus americanus</i>
Barnstable 10	<i>Potamogeton diversifolius</i>	<i>Panicum virgatum</i>	<i>Echinochloa crusgalli</i>
Braun	<i>Panicum virgatum</i>	<i>Xanthium strumarium</i>	<i>Setaria glauca</i>
Foster	<i>Eleocharis obtusa</i>	<i>Alisma plantago-aquatica</i>	<i>Rotala ramosior</i>
Gerber	<i>Eleocharis obtusa</i>	<i>Scirpus mucronatus</i>	<i>Digitaria ischaemum</i>
Nesbit	<i>Ludwigia palustris</i>	<i>Eleocharis obtusa</i>	<i>Echinochloa crusgalli</i>
Sultenfuss	<i>Leersia oryzoides</i>	<i>Potamogeton diversifolius</i>	<i>Echinochloa crusgalli</i>

Methods

Sampling and Analysis

We sampled water flowing from the 7 wetlands and water entering through up to 3 drainage leads per wetland for up to 10 dates, depending on the wetland, from February, 1994 through May, 1995. We designed our sampling to cope with the episodic and unpredictable nature of water flow through the wetlands. We installed polyethylene sampling bottles in drainage leads and near the outlets of the wetlands that would trap storm runoff. When possible, we also visited the wetlands during periods of runoff to collect samples by hand. However, because runoff was so intermittent, we could not collect complete sets of inflow and outflow samples from all the wetlands on each sampling date. Initially, we measured concentrations of dissolved inorganic nutrients, including phosphate, ammonium, and nitrate (plus nitrite). In the fall of 1994, we began measuring concentrations of suspended sediments, particulate nutrients and organic C, N and P. Standard techniques were used for analysis of N and P species. Samples to be analyzed for dissolved substances were filtered with prewashed 0.45 mm Millipore filters. Total P in filtered and unfiltered samples was digested to phosphate with perchloric acid (King 1932). Phosphate in the digestate and dissolved phosphate (DPO_4) in filtered samples were analyzed by reaction with stannous chloride and ammonium molybdate (APHA 1989). Total Kjeldhal N was digested with sulfuric acid, Hengar granules, and hydrogen peroxide (Martin 1972). The resultant ammonia was distilled and analyzed by Nesslerization (APHA 1989). In undigested aliquots, dissolved ammonium (DNH_4) was oxidized to nitrite by alkaline hypochlorite (Strickland and Parsons 1972), dissolved nitrate was reduced to nitrite by cadmium amalgam, and nitrite was analyzed by reaction with sulfanilamide (APHA 1989). We present data on the sum of nitrite and nitrate concentrations, which we refer to as NO_3 . Phosphate and ammonium bound to particles were extracted by collecting particles on 0.4 mm Nuclepore filters, and then rinsing with 1 M KCl (Keeney and Nelson 1982) to extract particulate ammonium (PNH_4), or with 0.5 N H_2SO_4 (Correll and Miklas 1975) to extract particulate phosphate (PPO_4). The extracts were analyzed with the same methods used for DNH_4 and DPO_4 .

From results of the above analyses we calculated particulate organic N (PON) and P (POP), and dissolved organic N (DON) and P (DOP). PON was calculated by subtracting Kjeldhal N in filtered samples and PNH_4 from Kjeldhal N in unfiltered samples. Similarly, POP was calculated by subtracting the total P in filtered samples and PPO_4 from total P in unfiltered samples. DON was calculated by subtracting DNH_4 from Kjeldahl N in filtered samples. Likewise, DOP was calculated by subtracting DPO_4 from total P in filtered samples.

Dissolved and particulate organic carbon (DOC and POC) were analyzed by drying samples at 60°C , followed by reaction with potassium dichromate in 67% sulfuric acid at 100°C for 3 h (Maciolek 1962). Organic carbon was calculated from the amount of unreacted dichromate measured colorimetrically (Maciolek 1962, Gaudy and Ramanathan 1964). Total suspended solids (TSS) were measured by filtering through prewashed, preweighed 0.4 mm filters, rinsing with distilled water to remove salts, drying, and reweighing.

Results and Discussion

Concentrations of total suspended solids and all forms of P, N, and organic C differed greatly among sampling dates (e.g., Fig. 2). However, the differences among dates did not seem to be part of a seasonal pattern at 5 of the wetlands where dissolved inorganic nutrients were sampled on 7-10 different dates throughout the year (e.g., Fig. 2). The extreme variability in concentrations among runoff events may have been caused by variable dilution from different runoff volumes, farming activities, or differences in soil conditions prior to the runoff event.

Because there were no clear temporal patterns, we averaged data from different dates to compare concentrations among different nutrient forms, among different wetlands, and between inflowing and outflowing water. We tested the statistical significance of differences between inflowing and outflowing water using Wilcoxon's signed-ranks test (Sokal and Rohlf 1981). We selected a non-parametric test because sporadic high concentrations resulted in a non-normal distribution of differences in concentration. For the test, we first calculated the difference between inflowing and outflowing concentration for each sampling date and then determined the probability that the differences for all the dates for each wetland are statistically different from zero. Pairing comparisons by date helped resolve differences when variance among dates is high.

Usually inflowing water had higher nutrient concentrations than outflowing water, suggesting that the wetlands remove nutrients from the water (Figs. 3 and 4). For most of the wetlands, mean DPO_4 concentrations were higher in inflowing than outflowing water. This difference was significant ($p < 0.05$) for 4 out of 7 wetlands (Fig. 3). Similarly, the concentration of DNH_4 was significantly higher in inflowing than outflowing water at two wetlands (Fig. 3). NO_3 concentrations were significantly higher in inflowing water at 3 of the wetlands (Fig. 3).

We had at most 5 pairs of measurements of inflowing and outflowing concentrations for total suspended solids and for particulate and organic forms of P, N, and C. With so few pairs, it is not possible to achieve a significance level of $p < 0.05$ with Wilcoxon's signed-ranks test. However, with 5 pairs, if the differences between inflowing and outflowing concentrations are all of like sign, then $p = 0.0625$, which is close to the traditional significance cutoff. In all cases where this level of significance was achieved, inflowing concentrations were higher than outflowing concentrations. This occurred for POP at one wetland, for DON at three wetlands, and for DOC at 2 wetlands, out of a total of 4 wetlands where these nutrients were measured (Fig. 4). In general, inflowing concentrations exceeded outflowing concentrations more for dissolved nutrients and TSS than for particulate forms of N, P, and organic C (Figs. 3 and 4).

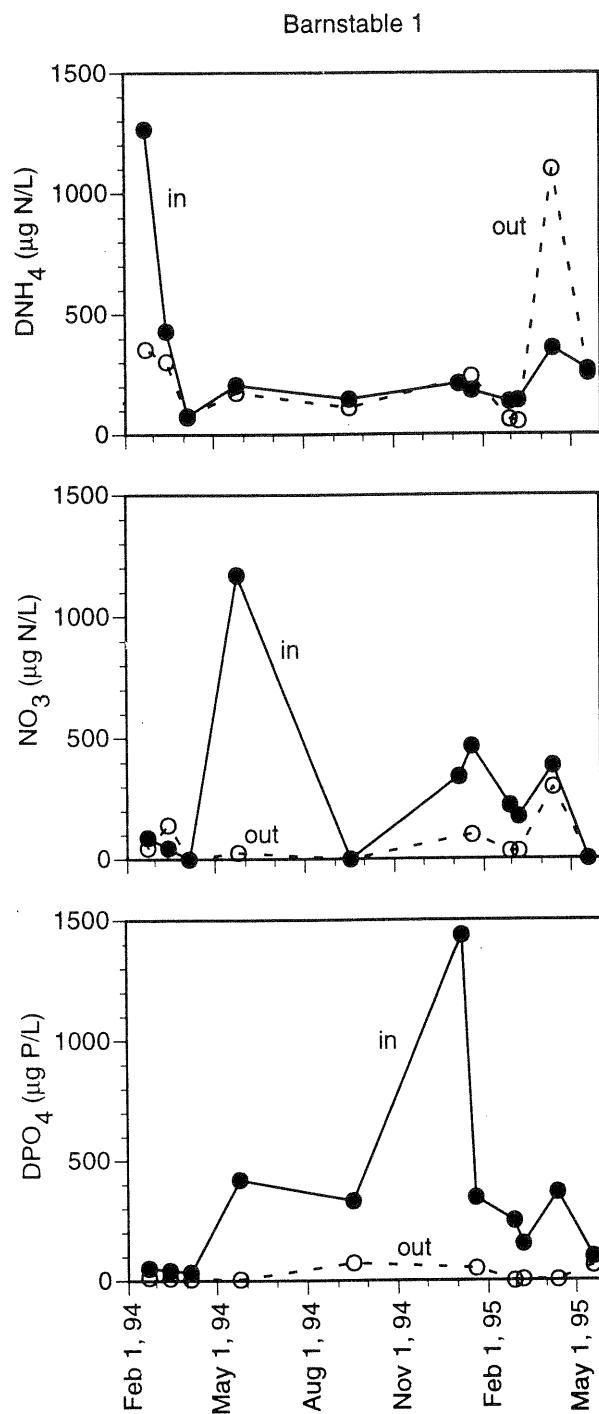


Fig. 2. Concentrations of DNH₄, NO₃, and DPO₄ in water entering (filled circles, solid lines) and leaving (open circles, dashed lines) the Barnstable 1 wetland versus time. Concentrations entering are averages of samples taken from 1-3 points of entry.

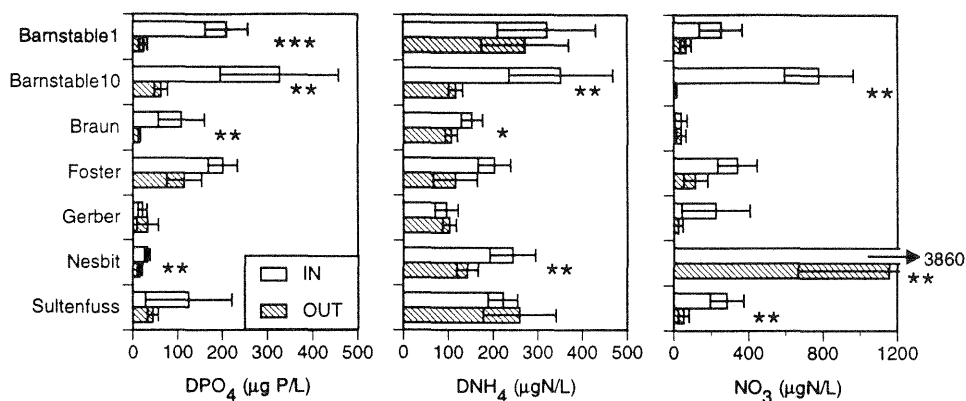


Fig. 3. Mean concentrations of DPO_4 , DNH_4 , and NO_3 in water entering (open bars), and leaving (shaded bars) seven different wetlands. Brackets are \pm standard errors. Asterisks indicate levels of significance of differences between inflowing and outflowing concentrations (*** $p < 0.01$, ** $0.01 < p < 0.05$, * $0.05 < p < 0.07$). Significance levels were calculated by Wilcoxon's signed ranks test.

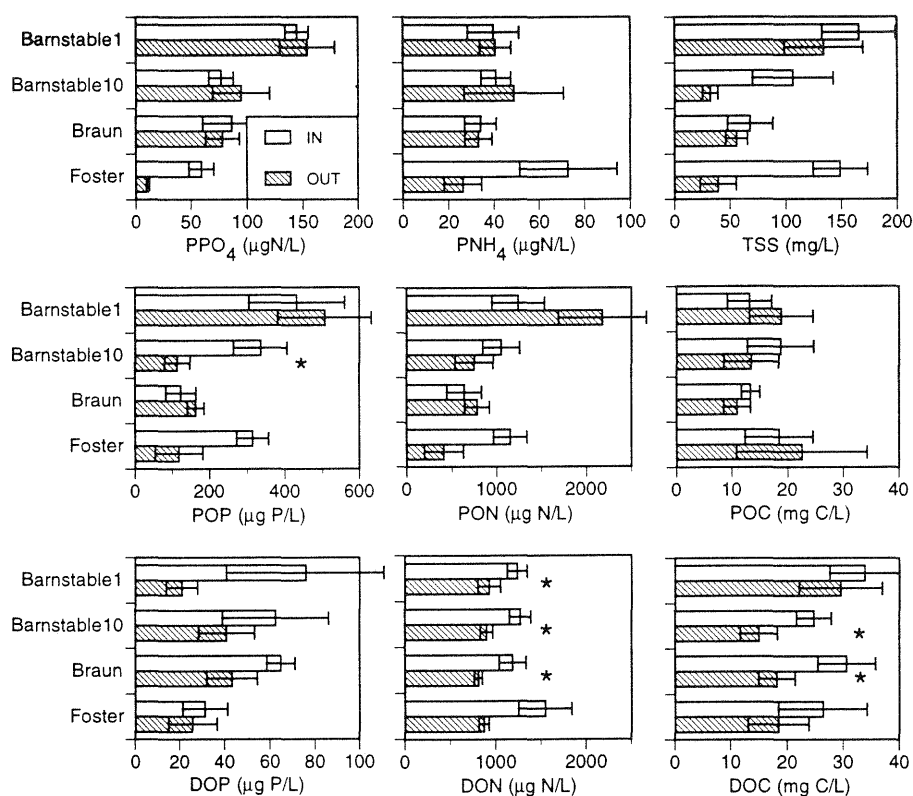


Fig. 4. Mean concentrations of PPO_4 , PNH_4 , TSS, POP, PON, POC, DOP, DON, and DOC in water entering (open bars), and leaving (shaded bars) four different wetlands. Brackets are \pm standard errors. Asterisk indicates that the difference between inflowing and outflowing concentrations is significant at $0.05 < p < 0.07$ as calculated by Wilcoxon's signed ranks test.

For four wetlands, we could compare concentrations of different forms of P, N, and C. In general, the most abundant form of P was POP while the least abundant was DOP in both inflowing and outflowing water (Figs. 3 and 4). In some cases, POP concentrations were more than 10 times DOP concentrations (Fig. 4). N was usually most abundant in organic forms, except at one wetland which had unusually high NO_3 concentrations (Figs. 3 and 4). PNH_4 was usually the least abundant form of N (Figs. 3 and 4). Organic C was usually more abundant in dissolved than in particulate form (Fig. 4).

For some forms of nutrients, the concentrations in water entering our wetlands were markedly different from those in water discharged from watersheds elsewhere on the Delmarva peninsula. Concentrations of N in watershed discharges increase as the proportion of cropland in the watershed increases (Jordan et al. 1997a). Watersheds with >60% cropland typically discharge water with NO_3 concentrations of 2000-3000 mg N/L and total organic N (DON+PON) concentrations of 1000-1300 mg N/L (Jordan et al. 1997a). By comparison, watersheds with similar percentages of cropland that drain into our wetlands discharged water with much lower concentrations of NO_3 (<1000 mg N/L, Fig. 3) and much higher concentrations of total organic N (>2000 mg N/L, Fig. 4). Concentrations of total organic C (DOC+POC) were also higher in water entering the wetlands (>40 mg C/L) than in discharges from other Delmarva watersheds (<14 mg C/L, Jordan et al. 1997a). These differences are probably related to the lack of groundwater flow from the watersheds that drain into the wetlands. Jordan et al. (1997c) found that NO_3 concentrations decrease and total organic N and C concentrations increase as the proportion of groundwater in watershed discharge decreases. It is consistent that the one wetland with relatively high concentrations of NO_3 and low concentrations of total organic N in inflowing water (Braun, Figs. 3 and 4) is also the only wetland that seems to receive some groundwater inflow, judging from the lack of impermeable clay near the soil surface and from the persistence of inflow during periods of low rainfall.

For some forms of nutrients, the concentrations in water entering our wetlands were similar to those found in watershed discharges elsewhere on the Delmarva peninsula. For example, total NH_4 ($\text{DNH}_4 + \text{PNH}_4$) concentrations in inflowing water were similar to those in watershed discharges measured by Jordan et al. (1997a). Also, concentrations of P forms and TSS in inflowing water are within the high end of the range reported by Jordan et al. (1997a).

From the differences in nutrient concentrations in inflowing and outflowing water we estimated the percentage of the inflowing material removed from the water passing through the wetland. For this estimation, we assumed that the amount of water entering each wetland is equal to the amount leaving so the net uptake (or net release) of material is proportional to the difference between concentrations in inflowing and outflowing water. Actually, this assumption should lead to underestimation of material removed because evaporation will result in less water leaving the wetland than entering. For example, our later mass balance study found that annually 8-18% of the water entering the Barnstable 1 wetland did not flow out but presumably evaporated (Table 2 in chapter 2). Therefore, a finding that concentrations of materials were the same in inflowing and outflowing water would imply that 8-18% of the materials were trapped within the wetland. Although we do not know the water budgets of the wetlands during the present study, an estimate of nutrient retention based on concentration differences and neglecting evapotranspiration is useful as a conservative approximation of the relative efficiency of nutrient removal. Thus, for each wetland, we calculated the proportion of inflowing nutrient removed as the difference of inflowing-outflowing concentration divided by the inflowing concentration. We then averaged the percentages of inflow removed for all the wetlands combined.

The average percentage of inflow removed ranged from 68% for NO_3 to -5% for POC (a negative percentage suggests net release, Fig. 5). Dissolved forms of nutrients were much more efficiently removed than particulate forms (Fig. 5). The average percentages of inflow removed were significantly greater than zero ($p < 0.05$, T test) for all the dissolved nutrients except for DNH_4 , which was close to the significance cutoff ($p = 0.070$). In contrast, the percentages removed were not significant for any particulate nutrients, although average removal of TSS (45% of inflowing TSS) was nearly significant ($p = 0.061$). The apparent trapping of TSS without removal of particulate nutrients suggests that the trapped TSS is relatively poor in associated PPO_4 , PNH_4 , and organic P, N, and C.

Our results suggest that restored wetlands could make a substantial contribution toward the Chesapeake Bay Program's goal of lowering nutrient inputs to the Bay by 40%. The average percentages of inflowing dissolved nutrients removed ranged from 25% for DNH_4 to 68% for NO_3 . However, the lack of efficient removal of particulate nutrients lowers the overall efficiency of removing total P, N, and organic C. Based on data from our four most intensively sampled wetlands, the average percentages of inflowing total P, N, and organic C removed were 43%, 23%, and 18%, respectively. Of these averages, only the average for total P was significantly greater than zero ($p = 0.027$).

Removal efficiencies reported from other wetland studies differ widely, in part due to differences in the rate of water flow through the wetlands, or to differences in the relative areas of the wetlands and their catchments. Studies reviewed by Verhoeven and van der Toorn (1990) found that natural and constructed wetlands receiving wastewater and natural wetlands with high inflows of nutrients removed 50-99% of the incoming N and 25-98% of the incoming P. Removal of P, which depends on accumulation within the wetland, may reach a limit (e. g., Richardson and Marshall 1986), but removal of N, which can result from denitrification, may persist indefinitely (Verhoeven and van der Toorn 1990). Data summarized by Mitsch and Gosselink (1993) suggest a rough correlation between nutrient loading and percentage removed. Jansson et al. (1994), comparing small lakes, ponds, and wetlands, concluded that the removal of nutrients increased as the retention time of water within the system increased. Water retention time increases as the volume of the wetland system increases in relation to the catchment area. The effect of catchment area may account for differences between the wetlands we studied and those studied by Fleischer et al. (1994). Three of the wetlands they studied received agricultural runoff and were morphologically similar to ours but covered only 0.3-0.02% of their catchment area and removed only 3-10% of the inflowing N. By comparison, our wetlands covered 4-16% of their catchment area (Table 1), and removed about 23% of the inflowing N. The efficiency of P removal by wetlands has been successfully predicted with a Vollenweider model, which considers both nutrient concentration and water through-flow (Mitsch et al. 1995). However, P removal is influenced not only by hydrological loading but also by the chemical composition of wetland sediments (Richardson 1985). Clearly, more research is needed to account for the enormous differences in N and P removal among wetlands.

It is surprising that our restored wetlands can act as depositional environments, trapping TSS, and yet be poor traps for particulate nutrients. Perhaps particle deposition is counter-balanced by export of particulate organic matter produced by wetland macrophytes, periphyton, benthic algae, and phytoplankton. In contrast to our restored wetlands, brackish tidal marshes on the western shore of the Chesapeake Bay trap particulate nutrients and release dissolved nutrients (Jordan et al. 1983). The opposite behavior of tidal marshes may compliment the nutrient removal effect of freshwater wetlands just upstream. Our results suggest that it is important to distinguish the fate of particulate and dissolved organic nutrients, but few studies have considered these fractions separately.

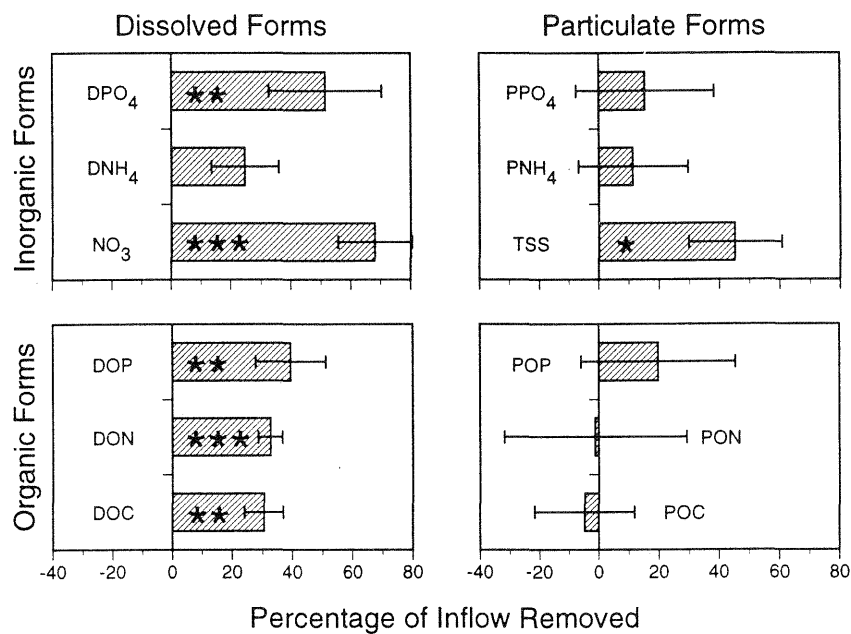


Fig. 5. Mean percentages of inflowing material removed as inferred from differences between inflowing and outflowing concentrations. Percentages for dissolved inorganic forms are averaged for 7 wetlands. Percentages for other forms are averaged for 4 wetlands. Brackets are \pm standard errors. Asterisks indicate levels of significance for difference from zero based on the t test (** $p < 0.01$, ** $0.01 < p < 0.05$, * $0.05 < p < 0.07$). TSS is grouped with particulate inorganic forms although it includes particulate organic matter.

To improve estimates of nutrient removal by our wetlands, we need measurements of the amount of water inflow and outflow. The estimates reported in this chapter, for example, are somewhat low since they ignore evaporation within the wetlands. Also, the high variance in concentrations among sampling dates and the paucity of dates sampled limits the precision of our estimates of nutrient trapping. At the four most intensively sampled wetlands, we have used automated samplers to measure water inflow and outflow collect samples of inflowing and outflowing water in volumes proportional to flow (see following chapter). This greatly improves the precision and accuracy of our measurements of nutrient trapping.

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NUTRIENT MASS BALANCE

Thomas Jordan, Dennis Whigham, Mary Pittek, and Kirsten Hofmockel

Introduction

Recent research has shown that constructed or restored herbaceous wetlands can also be used to remove sediments and nutrients from non-point sources including agricultural discharges (e.g., Fleischer et al. 1994, Mitsch 1994, Raisin and Mitchell 1995, Whigham 1995). Wetlands may act as filters, removing particulate material, or as sinks, accumulating nutrients, or as transformers, converting nutrients to different forms, including gaseous forms of nitrogen (N) and carbon (C) (Richardson 1989).

A central objective of this study was to measure the effect of the restored wetlands on water quality by comparing inflowing and outflowing water. By comparing several wetlands, we can also assess how wetlands differ with age and with differing physical and biological characteristics. Our broader goal was to assess the use of restored wetlands as a means of reducing nutrient inputs to Chesapeake Bay.

Study sites

The wetlands are located on the Delmarva peninsula on the Eastern Shore of the Chesapeake Bay (Fig. 1) in a very flat landscape that has a high percentage of the land in agriculture, primarily corn and soybeans. Soils throughout the study area typically have a high clay content and an impermeable clay layer near the soil surface. For crops to be successfully grown in these soils, excess water is removed from fields to avoid waterlogging. Most fields in the study area contain a network of connected drainage channels, created by plowing and ditching, that discharge water into wetlands, streams, riparian forests, or directly into the Bay. The drainage networks effectively convert wetlands to dry lands and non-point runoff into point source pollution. Ditches that are at the lowest topographic position within an agricultural field are typically in areas that were once wetland habitat. Wetlands restored in such areas are the subject of our study.

The study wetlands were restored by the Chesapeake Wildlife Heritage as part of their program to provide wildlife habitat and improve the quality of runoff water from agricultural fields. The restored wetlands (Table 1) were created 1-8 years before this study began. During restoration, a thin layer of soil was removed to create a shallow depression. Some of the excavated soil was used to create a dam to retain water. After excavation, top soil was returned to the surface and wetland vegetation was established by natural succession. Water levels in the wetland are controlled with stand-pipe drains installed in the dams.

Water enters and leaves all but one of the wetlands almost entirely as surface flow that is mostly restricted to times of high runoff associated with heavy rain. All the wetlands, except the Nesbit site, are underlain by an impermeable layer of clay within 0.5 m of the soil surface. We concluded that the clay layer blocks water infiltration because we found that clay sampled from beneath inundated areas appears to be dry.

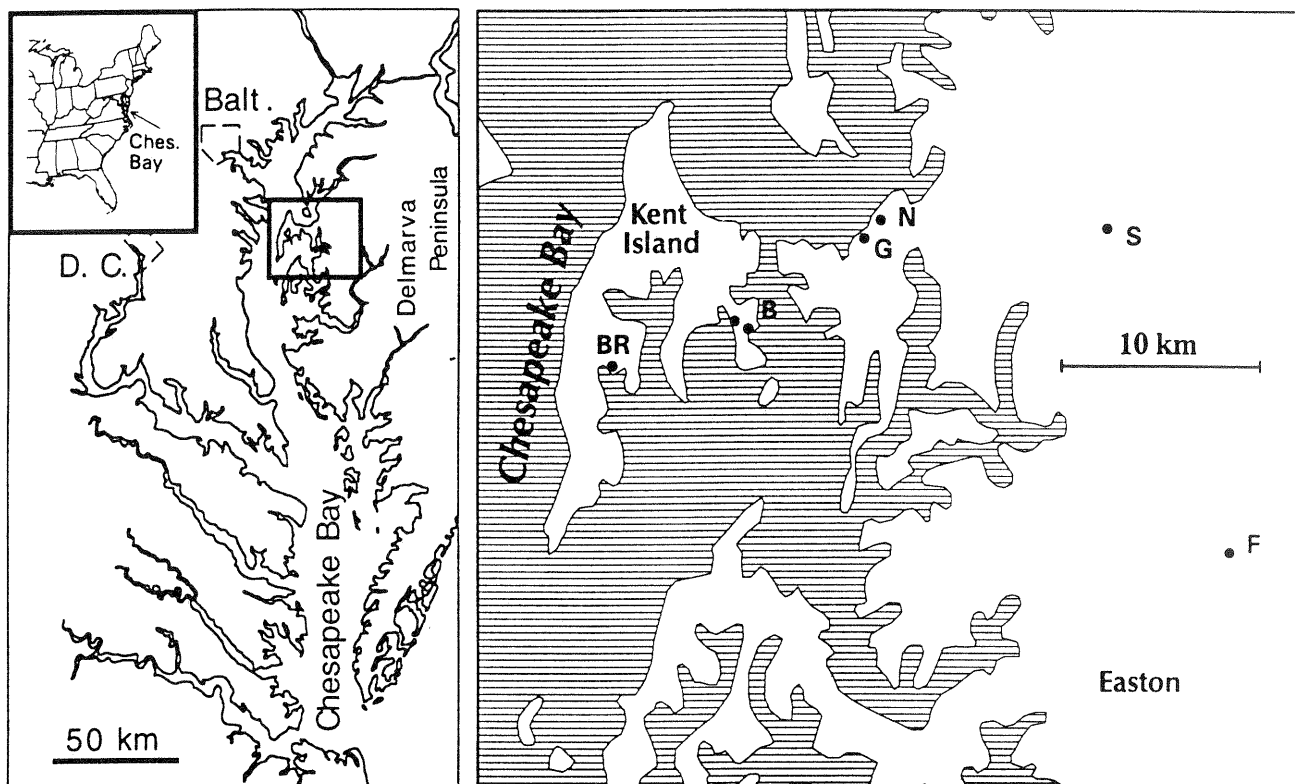


Fig. 1. Inset: Location of Chesapeake Bay on the east coast of the United States. Left: Chesapeake Bay and the cities of Baltimore and Washington, D. C. The box outlines the area of the study wetlands on Kent Island and the Delmarva Peninsula. Right: Locations of the study wetlands on Kent Island and the Delmarva Peninsula near the town of Easton. The different wetlands are Braun (BR), Barnstable (B, two wetlands), Gerber (G), Nesbit (N), Sultenfuss (S), and Foster (F).

Table 1. Characteristics of the study wetlands and their watersheds.

Site	Watershed			Wetland	
	Soils	%Crops	Area (ha)	Area (ha)	Restored
Barnstable 1	Mattapex/Elkton	85	14	1.3	1986
Barnstable 10	Mattapex/Elkton	70	19	3.7	July, 1992
Braun	Mattapex	80	12	2.3	Sept., 1992
Sultenfuss	Falsington	95	19	1.4	Nov., 1992
Nesbit	Falsington/Sassafras	95	10	0.39	July, 1989
Gerber	Falsington	30	3.6	0.41	July, 1990
Foster	Falsington	60	4.4	0.49	Oct., 1993

Methods

Sampling

In the first year of the project, we collected grab samples of water entering and leaving the wetlands during flow events. We sampled water draining from 7 wetlands and water entering each wetland through up to 3 drainage leads for up to 10 dates, depending on the wetland, from February, 1994 through May, 1995. We designed our sampling to cope with the episodic and unpredictable nature of water flow through the wetlands. We installed polyethylene sampling bottles in drainage leads and near the outlets of the wetlands that would trap storm runoff. When possible, we also visited the wetlands during periods of runoff to collect samples by hand. However, because runoff was so intermittent, we could not collect complete sets of inflow and outflow samples from all the wetlands on each sampling date. Initially, we measured concentrations of dissolved inorganic nutrients, including phosphate, ammonium, and nitrate (plus nitrite). In the fall of 1994, we began measuring concentrations of suspended sediments, particulate nutrients and organic C, N and P. Results of the grab sampling study are reported in the previous chapter and in Jordan et al. (1999).

Later in the project, we installed automated systems in four wetlands to measure flow and collect water samples in volumes proportional to flow. Each automated sampler has a float and counter weight suspended in a stilling-well, which was connected to the ponded water in the wetland. A data logger records the position of the float to monitor the pond depth. In three of the wetlands, one or more V-notch weirs are located at the drain pipe. For these wetlands, the rate of outflow is calculated from the depth of water in V-notch. One wetland, Foster, has a 6" parshall flume in the ditch that collects outflowing water. There the outflow is calculated from the depth in the flume, which, like the pond depth, is measured with a float and counter weight suspended in a stilling well. At all the wetlands, the rate of inflow is calculated from the outflow rate and the rate of change of the wetland pond volume. The data logger controls pumps that collect separate samples of inflowing and outflowing water in volumes proportional to the flow rates. This system continuously monitors water flow and collects composite samples that accurately represent the water quality of the inflowing and outflowing water. The samples of both inflowing and outflowing water are split into two jugs, one with acid added as a preservative. Each week the samples that accumulated during the week are brought into the laboratory for analysis. The acid-preserved samples are analyzed for nutrient concentrations, but, because of the acid preservative, the concentrations represent the total of dissolved nutrients and nutrients bound to particles that are released in the presence of acid. The relative proportions of particulate and dissolved nutrients were measured by our grab sampling

program (previous chapter). The unpreserved samples collected by the automated sampling system are analyzed for total particulate matter. To complement the automated sampling, weekly grab samples are taken for pH and conductivity. In the Barnstable 1 wetland, the automated system has been collecting flow data since February 1995, and pumping samples since May 1995. At the Barnstable 10, Braun, and Foster wetlands automated samplers have been operating since December 1996.

Chemical Analysis

Standard techniques were used for analysis of N and phosphorus (P) species. Dissolved and particulate species were analyzed separately in grab samples, but in automatically composited samples the combined totals of particulate and dissolved species were measured. Samples to be analyzed for dissolved substances were filtered with prewashed 0.45 mm Millipore filters. Total P in filtered and unfiltered samples was digested to phosphate with perchloric acid (King 1932). Phosphate in the digestate and dissolved phosphate (DPO_4) in filtered samples were analyzed by reaction with stannous chloride and ammonium molybdate (APHA 1989). Total Kjeldhal N was digested with sulfuric acid, Hengar granules, and hydrogen peroxide (Martin 1972). The resultant ammonia was distilled and analyzed by Nesslerization (APHA 1989). In undigested aliquots, dissolved ammonium (DNH_4) was oxidized to nitrite by alkaline hypochlorite (Strickland and Parsons 1972), dissolved nitrate was reduced to nitrite by cadmium amalgam, and nitrite was analyzed by reaction with sulfanilamide (APHA 1989). We present data on the sum of nitrite and nitrate concentrations, which we refer to as NO_3 . For grab samples, phosphate and ammonium bound to particles were extracted by collecting particles on 0.4 mm Nuclepore filters, and then rinsing with 1 M KCl (Keeney and Nelson 1982) to extract particulate ammonium (PNH_4), or with 0.5 N H_2SO_4 (Correll and Miklas 1975) to extract particulate phosphate (PPO_4). The extracts were analyzed with the same methods used for DNH_4 and DPO_4 .

From results of the above analyses we calculated particulate organic N (PON) and P (POP), and dissolved organic N (DON) and P (DOP). PON was calculated by subtracting Kjeldhal N in filtered samples and PNH_4 from Kjeldhal N in unfiltered samples. Similarly, POP was calculated by subtracting the total P in filtered samples and PPO_4 from total P in unfiltered samples. DON was calculated by subtracting DNH_4 from Kjeldahl N in filtered samples. Likewise, DOP was calculated by subtracting DPO_4 from total P in filtered samples.

Dissolved and particulate organic carbon (DOC and POC) were analyzed by drying samples at 60° C, followed by reaction with potassium dichromate in 67% sulfuric acid at 100° C for 3 h (Maciolek 1962). Organic carbon was calculated from the amount of unreacted dichromate measured colorimetrically (Maciolek 1962, Gaudy and Ramanathan 1964). Total suspended solids (TSS) were measured by filtering through prewashed, preweighed 0.4 mm filters, rinsing with distilled water to remove salts, drying, and reweighing.

Results

Water Flow

The four wetlands with automated samplers showed similar changes in water depth through the seasons, with a period of decreasing depth in the summer of 1997 (due to evapotranspiration exceeding water inflow) and a period of refilling in late fall (Fig. 2). Data from Barnstable 1 include three years. The driest summer with the greatest decrease in water depth was in 1995. The summer of 1996 was the wettest, with flow continuing all summer and virtually no period of low depth. Flow in the summer of 1997 was intermediate, but the depth in Barnstable 1 remained low from October 1997-February 1998 because of a leak in the wetland berm.

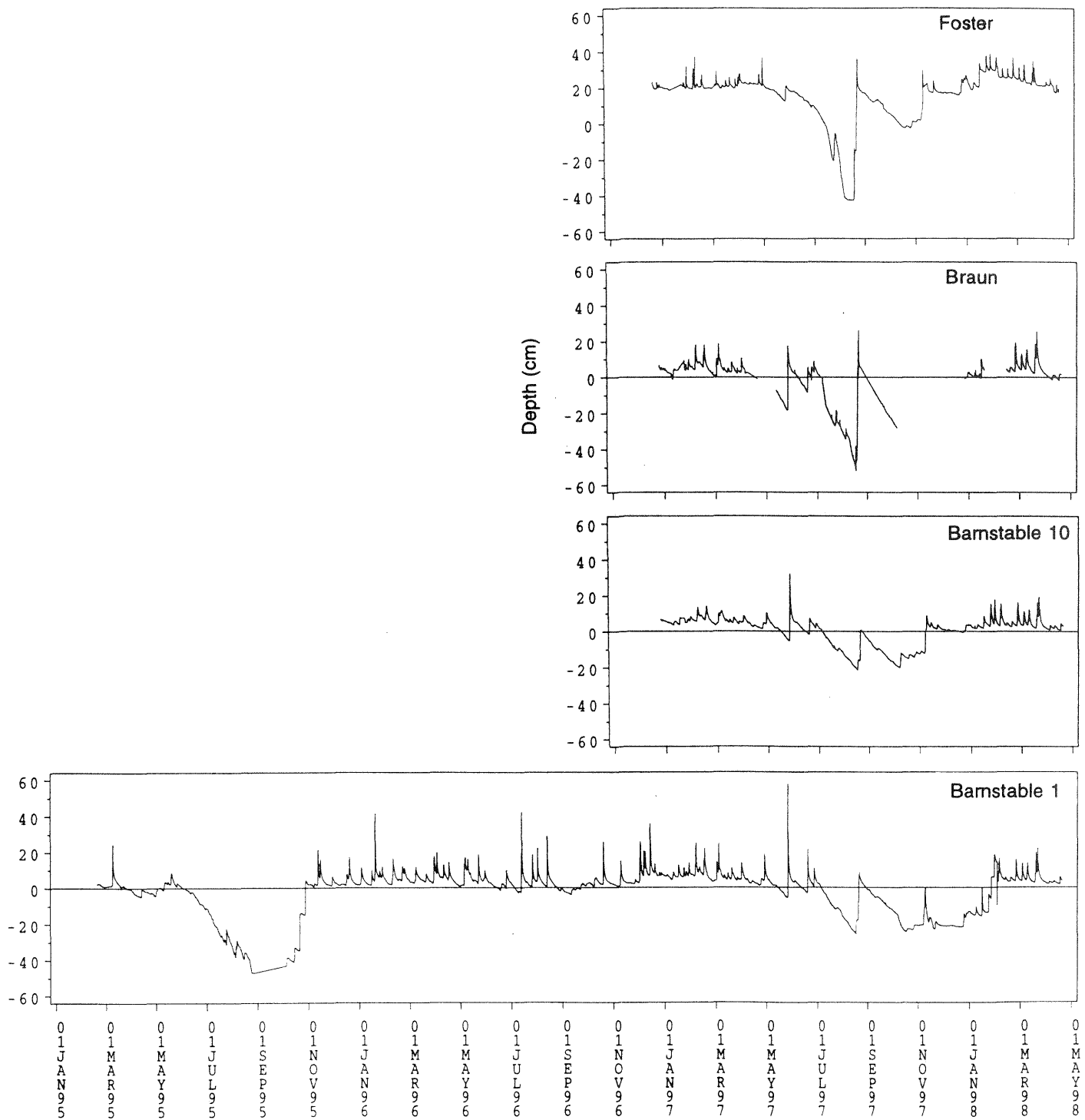


Fig. 2. Water depth (cm) vs. time in four wetlands equipped with automated samplers (Foster, Braun, Barnstable 10, and Barnstable 1). For all wetlands except Foster, depth is relative to the bottom of the V-notch in the weir at the wetland drain. Thus, for those wetlands outflow occurs only when depths are above zero. Foster has no weir but drains through a standpipe. Depths at Foster are relative to an arbitrary benchmark elevation. Gaps in the depth record at Braun occurred due to equipment failures.

At some times flow could not be measured at some of the wetlands. At Barnstable 1, flow could not be measured while the berm was leaking. At Foster, there were some malfunctions of the depth sensor for the flume. At Braun, there were some failures of the data logger resulting in gaps in the depth data (Fig. 2). At Barnstable 10, water flowed over the berm during high flow conditions prior to October 1997. When the berm overflowed, flow over the weir became an underestimation of total flow. The problem of overflows at Barnstable 10 was corrected in October 1997 by lowering the weir and adding a second weir at the same height. We will continue automated sampling with funding from NRCS to obtain at least one full year of concurrent automated sampling at all four wetlands. Presently our automated sampling is distributed unevenly through the seasons at the Foster, Braun, and Barnstable-10 wetlands.

At Barnstable 1, we accomplished two full years of automated sampling including a dry year (May 1995-May 1996) and a wet year (May 1996-May 1997). Flow through the wetland was very episodic, depending almost entirely on storm events (Fig. 3). Most of the flow occurred within a day of a storm event. During major flow events, the amounts of daily inflow and outflow often approached and sometimes exceeded the total volume of standing water in the wetland (Fig. 3). When throughflow equals standing volume, about half of the standing water would be discharged and half of the discharged water would be water that had just entered, assuming complete mixing of standing and inflowing water.

Even on a weekly basis, flow through the Barnstable-1 wetland was very uneven (Fig. 4). During many weeks there was no flow at all (especially in the summer and early fall of 1995). Flow during a few weeks exceeded the average weekly flow by about a factor of ten (Fig. 4). Therefore, the weekly composite samples from weeks with high flow were very important in calculating the total annual flow of nutrients and sediments.

On an annual basis, inflow exceeded outflow at the Barnstable-1 wetland because of evapotranspiration within the wetland (Table 2). In the dry year, inflow was about 20% higher than outflow, but in the wet year inflow was only about 9% higher than outflow. Outflow during the wet year was about double the outflow during the dry year. Inflow during the wet year was about 40 times the water holding capacity of the wetland.

Table 2. Water flow (m^3) into and out of the Barnstable 1 wetland and percentage of inflow water that evaporated in the wetland.

<u>Period</u>	<u>inflow (m^3)</u>	<u>outflow (m^3)</u>	<u>evaporated</u>
May 95-May 96 (dry year)	51,300	42,300	17.5%
May 96-May 97 (wet year)	<u>93,900</u>	<u>86,200</u>	<u>8.2%</u>
May 95-May 97 (both years)	145,200	128,500	11.5%

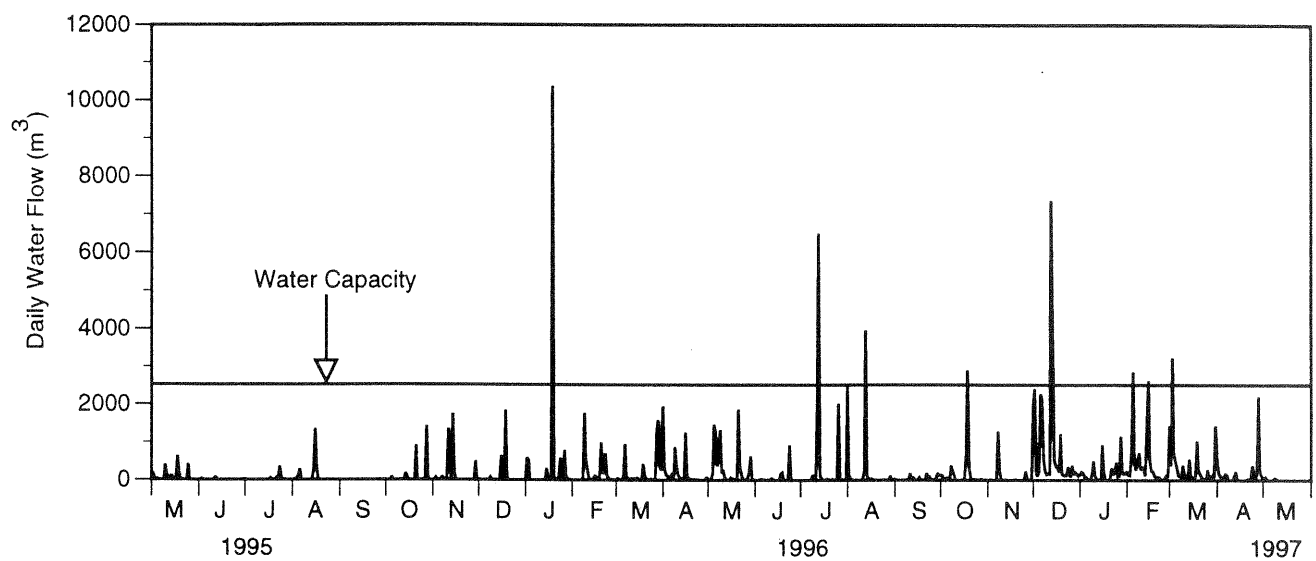


Fig. 3. Daily outflow of water (m^3) vs. day for the Barnstable 1 wetland. The volume held by the wetland before outflow occurs is indicated by the horizontal line at 2500 m^3 .

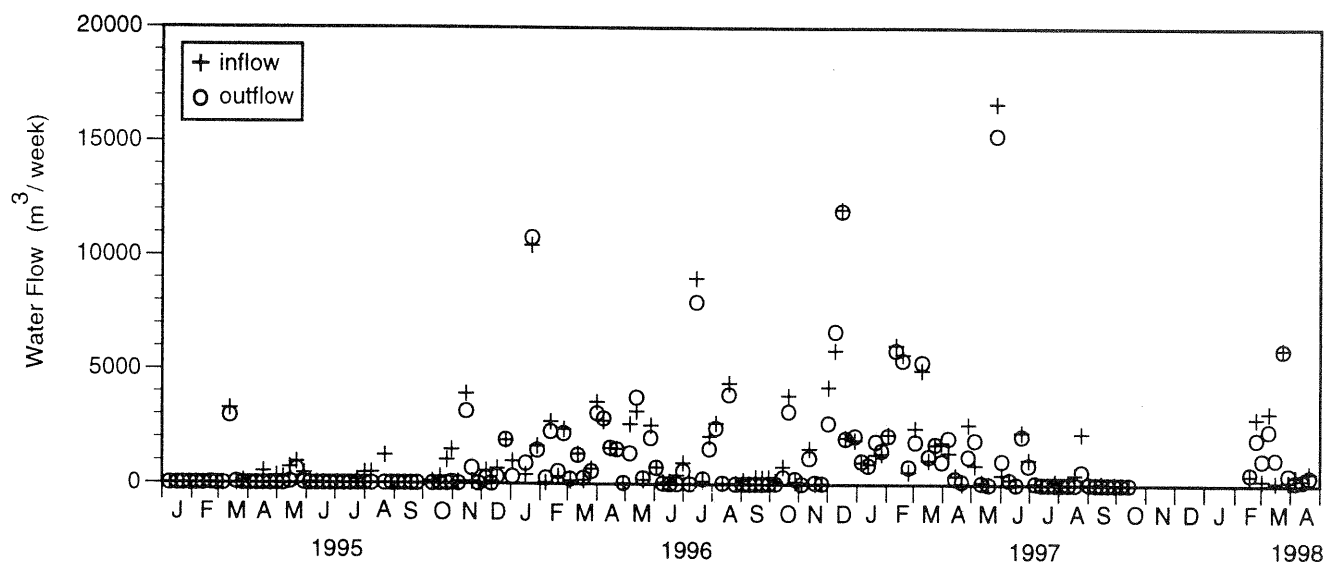


Fig. 4. Weekly inflow and outflow of water (m^3) vs. time at Barnstable 1.

Fluxes of Nutrients and Suspended Solids

Barnstable-1 wetland-- Fluxes of total suspended solids (TSS) and most nutrients were even more episodic than water flows because concentrations of suspended solids and particulate nutrients were highest during high flow conditions. Our grab sampling showed that most of the organic phosphorus and a large proportion of phosphate was particulate (previous chapter and Jordan et al. 1999). Thus, the annual flux of P was dominated by a few weeks with both high water flow and high P concentrations (Fig. 5). In general, the P concentrations were higher in inflowing water than in outflowing water. NO_3 was essentially all dissolved, but NO_3 flux was still very variable among weeks (Fig. 5), reflecting both the variability of water flow and NO_3 concentration. Usually, NO_3 concentrations were higher in inflowing water than in outflowing water. NH_4 concentrations varied greatly but did not show a systematic pattern of difference between inflowing and outflowing water. Fluxes of organic N and C, which were mostly dissolved (previous chapter and Jordan et al. 1999), were more uniform among weeks with inflow generally exceeding outflow (Fig. 5). TSS fluxes were very variable among weeks, with occasional high inflows (Fig. 5). One week in the spring of 1995, TSS outflow exceeded inflow and the fluxes were sufficiently high to dominate the annual total flux.

For some weeks, data on concentrations of some materials were not available due to technical problems. However, water flow was measured for all weeks in the two year period from May 1995-May 1997. Therefore, to calculate the total annual fluxes of materials, we first calculated the annual flow-weighted mean concentrations and then multiplied by the total annual water flow.

We calculated the 95% confidence limits around the annual fluxes using the bootstrap technique (Efron 1982). Differences among annual fluxes may arise due to the variability among weekly fluxes because a few weeks with high water flow can dominate the calculation of the annual flux. The bootstrap technique measures the consequences of randomly including or excluding certain weekly fluxes from the calculation of the annual flux. In other words, it accounts for the chance occurrence of weeks with differing water and nutrient flow within a given year. The bootstrap procedure begins by creating 1,000 sets of data by selecting data points at random from the original data set, replacing the selected points so they can be chosen again. In this case the data points are the weekly fluxes within the year. Each of the data sets created by the bootstrap procedure has the same number of samples as the original data set. The means of the created sets are calculated, and the 2.5 and 97.5 percentiles of these means represent the 95% confidence limits of the original mean (Efron 1982). Dividing the means and confidence limits of the weekly fluxes by the mean weekly water flow produces the flow-weighted mean concentrations and their confidence limits. If the confidence limits of concentration in inflowing water do not overlap the limits of concentration in outflowing water, then the concentrations are significantly different at the $p < 0.05$ level. However, even if inflowing and outflowing concentrations of a given nutrient do not differ, the wetland could still be a trap for that nutrient because more water enters the wetland than leaves the wetland. The annual inflow and outflow of each nutrient was calculated by multiplying its annual flow-weighted mean concentration in inflowing and outflowing water by the annual water inflow and outflow, respectively. The amount of nutrient trapped (or released) was calculated by subtracting its outflow from its inflow. The 95% confidence limits of the amount trapped was estimated from the confidence limits of the flow weighted mean concentrations and by propagating the error estimate, assuming that variances are additive.

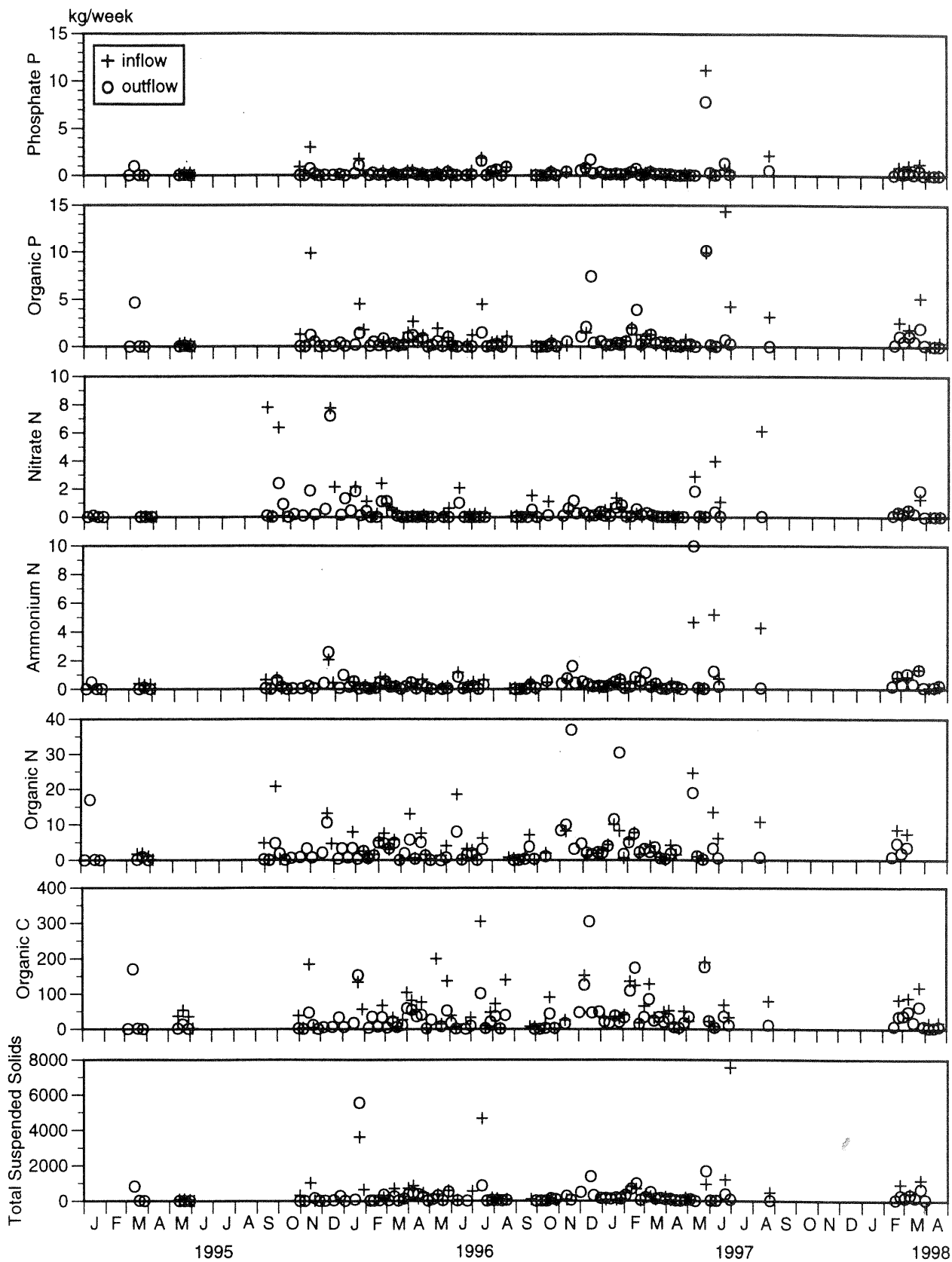


Fig. 5. Weekly inflow (+) and outflow (o) of phosphate P, organic P, nitrate N, ammonium N, organic N, organic C and total suspended solids (kg/week) vs. time at Barnstable 1.

Comparing the annual flow-weighted mean concentrations in inflowing and outflowing water revealed differences in the function of the Barnstable-1 wetland during the wet and dry years. During the dry year (May 95-May 96), the annual flow-weighted mean concentrations of PO_4 and TOP were significantly higher ($p < 0.05$, bootstrap) in inflow than in outflow (Fig. 6), and the magnitude of the difference suggested that the wetland trapped more than half of the inflowing P. During the wet year, P concentrations were about the same in inflow and outflow (Fig. 6). Patterns of N concentration also suggested greater trapping of N during the dry year than during the wet year (Fig. 6). However, the difference between inflow and outflow concentrations was statistically significant only for NO_3 in the wet year. Organic C concentrations were significantly higher in inflowing water than in outflowing water in both years, although the difference was greatest in the wet year (Fig. 6). TSS concentrations also suggests trapping of TSS in the wetland in both years, but the differences between inflow and outflow concentrations were not statistically significant (Fig. 6).

Based on the annual flow-weighted mean concentrations and annual water flow we calculated what percentages of the inflowing materials were trapped in the wetland in the wet and dry years and over the whole two-year period. There was more trapping of N and P during the dry year than during the wet year (Table 3). During the dry year, 49% of the total N and 69% of the total P entering the wetland was trapped, but during the wet year there was essentially no trapping of total N and total P. Although 49% of the NO_3 inflow was trapped during the wet year this was offset by a slight net loss of TON resulting in no net trapping of total N. About half of the TOC inflow was trapped in both years (Table 3). There appeared to be a net trapping of TSS, but due to the extreme variability among weekly fluxes the apparent trapping was not statistically significant (Table 3). Over the whole two-year period, trapping of NO_3 , total N, TOC, and all forms of P was statistically significant.

Table 3. Percentages of inflows trapped in Barnstable 1 wetland during a dry year (May 1995-May 1996) and a wet year (May 1996-May 1997).

<u>Material</u>	<u>Percentage of inflow trapped</u>		
	<u>dry year</u>	<u>wet year</u>	<u>whole period</u>
Ammonium	23	-0.33	10
Nitrate	52	49*	51*
Organic N	50*	-5.4	19
Total N	49*	-0.84	23*
Phosphate	65*	1.3	34*
Organic P	71*	-1.3	40*
Total P	69*	-0.46	39*
Organic C	57*	42*	44*
Suspended Solids	24	40	34

* $p < 0.05$, bootstrap (repeated random sampling of weekly data)

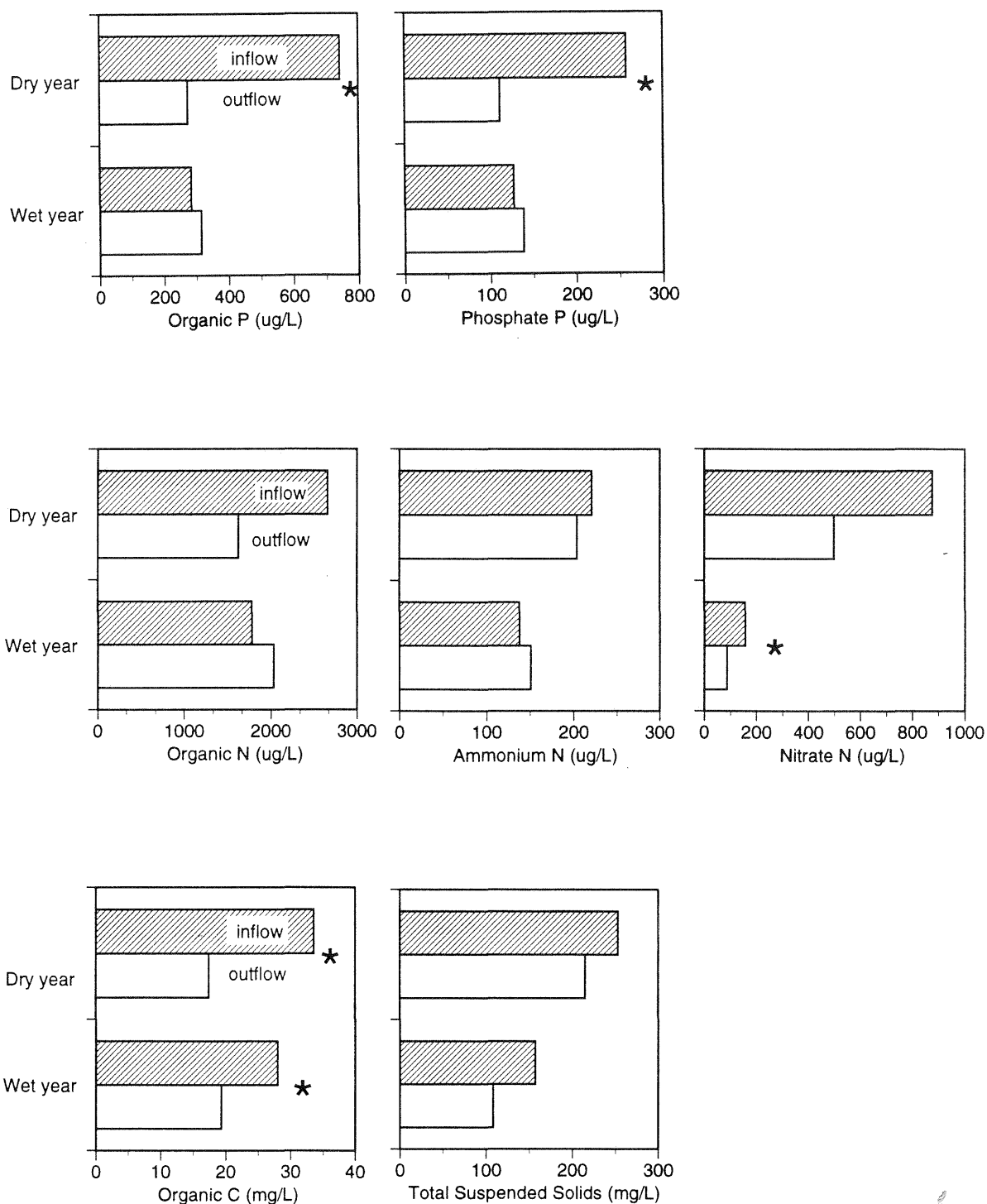


Fig. 6. Annual flow-weighted mean concentrations of organic P, phosphate P, organic N, ammonium N, nitrate N ($\mu\text{g N or P /L}$), organic C (mg C/L) and total suspended solids (mg/L) in inflow and outflow water during the dry year (May 1995-May 1996) and the wet year (May 1996-May 1997) at Barnstable 1. Asterisks indicate statistically significant differences ($p < 0.05$, bootstrap).

Four wetlands with automated samplers-- Flow-weighted mean concentrations differed among the four wetlands with automated samplers during the period when all the samplers were running (10-30 weeks in the time from February, 1997 - April, 1998). PO_4 concentrations in inflowing water were highest at Barnstable 10, but TOP concentrations in inflowing water were highest at Braun (Fig. 7). In all the wetlands except Foster, comparison of inflowing and outflowing concentrations suggests a trapping of about half the inflow of total P. Trapping of total N is less evident (Fig. 7), although NO_3 concentrations in inflowing water were higher than in outflowing water (Fig. 7). NH_4 concentrations in inflowing water at Braun were unusually high and greatly exceeded concentrations in outflowing water. At all wetlands except Foster, TOC concentrations in inflowing water exceeded concentrations in outflowing water (Fig. 7), suggesting a trapping of TOC. At Foster, comparison of concentrations suggests a net export of TOC. TSS concentrations suggested trapping of TSS at Barnstable 1 and Braun. When we complete a full year of concurrent sampling at the four wetlands, we will be able to make more definitive conclusions.

Discussion

In general, the Barnstable-1 wetland was much less effective at trapping nutrients during the wet year than during the dry year. This suggests that the rate of water flow through the wetland may be critical to its function as a nutrient sink. During high flow conditions daily flow of water into the wetland may approach or exceed the water holding capacity of the wetland (Fig. 3). At such times much of the water entering the wetland flows out within hours.

We have made preliminary estimates of the rates of nutrient removal from the water column in the Barnstable-10 wetland. We enclosed portions of the wetland water column and underlying sediment in plastic cylinders (approximately 0.5 m diameter X 1 m high). We then added dissolved PO_4 , NH_4 , and NO_3 to the enclosures at concentrations similar to the highest found in inflowing water. The concentrations gradually decreased within the enclosures, but did not approach pretreatment levels until more than a week passed. Thus, we would expect little removal of dissolved nutrients from water that passes through the wetlands in a few hours during high flow conditions.

The estimates of nutrient uptake rates from the enclosure experiments and the lack of trapping efficiency during wet conditions suggest that the turnover time of water within the wetland is a critical factor controlling nutrient uptake, as found by Jansson et al. (1994). The nutrient trapping by wetlands would probably be enhanced by maximizing the residence time of water within the wetland. This should be a consideration in designing water flow control structures such as berms and drains used in wetland restoration.

Automated sampling is essential for quantifying unpredictable episodic transport of materials into and out of wetlands. However, the need to preserve field samples for nutrient analysis presents problems. The sulfuric acid preservative we used is convenient and effective, but it alters the proportions of dissolved and particulate forms of N, P, and C. Thus, we can only measure the total of dissolved and particulate fractions. Our grab sampling (see previous chapter) did not require preservative because the samples were collected immediately after the flow events. The grab sampling results indicated differences in the trapping of dissolved and particulate nutrients. Comparison of concentrations in inflowing and outflowing water suggested that dissolved PO_4 , and dissolved organic P, N, and C were trapped while particulate PO_4 and particulate organic P, N, and C were not (Jordan et al. 1999, and previous chapter). This is surprising because the wetlands seem likely to trap particulate matter. Trapping of suspended particulate matter should occur because water flow is slowed down by the vegetation and the containment of water within the wetland. Trapping of TSS is suggested by grab sampling data showing higher TSS

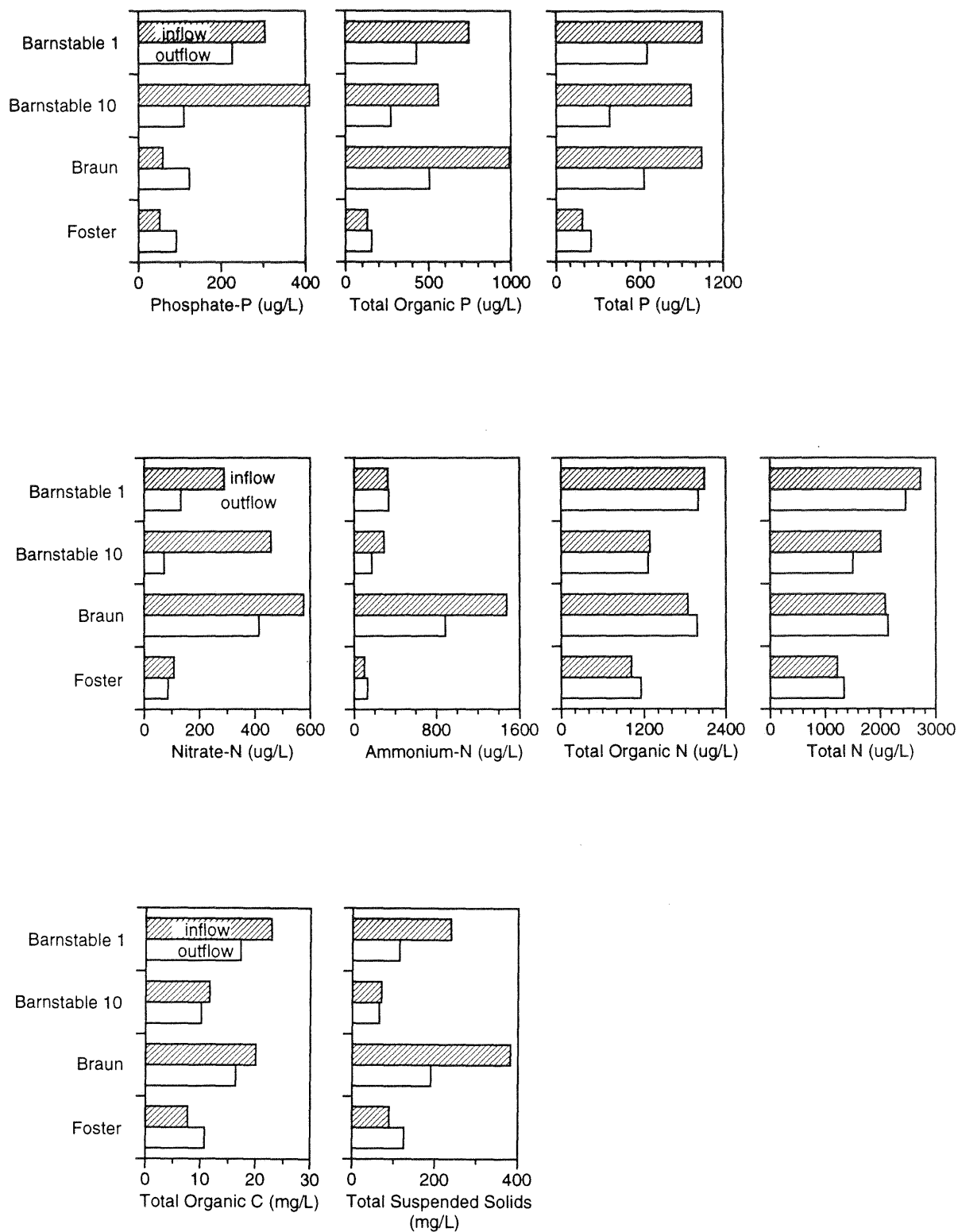


Fig. 7. Annual flow-weighted mean concentrations of phosphate P, organic P, total P, nitrate N, ammonium N, total organic N, total N ($\mu\text{g P or N/L}$), organic C (mg C/L), and total suspended solids (mg/L) in inflow and outflow water at four wetlands during the time when all samplers were running (February 1997- April 1998).

concentrations in inflowing water than in outflowing water (Jordan et al. 1999 and previous chapter). The trapping of TSS without trapping of particulate nutrients suggests that nutrient concentrations are higher in particulate matter leaving the wetlands than in particulate matter entering the wetlands. This could occur if TSS entering the wetlands is predominantly mineral rich soil particles while TSS leaving the wetlands includes biota and organic detritus produced within the wetlands.

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BIOMASS AND NUTRIENT DYNAMICS OF VEGETATION

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Introduction

Three general approaches are used in restoring vegetation in wetland restoration and creation projects (Mitsch and Wilson 1996, Stauffer and Brooks 1997). Wetlands can be designed and planted so that the species composition approximately mimics the species composition of natural wetlands from the very beginning of the restoration effort. A second approach is to transplant soils or sods (referred to as 'salvaged marsh surface') from natural wetlands into restored or created wetlands (Brown and Bedford 1997, Stauffer and Brooks 1997). The third approach emphasizes 'self-design' or 'self organization' by letting vegetation development occur naturally on the assumption that vegetation will rather quickly resemble the vegetation of natural wetlands. In the latter instance, it is assumed that all species that can grow at the site will eventually become established from seeds in the seed bank or by dispersal of propagules to the site (Galatowitsch and van der Valk 1996a, 1996b). Mitsch (1997) has hypothesized that planned and self-designed wetlands will "be similar in function in the beginning, diverge in function during the middle years, and ultimately converge in structure and function". In this scenario, the initial conditions of the vegetation (e.g., planted or self-designed) will have little impact on wetland functions because the vegetation cover may be sparse and wetland features influenced by vegetation (e.g., litter layer, oxidized root channels, soil organic matter) will not be well developed. As succession and development continues, functions of planted and self-designed restored wetlands would diverge, most likely due to significant differences in the rate of vegetation development and species composition of the vegetation. In later stages of development, functions would converge again in planted and self-designed wetlands because of convergence in characteristics of wetland vegetation (e.g., biomass and species composition). There are arguments in favor of all three restoration/creation methods (Brown and Bedford 1997, Mitsch and Gosselink 1993) but to date there have been few long-term studies in which success of one method or the other has been thoroughly evaluated.

Galatowitch and van der Valk (1996a), for example, found that the self-design approach (they referred to it as the 'efficient community' hypothesis) only partially resulted in vegetation that was similar to natural wetlands in a study of ten restored wetlands in Iowa. They found that after three years of self-design that natural wetlands had more species in all zones but the submersed zone and that some guilds of species were very different from natural wetlands in all zones. They concluded that the seed bank, a source of potential colonizers, contained fewer species in the restored wetlands and, with the exception of submersed species, that dispersal to the restored wetlands by animals was less rapid than anticipated. Brown (1998) also found that the seed bank was a poor indicator of vegetation in restored wetlands. Galatowitch and van der Valk suggested that the efficient community hypothesis needed to be modified so that seed/propagule dispersal to the wetland is more important than establishment from a seed bank and that development of vegetation will take longer than is typically projected for depressional wetlands in the Prairie Pothole region. Hunt (1996) found similar results for a created wetland in the mid-West after five years of vegetation development. In contrast, Brown and Bedford (1997) and Stauffer and Brooks (1997) found that vegetation development occurred faster in restored and created wetlands that had received salvaged marsh surface material.

The approach used by the Chesapeake Wildlife Heritage in restoring the wetlands that we have studied is similar to the self-design (Mitsch and Wilson 1996) and efficient community approaches (Galatowitch and van der Valk 1996a). The study sites had all been

ditched agricultural fields before restoration. We do not know what type of vegetation existed prior to conversion to agricultural land but, given land-use practices on the Eastern Shore of Maryland, it is likely that the sites had originally been either forested depressional or slope wetlands in the context of wetland classification developed by Brinson (1993). The sites were all restored as depressional wetlands (e.g., basins with closed contour intervals) that had outlets. All of the sites except the 3 wetlands sampled at Eastern Neck Wildlife Refuge were restored by the Chesapeake Wildlife Heritage (CWH). The basin topography at each site (Jordan et al. 1996) is very similar to shallow, closed depressions typical of wetlands in the Prairie Pothole Region (Galatowitsch and van der Valk 1996b, Steward and Kantrud 1971) in the mid-west and Carolina Bays along the Atlantic Coastal Plain (Lide et al. 1995, Sharitz and Gibbons 1982).

Our objectives were to monitor vegetation to evaluate vegetation development using two approaches. First, we used permanent plots in each wetland to monitor species composition over the three years of the study. We assumed that the vegetation would be very dynamic in young wetlands (i.e., 1-3 years following restoration) and more stable in older wetlands (i.e., approximately 10 years since restoration). We also measured aboveground biomass to test the assumption that biomass would be greater in older wetlands as annual and short-lived species were replaced by perennials that reproduce primarily by clonal propagation (e.g., Cattail). In this chapter, results of the biomass study are reported. We tested both assumptions by selecting restored sites that were of different ages (Table 1) at the beginning of the project. By using wetlands of different ages since restoration and by sampling them for three consecutive years, we are able to evaluate vegetation development over short- and intermediate time periods.

Table 1. Characteristics of restored wetlands selected for this study and their watersheds.

Site	Watershed			Wetland	
	Hectares	Soils	% Crops	Hectares	Year Restored
Barnstable 1	14	Mattapex/Elkton	85	1.3	1986
Barnstable 3	4.0	Elkton	55	1.3	1991
Barnstable 10	19	Mattapex/Elkton	70	3.7	1992
Braun	12	Mattapex	80	2.3	1992
Eastern Neck 1	20	Mattapex/Othello	70	1.8	@1964
Eastern Neck 2	10	Mattapex/Othello	25	0.51	@1964
Eastern Neck 3	---	Mattapex/Othello	---	7.2	@1964
Foster	4.4	Falsington	60	0.49	1993
Gerber	3.6	Falsington	30	0.41	1990
Hope	3.2	Elkton	60	0.88	1993
Nesbit	10	Falsington/Sassafras	95	0.39	1989
Sultenfuss	19	Falsington	95	1.4	1992

Methods

In 1994, 2 X 2 meter plots were established in each wetland in three hydrologic zones. The three zones within each wetlands were characterized as follows: The temporary zone is closest to adjacent uplands and is usually flooded only during the non-growing season months. Plant species in the temporary zone represent a range of wetland species from obligate upland to obligate wetland. The emergent/seasonal zone lies between the temporary zone and the portion of the wetland that is usually permanently flooded and dominated by submersed species. The emergent/seasonal zone is flooded for longer periods of time than the temporary zone and, depending on the amount of summer precipitation, may be flooded for the entire or for only part of the growing season. The emergent/seasonal zone supports mostly facultative and obligate emergent wetland species. The submersed zone is the deepest zone and supports no vascular plants, submersed species, and/or scattered emergent species. The submersed zone is usually flooded for the entire year but, at times of extended summer drought, could have little or no standing water. All of the plots established in 1994 were assigned to one of the three zones based on their positions within the wetlands and relative water depth at the time they were established. In 1995, all of the plots were surveyed to determine their elevation relative to a fixed point established near the outlet of each wetland. Elevation data and water level data were used to evaluate the original assignments given to the plots in 1994 and, where appropriate, plots were assigned to different zones.

Each plot was divided into four 1 X 1 meter subplots which were used to monitor species composition and measure annual aboveground biomass (g/m^2), nutrient concentrations in biomass, and total standing stocks of nutrients in biomass (g/m^2). Biomass was harvested in the autumn (mid- to late-October) by cutting and removing all aboveground plant material in one of the subplots each year. Thus, one subplot was harvested in 1994, a second in 1995, and the third in 1996. Harvested plant material was returned to the laboratory, dried in a forced air oven to constant weight at 70°C , and weighed to determine the amount of biomass per m^2 . The fourth subplot was not harvested during the study but was used as a permanent plot to monitor the aerial coverage of each plant species at least once during each growing season. Details of the procedures used to monitor vegetation are described in the next chapter.

Aboveground biomass from each year was analyzed for nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and sodium (Na). The carbon (C) content of biomass was only measured in 1995 and 1996. Nutrient concentrations and biomass data were combined to calculate nutrient standing stocks. Biomass samples were prepared for nutrient analyses by first grinding subsamples of the dried and weighed biomass from each plot in a food processor followed by grinding in a Wiley Mill (40 mesh screen). Powdered samples were stored dry at room temperature until they were analyzed. All samples were analyzed at Pennsylvania State University in 1994 for N, P, Ca, Mg, Na, and K. Nitrogen was determined by standard Kjeldahl procedures (Martin 1972). The other nutrients were analyzed on an individually coupled plasma emission spectrometer (Applied Research laboratory Model 137) using procedures described in Dahlquist and Knoll (1978). In 1995 and 1996, N and C were analyzed at SERC with a Perkin-Elmer CHN analyzer. Calcium, Mg, Na, and K in the 1995 and 1996 samples were analyzed at Pennsylvania State University using the procedures described. Biomass, nutrient concentration, and nutrient standing stock data were analyzed by analysis of variance (ANOVA) using SAS for year (1994, 1995, 1996), zone (submerged, emergent/seasonal, temporary), or wetland (12 wetland sites) differences. Interaction terms were also compared using ANOVA. Multiple comparisons of the means were performed using the LSMEANS and Tukey's procedures

in the GLM protocol in SAS. Percentage data for nutrients were arcsine-transformed before analysis with SAS. Analyses of nutrient concentrations were performed only on data from plots which contained vegetation. Analyses of biomass and total nutrients were performed on all plots, including those in which there were biomass and nutrient standing stocks were zero.

Results

There were highly significant differences among and within wetlands for almost all variables and significant differences between years for more than half (7 of 13) of the variables (Table 2). Overall, there were significant differences for 82.4% of the variables tested demonstrating that biomass, nutrient concentrations, and nutrient standing stocks were highly variable within and between wetlands.

Table 2. Results of ANOVA tests for Years (Y), Sites (S), Zones (Z), and interactions between Y, S, Z for aboveground biomass, nutrient concentrations, and nutrient standing stocks. Values in the Table are probability levels.

Variable	Year (Y)	Site (S)	Zone (Z)	Y*S	Y*Z	S*Z	Y*S*Z
Biomass	.1304	.0001	.0001	.0001	.0005	.0001	.0005
%P	.0001	.0001	.0001	.0001	.3992	.0001	.0001
Total P	.0001	.0001	.0001	.0001	.0001	.0001	.0001
%N	.0073	.0001	.0001	.0001	.0001	.0001	.0001
Total N	.0528	.0001	.0477	.0001	.0150	.0001	.0074
%Ca	.0183	.0001	.0001	.0001	.0001	.0001	.0001
Total Ca	.1373	.0001	.0556	.0001	.4689	.0001	.2394
%Mg	.1842	.0001	.0001	.0001	.2566	.0001	.0001
Total Mg	.7360	.0001	.0001	.0001	.3910	.0001	.0001
% K	.0001	.0001	.0001	.0001	.0605	.0001	.0001
Total K	.0001	.0001	.0001	.0001	.0001	.0001	.0001
%C	.0001	.0001	.0001	.0001	.0370	.0001	.0044
Total C	.4351	.0001	.0001	.0001	.2903	.0001	.2305

Aboveground biomass averaged 229.3 ± 9.1 g/m² for all sites combined for the three years and there were no significant differences between years (Fig. 1). Biomass, however, varied widely between wetlands each year and, for almost all wetlands, biomass also varied from one year to another (Fig. 2). The highest average biomass occurred at Braun (464.7 ± 93.2 g/m²) in 1994, at Braun (285.3 ± 59.1 g/m²), Eastern Neck 2 (330.7 ± 51.7 g/m²), and Nesbit (328.1 ± 57.0 g/m²) in 1995 and at Barnstable 3 (415.3 ± 50.8 g/m²) in 1996. The greatest annual variation occurred at Barnstable 10 where average biomass was 244.7 ± 50.7 g/m² in 1994 and 9.4 ± 5.0 g/m² in 1996. The biomass data clearly demonstrate that the wetlands followed no overall temporal or spatial pattern.

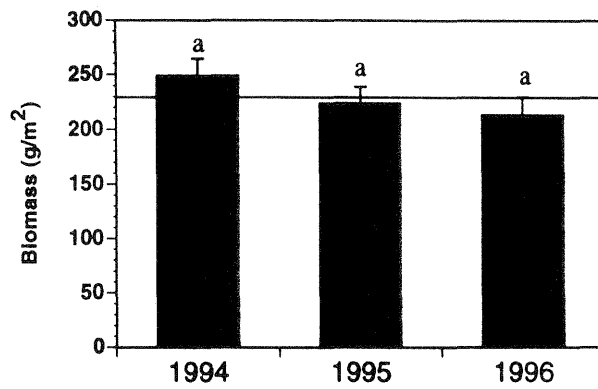


Figure 1. Mean annual biomass of all restored wetlands in 1994, 1995 and 1996. Values are means (g/m^2) \pm 1 standard error. The horizontal line is the mean for all three years combined. There were no significant differences between years as indicated by the same letters above each bar. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

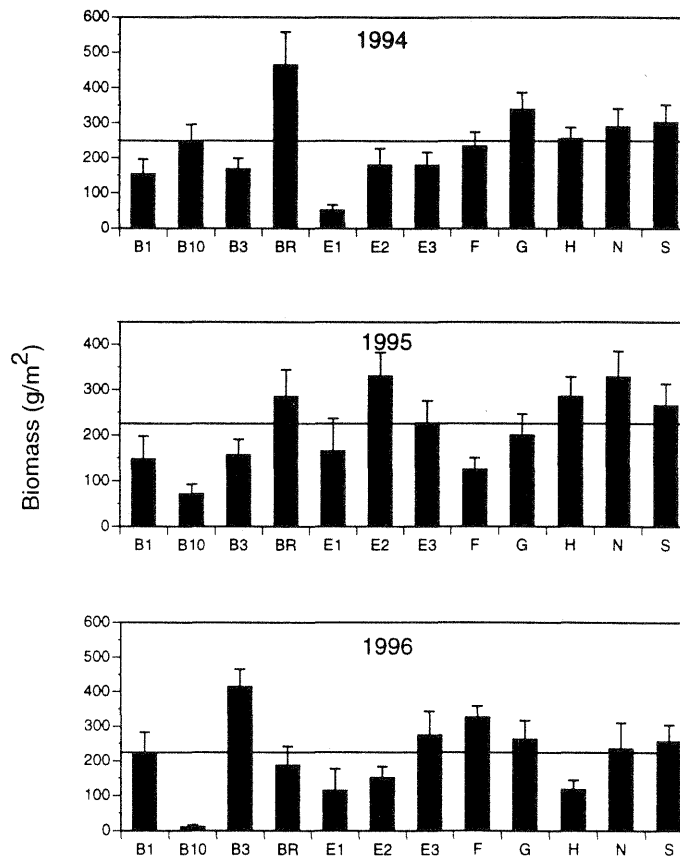


Figure 2. Mean annual biomass for each of the restored wetlands in 1994, 1995 and 1996. Values are means (g/m^2) \pm 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

There was, however, a consistent pattern of biomass distribution within wetlands (Fig. 3). Aboveground biomass was always least in the submersed zone (range: 69.2 ± 13.4 - 137.8 ± 35.8 g/m²) and there were no significant differences between years. Average biomass in the seasonal/emergent zone was intermediate (range: 167.8 ± 23.6 - 232.3 ± 22.7 g/m²) and biomass in 1996 was significantly less than in 1995 and 1994 (Fig. 3). The temporary zone had the greatest biomass in each of the three years (range: 297.6 ± 23.5 - 358.6 ± 26.3 g/m²) and there were no significant differences between years (Fig. 3).

Except for Mg, nutrient concentrations in aboveground biomass differed significantly between years (Figs. 4-6). Nitrogen concentrations were highest in 1996 ($1.32 \pm 0.04\%$), significantly lower ($1.16 \pm 0.04\%$) in 1995, and intermediate ($1.23 \pm 0.06\%$) in 1994. Phosphorus concentrations were significantly lower in 1995 ($0.17 \pm 0.007\%$) than in 1994 ($0.22 \pm 0.01\%$) and 1996 ($0.21 \pm 0.007\%$). Potassium concentrations followed the same pattern as P with a significantly lower average in 1995 ($0.76 \pm 0.04\%$) compared to 1994 ($1.19 \pm 0.05\%$) and 1996 ($1.12 \pm 0.04\%$). Calcium concentrations were significantly lower in 1994 ($0.49 \pm 0.017\%$) than in 1995 ($0.55 \pm 0.017\%$) and 1996 ($0.57 \pm 0.018\%$). Carbon differed significantly in the two years that it was measured.

Similar to the distribution of biomass within the wetlands, nutrient concentrations also differed between zones (Fig. 7) but the general pattern was opposite the pattern for biomass and it was more variable from year to year. For all nutrients except C, Ca in 1995 and 1996 and P in 1994, concentrations were highest in the submersed zone and decreased toward the outer seasonal zone (Fig. 7). In the submersed zone, significantly higher nutrient concentrations occurred in 1994 with the exception of P and there were no significant differences between 1995 and 1996. There was no consistent pattern for nutrient concentrations in the seasonal/emergent zone. Tissue concentrations were significantly lower in 1995 for P and K, significantly higher for Ca in 1996 and there were no significant differences for Mg and N. Carbon concentrations in the seasonal zone were significantly higher in 1995 ($37.9 \pm 0.80\%$) than 1996 ($34.4 \pm 1.04\%$).

Nutrient concentrations varied significantly between wetlands and the wetland*year interactions were significant for all variables (Table 2). Examples of variations between wetlands and years are shown for %N and %P in Figs. 8 and 9. Percent N was more variable among site and years. Percent N was highly variable among sites in 1994 and less variable in 1995 and 1996 (Fig. 8). Phosphorus concentrations, while differing among wetlands, showed the same general pattern in each of the three years. The highest %P occurred at Barnstable 10 in all three years and the lowest levels were found in plants at Eastern Neck 2 (Fig. 9).

Biomass and nutrient concentration data were combined to estimate total standing stocks of nutrients. There were significant differences between wetlands (Table 2) for all variables and the differences between wetlands showed a pattern that was similar to the pattern for biomass (i.e., large differences between wetlands and variable nutrient standing stocks from year to year within wetlands). Examples of the differences between wetlands and years are demonstrated for N and P in Figs. 10 and 11. Total N at two sites (Eastern Neck 1 and Hope) was less than average for all three years and vegetation at Nesbit and Sultenfuss had higher than average Total N for all three years (Fig. 10). Total N was highly variable between years at all other sites. Only Sultenfuss had higher than average Total P in all three years (Fig. 11). Four sites (Barnstable 1, Eastern Neck 1, Eastern Neck 2, and Hope) had Total P standing stocks that were less than average for all three year. The other seven sites had Total P standing stocks that varied from above to below the average for all sites combined.

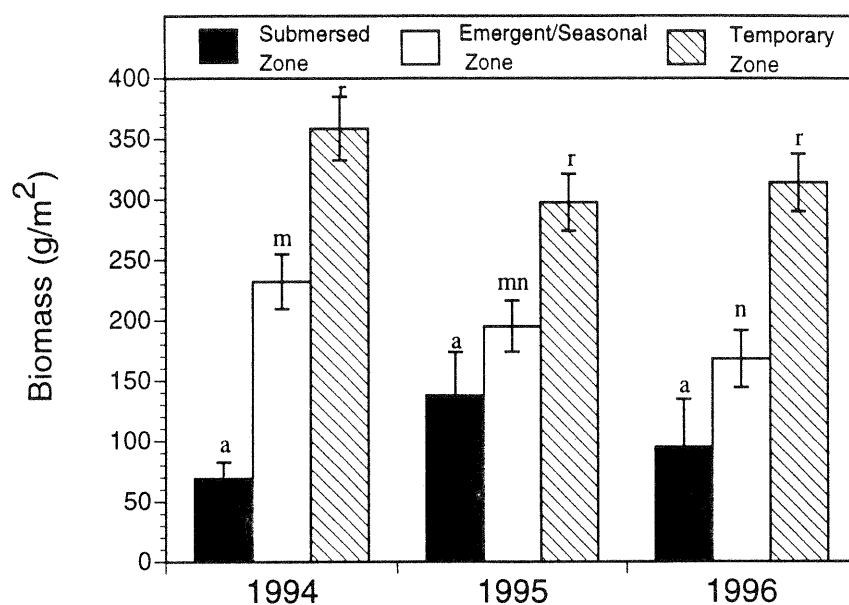


Figure 3. Mean annual biomass in each of the zones for all restored wetlands in 1994, 1995 and 1996. Values are means (g/m^2) \pm 1 standard error. Statistical comparisons were made between years for each zone. There were no significant differences between years for the submersed and temporary zones as indicated by the same letters above the bars for those two zones. There were differences between years for the emergent/seasonal zone as indicated by the letters above the bars. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

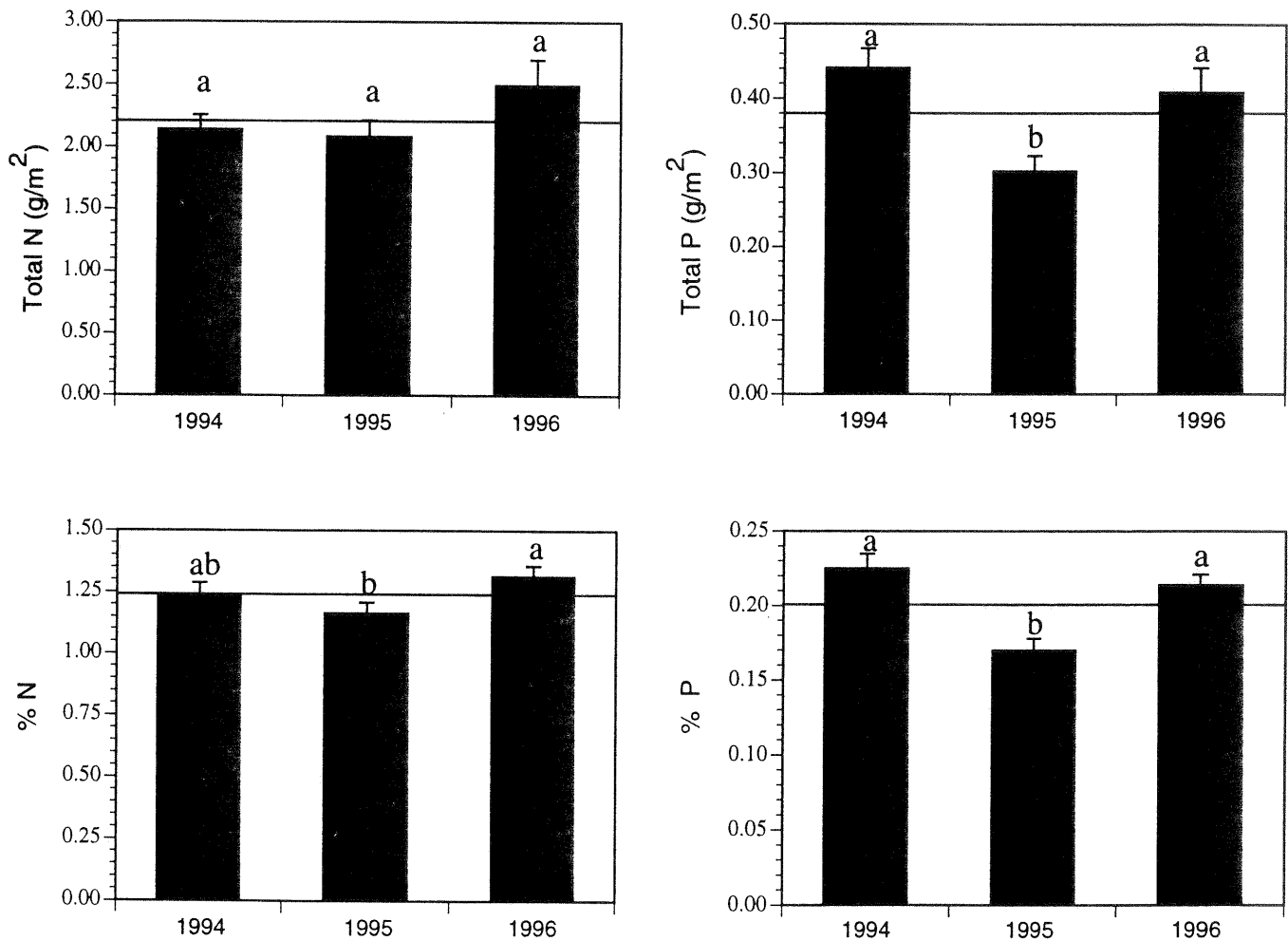


Figure 4. Mean concentrations (%) and standing stock (g/m^2) of nitrogen (N) and phosphorus (P) in aboveground biomass for all wetlands combined in 1994, 1995 and 1996. Values are means \pm 1 standard error. Results of statistical comparisons between years are indicated by the letters above the bars. There were no significant differences between 1994 and 1996 for any of the variables. N and P concentrations and P standing stock were significantly lower in 1995. The horizontal line in each graph is the mean for all three years. Concentration data were only based on subplots which had vegetation. Standing stocks were based on all subplots.

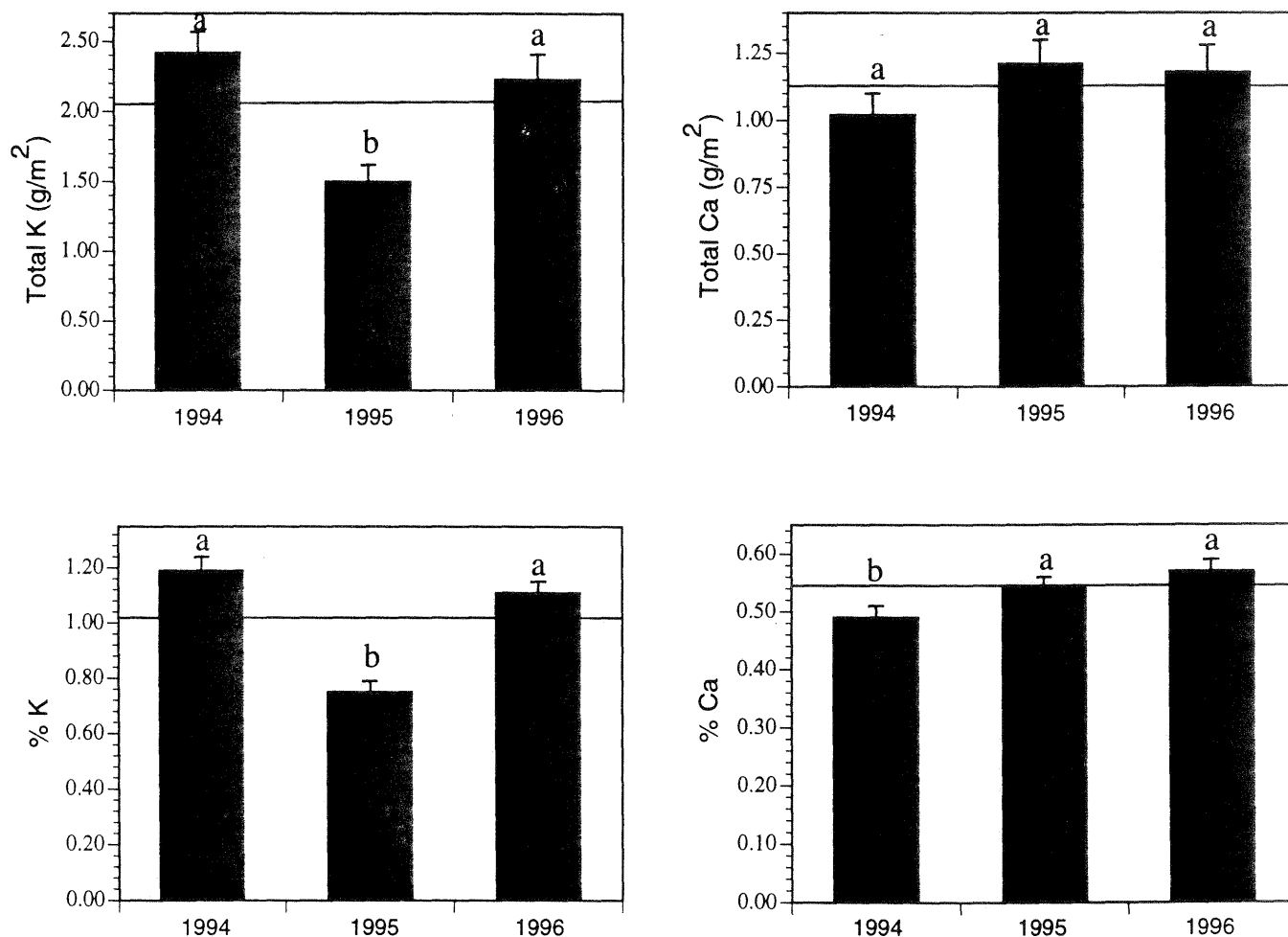


Figure 5. Mean concentrations (%) and standing stocks (g/m²) of potassium (K) and calcium (Ca) in aboveground biomass for all wetlands combined in 1994, 1995 and 1996. Values are means \pm 1 standard error. Results of statistical comparisons between years are indicated by the letters above the bars. K and Ca concentrations were significantly lower in 1995 and 1994, respectively. Total K was significantly lower in 1995. The horizontal line in each graph is the mean for all three years. Concentration data were only based on subplots which had vegetation. Standing stocks were based on all subplots.

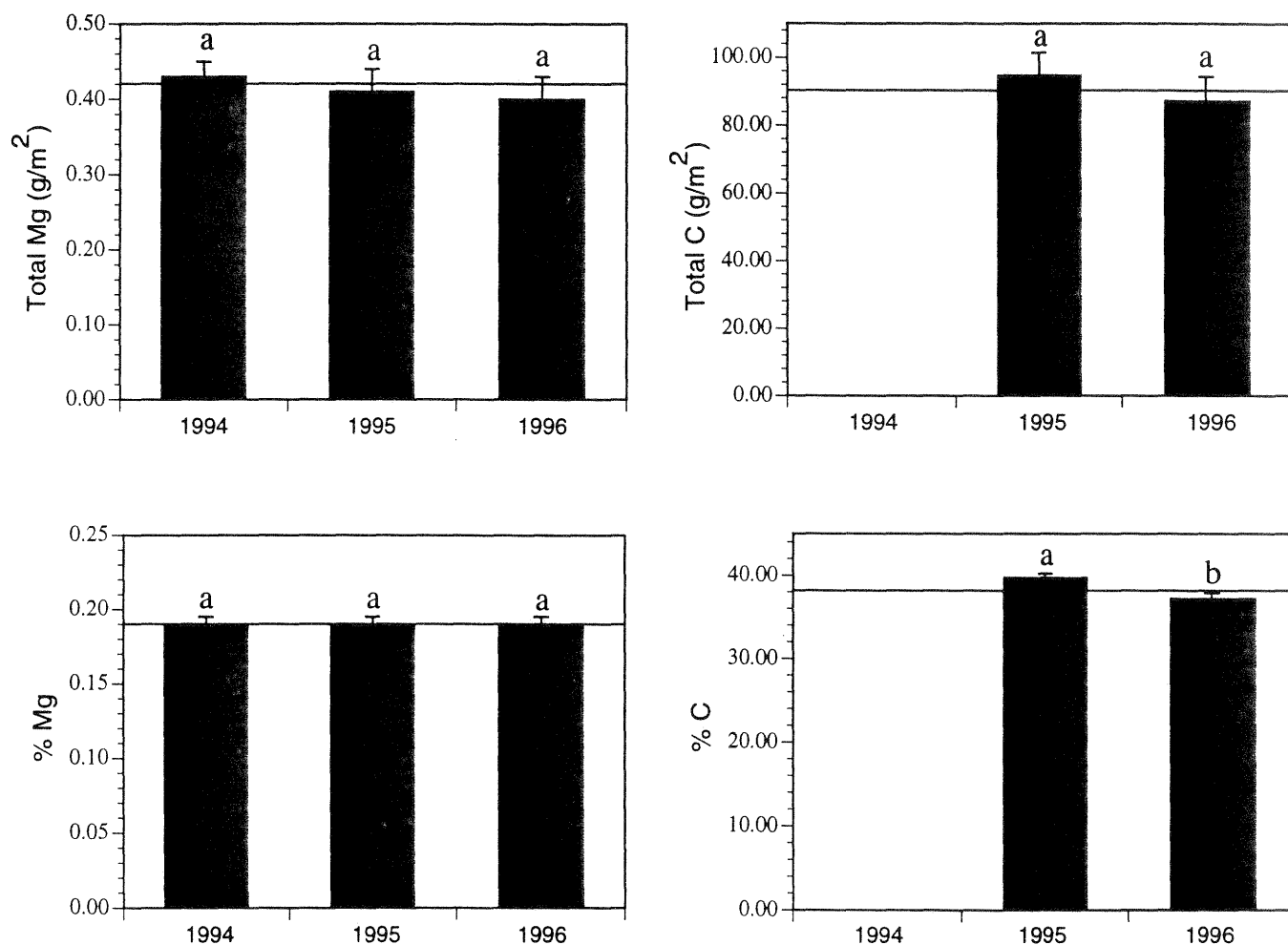


Figure 6. Mean concentrations (%) and standing stocks (g/m^2) of magnesium (Mg) in aboveground biomass for all wetlands combined in 1994, 1995 and 1996 and for carbon (C) in 1995 and 1996. Values are means ± 1 standard error. Results of statistical comparisons between years are indicated by the letters above the bars. C concentrations were significant between 1995 and 1996. The horizontal line in each graph is the mean for all three years. Concentration data were only based on subplots which had vegetation. Standing stocks were based on all subplots.

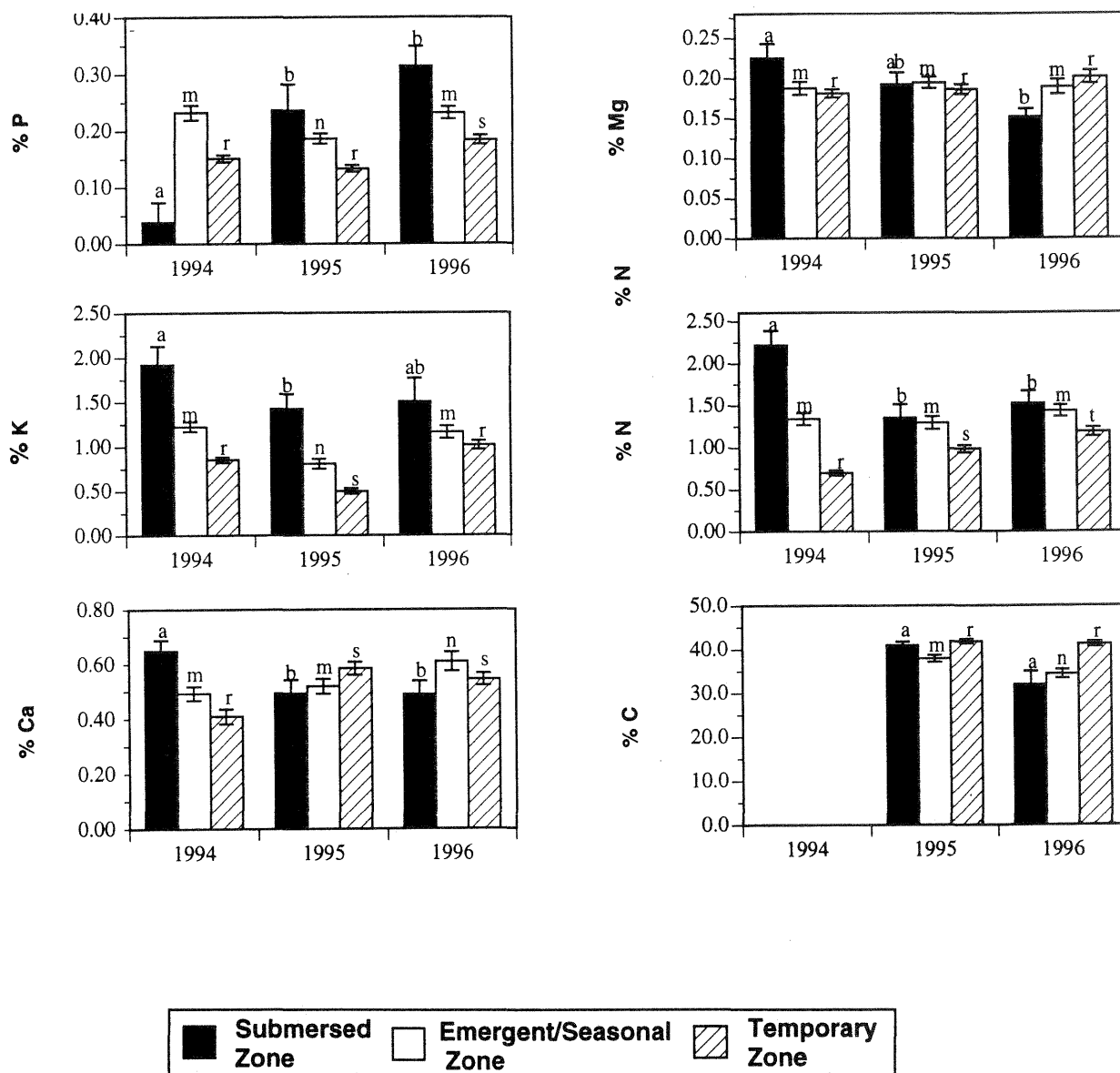


Figure 7. Mean concentrations (%) of Ca, K, P, C, N and Mg in aboveground biomass in each of the zones for all the restored wetlands in 1994, 1995 and 1996. Values are means ± 1 standard error. Statistical comparisons were made between years for each zone and the results, within zones, are indicated with the letters above the bars. There were significant differences between years for the submersed for all nutrients. Significant differences between years in the emergent/seasonal zone were found for Ca, K, P and C. Significant differences between years in the temporary zone were found for Ca, K, P and N. Only subplots which had vegetation were used in this analysis.

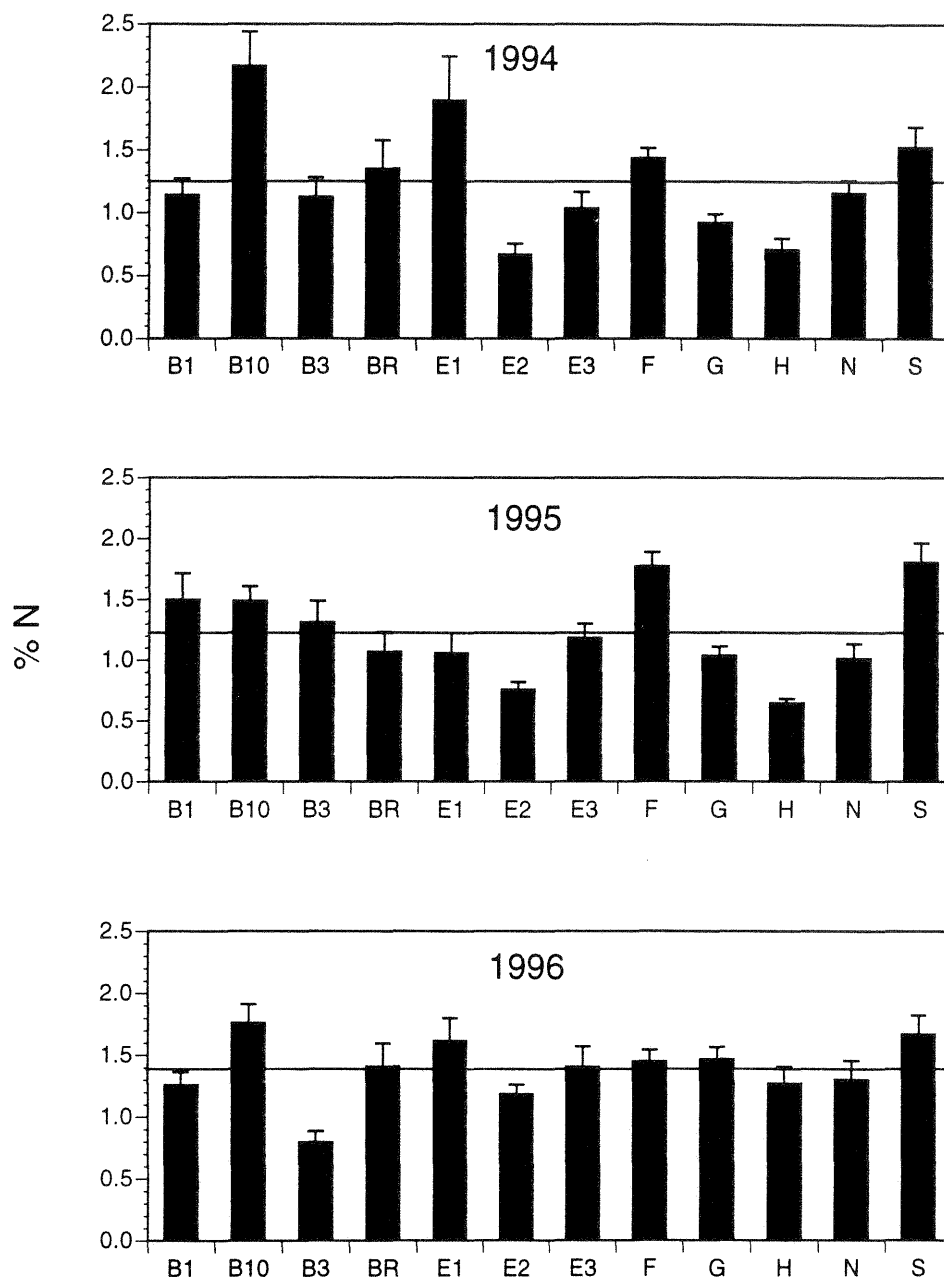


Figure 8. Mean nitrogen concentration of aboveground biomass for each of the restored wetlands in 1994, 1995 and 1996. Values are means \pm 1 standard error. The horizontal line in each graph is the mean for all three years combined. Only subplots with aboveground biomass were used in this analysis.

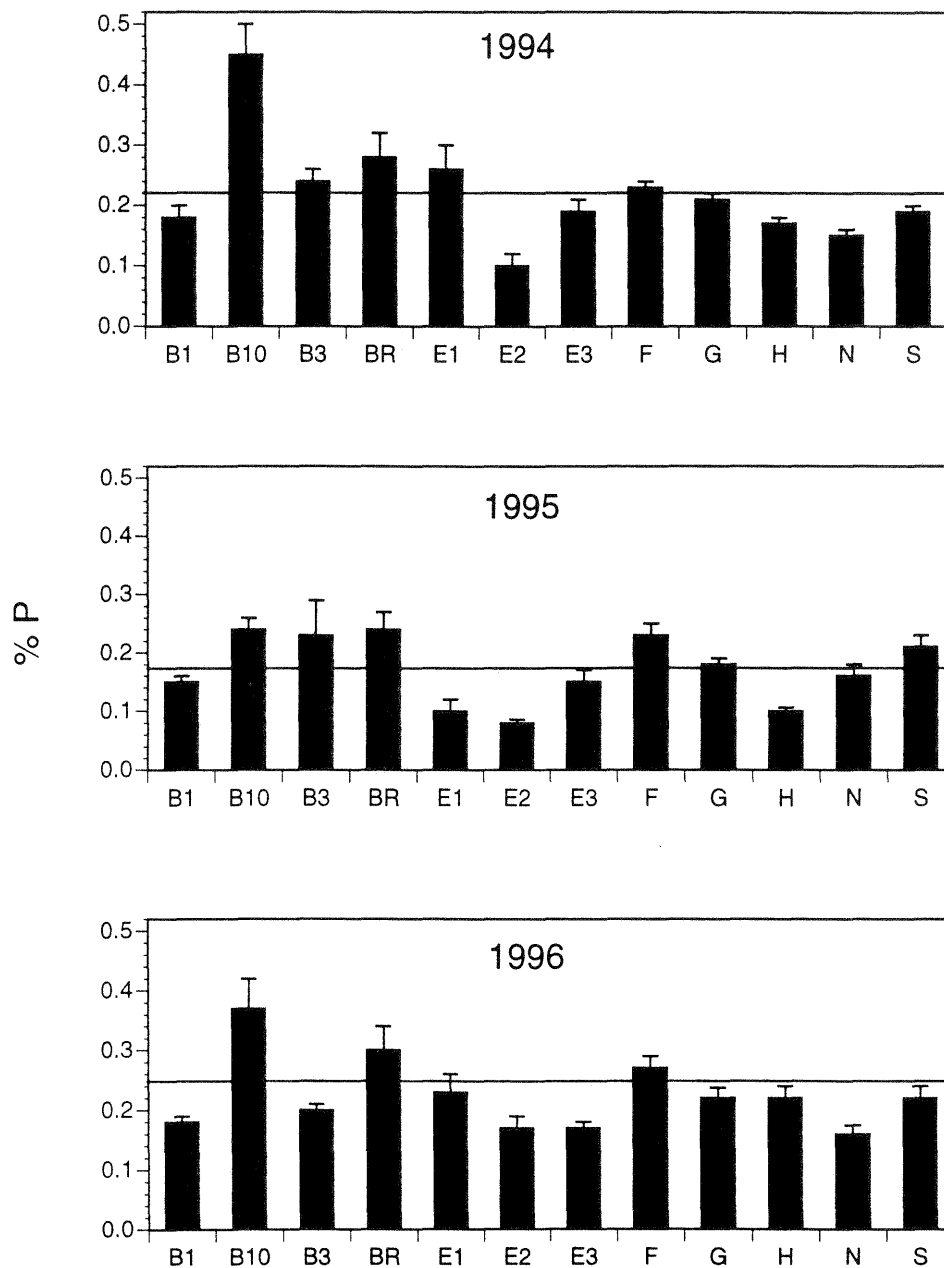


Figure 9. Mean phosphorus concentration of aboveground biomass for each of the restored wetlands in 1994, 1995 and 1996. Values are means \pm 1 standard error. The horizontal line in each graph is the mean for all three years combined. Only subplots with aboveground biomass were used in this analysis.

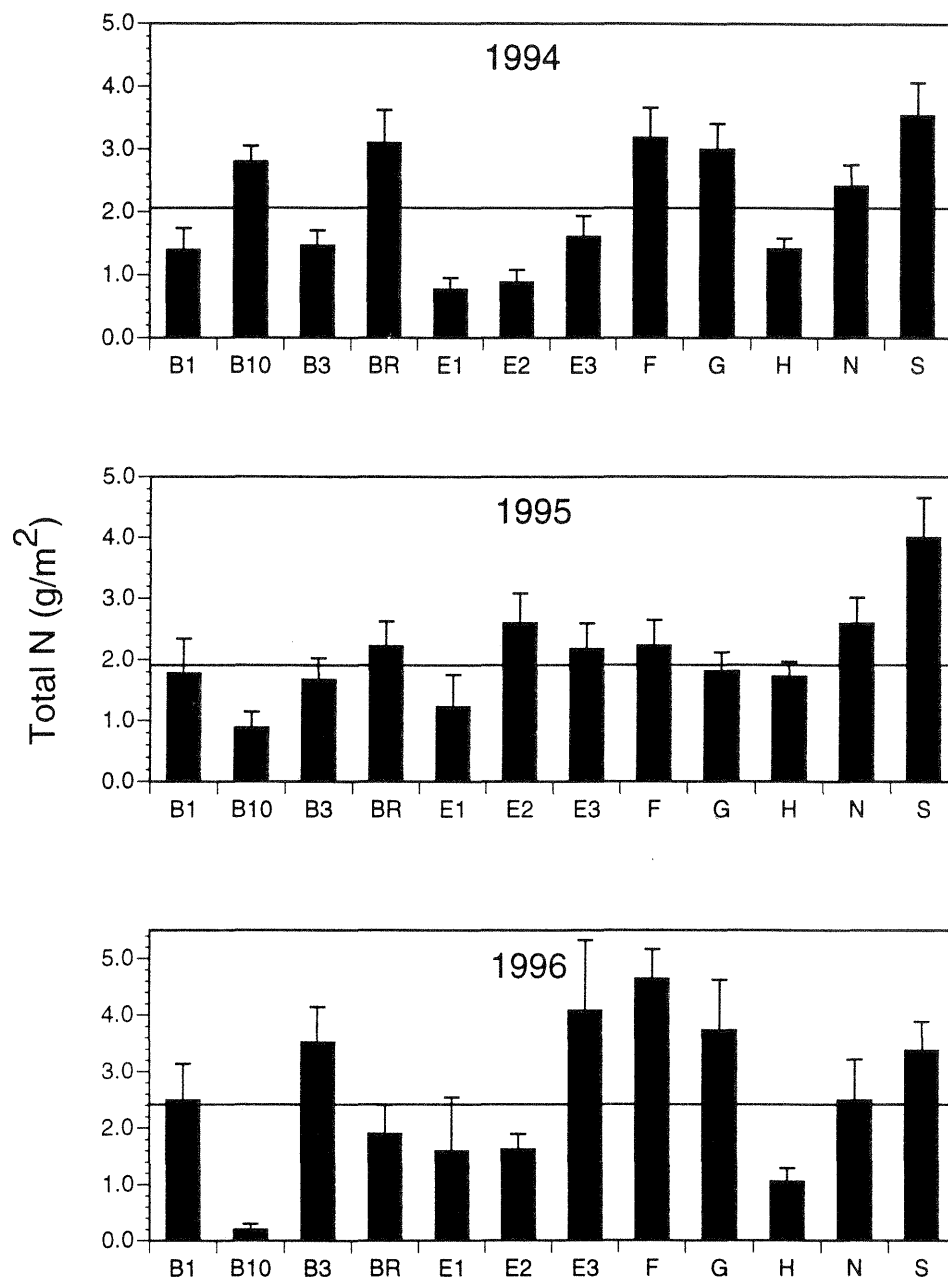


Figure 10. Mean Total N in aboveground biomass for each of the restored wetlands in 1994, 1995 and 1996. Values are means \pm 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in the analysis.

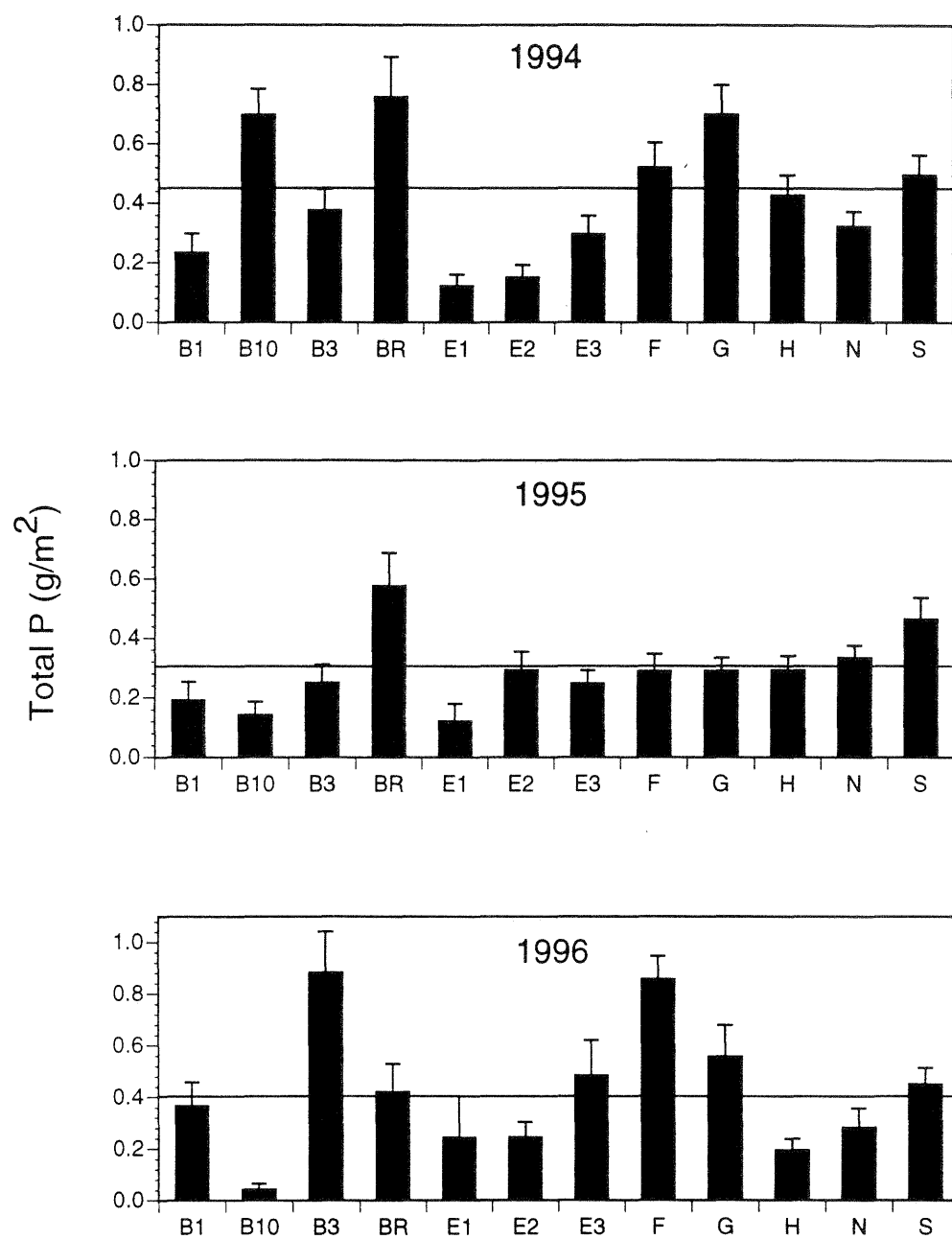


Figure 11. Mean Total P in aboveground biomass for each of the restored wetlands in 1994, 1995 and 1996. Values are means \pm 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in the analysis.

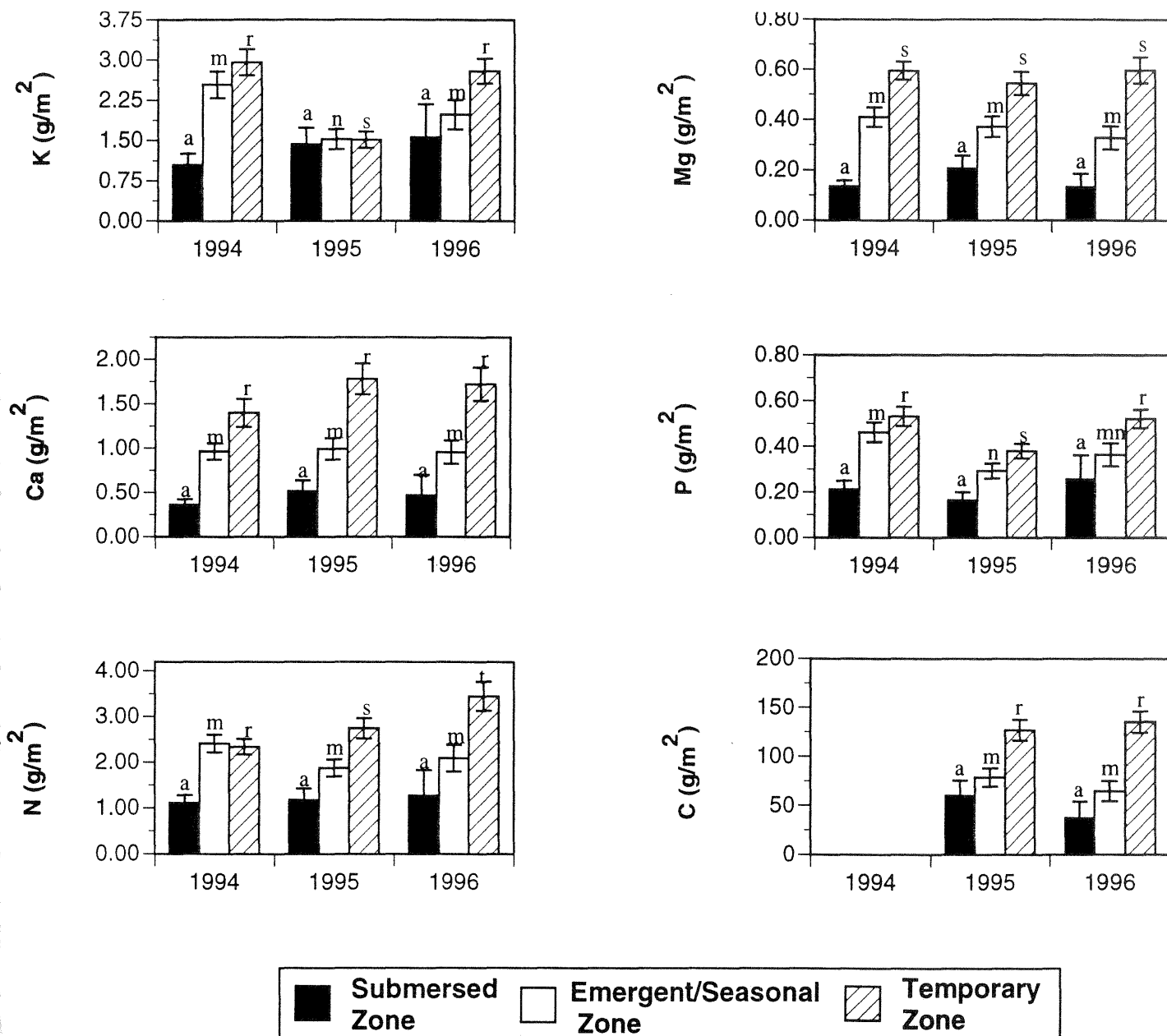


Figure 12. Mean total amounts of Ca, K, P, C, N and Mg in aboveground biomass in each of the zones for all restored wetlands in 1994, 1995 and 1996. Values are means (g/m²) \pm 1 standard error. Statistical comparisons were made between years for each zone and the results, within zones, are indicated with letters above the bars. There were no significant differences between years for the submersed zone. Significant differences between years in the emergent/seasonal zone were found for N, K, and P. All subplots were used in this analysis.

Total nutrient stocks differed little between years (Figs. 4-6, 12) and significant differences were found only for K and P. Total K (Fig. 5) was significantly lower in 1995 ($1.50 \pm 0.11 \text{ g/m}^2$) than 1994 ($2.42 \pm 0.15 \text{ g/m}^2$) and 1996 ($2.24 \pm 0.19 \text{ g/m}^2$). Total P was also significantly lower in 1995 ($0.31 \pm 0.02 \text{ g/m}^2$) than in 1994 and 1996 (Fig. 4). Total biomass distribution in the three zones also varied little from one year to the next and the pattern just described was similar. There were no differences in nutrient standing stocks for any nutrient in the submersed zone (Fig. 12). In the emergent/seasonal and temporary zones, Total K and Total P were significantly lower in 1994 than in the other two years (Fig. 12). Total N was significantly different in all three years in the temporary zone (Fig. 12).

Discussion

Confer and Niering (1992) studied five created wetlands in Connecticut and concluded that after four years of development that they were still very different from natural wetlands of the same type. They also found that the created wetlands were different from each other in the amount of the wetland that was vegetated after four years and in the characteristics of water level fluctuations during the period of study. Confer and Niering also found differences in species composition between the created wetlands even though a few species (*Typha latifolia*, *Juncus effusus*, *Leersia oryzoides*, *Impatiens capensis*, *Echinochloa crusgalli*) were common at all sites. Galatowitsch and van der Valk (1996a) also found that the vegetation in most restored wetlands was different than vegetation in natural depressional wetlands. Galatowitsch and van der Valk, however, did not provide any information on within wetland differences. We have not found any studies in which continuous annual measurements have been made of biomass and nutrients in restored wetlands. Our results can, therefore, only be compared in a general way with related studies. In general, we found patterns that were similar to those described by Confer and Niering (e.g., the individual sites differ from each other on an annual basis). The biomass and nutrient data also demonstrate that there is considerable variation from year to year for individual wetlands. Similar patterns have been shown in other studies in which species composition and percent cover of the vegetation have been examined for more than one year. Stauffer and Brooks (1997), for example, found differences in species and cover over two years in a restored wetland that experiences different hydrologic conditions from one year to the next. Brown and Bedford (1997) also found differences between years in the number of species and percent cover of vegetation. Our results suggest that during at least the first ten years following restoration that created wetlands will be very dynamic both in terms of species composition and biomass production.

The dynamic nature of the wetlands sampled during this study was also demonstrated by changes in vegetation cover and species composition of the permanent subplots which were in the same locations as the subplots that were harvested for biomass and nutrient determinations. Characteristics of the vegetation, more fully described in the next chapter, are only summarized here to demonstrate the temporal dynamics that occurred in the sites restored by CWH. Seventy-two species were identified in the permanent plots during the three years in which the 9 CWH were sampled. *Echinochloa crusgalli*, *Eleocharis obtusa* and *Ludwigia palustris* were the only species that occurred in permanent plots at all sites in each of the three years. Forty-four percent of the species were present at only one site during the three years, 19 species occurred in only one plot during the three years and 4 species were recorded in only two plots. Yearly differences in hydrologic conditions appear to have a particularly strong influence on vegetation dynamics. Species characteristic of drawdown conditions (*Bidens polylepis*, *Cyperus erythrorhizos*, *Eclipta alba*, *Fimbristylis autumnalis*, *Hypericum mutilum*) were more abundant during the driest year (1995). Other species (*Polygonum punctatum*, *Scirpus mucronatus*) were more abundant during wetter years.

Time and manpower limits did not enable us to attempt to accurately measure annual biomass production by sampling individual species when they were at peak biomass or by repeated measurements of shoot density and shoot size that could be used to more accurately estimate production. The approach that we used, measurements of biomass at the same time each year in adjacent subplots, was chosen to provide biomass comparisons between and within sites rather than accurate measurements of annual aboveground biomass. Accordingly, by sampling only once per year and sampling later in the growing season, the measurements of aboveground biomass were lower than would be expected for nutrient rich early successional wetlands (Mitsch and Gosselink 1993). While there were no overall differences in aboveground biomass across all sites, there were significant annual differences between wetlands. We believe that several factors were responsible for the measured differences. *Typha latifolia*, for example was spreading rapidly at the Hope site and in 1995 the site managers reduced that species by applying herbicides, thus resulting in lower biomass in 1996. Barnstable 10 had very low biomass in 1996 because most of the biomass that was present during the early and middle parts of the growing season had senesced because of dry conditions. Variations in management, the impacts of herbivores such as muskrats and variations in water levels during the growing season would all have site specific impacts on biomass production. Thus at the level of individual wetlands, variation from year to year is the most obvious pattern. At the landscape level, however, variation among years is minimal for both biomass, nutrient concentrations, and nutrient standing stocks (e.g., Fig. 1).

We are also measuring differences between years and between wetlands in the amounts of nutrients that were annually retained or released. The only site for which we currently have more than one full year of data for nutrient inputs and outputs is Barnstable 10. Similar to biomass and nutrients standing stocks, there were also large annual differences in the amounts of nitrogen, phosphorus retained or released (Chapters 2 and 3), further demonstrating the dynamic nature of these wetlands.

Finally, data on N:P ratios in the vegetation (range for the three years: 5.7 ± 0.15 - 7.6 ± 0.20) suggest that these systems are rich in P and that production may be limited by N. Koerselman and Meuleman (1996) suggested that N:P ratios less than 14 are indicative of N limiting conditions. Bedford et al. (In press) analyzed N:P ratio data for North American wetlands and suggested that most marshes (e.g., wetlands similar to those examined in this study) had N limited vegetation.

Conclusions

Over the three years of this study, the emergent vegetation was quite dynamic at the level of individual wetlands. Biomass varied from year to year and we believe that the differences were due to annual variations in management and hydrologic conditions. While the level of variation was high at the level of individual wetlands, at the landscape level (e.g., the geographic area over which the set of study wetlands was distributed), annual variations are very small suggesting that the overall level of plant resources are relatively similar. The pattern of distribution of biomass within wetlands zones was anticipated (e.g., decreasing biomass from the outside to inside of each wetland) and differences between zones in nutrient concentrations resulted in a fairly even distribution of nutrients from the outer seasonal zone to the submersed zone. These results suggest that nutrient dynamics within the wetlands are less variable than annual differences in biomass. Plant nutrient data also suggest that these wetlands are rich in phosphorus and that nitrogen may limit plant growth.

We did not observe any successional patterns in biomass production over the three years of the study and given the varying ages of the wetlands and results from the permanent plot study of species composition and cover (described in the next chapter), we conclude that the vegetation of these wetlands will be quite dynamic for one or more decades.

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SPECIES DYNAMICS OF VEGETATION

Antoinette L. Pepin and Dennis F. Whigham

Introduction

The vegetation dynamics of non-tidal freshwater wetlands have been the subject of many studies (see Spence 1982 for a review). However, the processes that produce the characteristic zonation of freshwater wetland plant species along gradients of water depth are not well understood (Keddy 1983, Wilson et al. 1985, Welling et al. 1988a).

In the broadest sense, wetland ecosystems are defined by their hydrology, soils and vegetation (Gosselink and Turner 1978, Carter et al. 1979, Hammer 1992, Mitsch and Gosselink 1993). Of these three, hydrology is probably the single most important factor that determines the establishment and maintenance of specific wetland types through interactions between hydrologic conditions and individual species life history strategies (Mitsch and Gosselink 1993). Hydrology also influences the biogeochemistry of soils and impacts patterns of species distribution through its influence on nutrient cycling and energy inputs (Gosselink and Turner 1978).

Yet within a specific wetland type, what processes determine the development of its characteristic vegetation? Particularly in the restoration and creation of wetlands, an understanding of these ecological processes is essential (Niering 1990) and yet these processes remain poorly understood. Vegetation development through time is often described in terms of succession. As first proposed by Clements (1916), succession was an autogenic process in which vegetation changes are brought about by the biota. Each community "prepares the way" for subsequent communities. Gleason (1917, 1926) proposed an alternate individualistic hypothesis, suggesting that a species' distribution is determined by its response to environmental conditions (allogenic succession). Odum (1969) combined these theories, suggesting that succession is really the same process everywhere, with the same driving forces and properties. It is now generally recognized that both autogenic and allogenic factors are important in the development of plant communities (Niering 1990).

Van der Valk (1981, 1982) applied the Gleasonian concept of succession to freshwater wetlands. Van der Valk's model recognizes twelve basic life history types based on life-span, propagule longevity and propagule establishment requirements. If environmental (i.e., hydrologic) conditions change, the presence or absence of a life history type can be predicted with this model and thus vegetation patterns can be explained. Whether or not a species becomes established on a site will be determined by the life history requirements of that species and its presence or absence in the seed bank. For this reason, Niering (1990) suggested that "No two sites, even though similar, will support exactly the same plant association."

Van der Valk's (1981) model of succession in freshwater wetlands, the more recent model of Poiani and Johnson (1993) and other studies of non-tidal freshwater wetlands (e.g., Heinselman 1970, Walker and Wehrhahn 1971, Millar 1973, Weller and Frederickson 1974, van der Valk and Davis 1976, Gosselink and Turner 1978, Nilsson and Keddy 1988, Schot et al. 1988, van der Valk and Welling 1988, Poiani and Johnson 1989, Charman 1993, van der Valk et al. 1994, Best et al. 1995, Vivian-Smith and Handel 1996) have shown the importance of hydrology and water regime in determining the relative abundance and distribution of freshwater wetland species. There is however a significant body of research that supports the importance of substrate in the vegetation dynamics of freshwater wetlands (Pearsall 1918, 1921, Gaudet 1977, Keddy 1983, Wilson and Keddy 1985a, b, 1986a, b, Wilson et al. 1985, Dunham 1989, Gaudet and Keddy 1995).

Nutrient availability has been shown to affect freshwater wetland species composition and distribution (e.g., Ingram 1967, Verhoeven 1986, Verhoeven et al. 1988, Koerselman et al. 1990, Wassen et al. 1990, Verhoeven and Schmitz 1991, Walbridge 1991, Mitsch and Gosselink 1993). Stochastic factors also play a role in the development of vegetation in created and restored wetlands (McCune and Cottam 1985, Niering 1989). Erwin and Best (1985) and Galatowitsch and van der Valk (1996b) suggest that fast-growing species that become established initially may preclude the subsequent establishment of other species through competitive interactions. While competition can be important in determining species distribution in other communities such as old fields (Gross and Werner 1982) and rocky inter-tidal zones (Connell 1961), relatively few studies have demonstrated the importance of competition in the distribution of freshwater wetland plant species (e.g., Buttery and Lambert 1965, Grace and Wetzel 1981, Grace and Tilman 1990, Gaudet and Keddy 1995).

In this study, the species diversity and relative abundance of species in twelve restored freshwater wetlands were compared. The first objective was to compare patterns of vegetation succession in wetlands of different ages. The second objective was to compare vegetation patterns across hydrologic zones within the wetlands. It was assumed that the vegetation would be more dynamic in young wetlands (i.e., 1-3 years following restoration) and that within individual wetlands, vegetation stability would be controlled by seasonal variations in water level fluctuations. Since sites selected for this study were restored on three different soil types, the third objective was to compare vegetation patterns for different soil types.

Study Area

Nine of the 12 sites selected for this study (Table 1) were restored by Chesapeake Wildlife Heritage (CWH) to control agricultural runoff and provide wildlife habitat. Located in topographically low areas of agricultural fields, the wetlands have hydrologic conditions similar to depressional wetlands as described by Brinson (1993). Overland flow of surface water runoff provides the primary source of hydrology. Water levels are usually the highest in winter after a pronounced drawdown that typically occurs during the growing season. Sites were allowed to re-vegetate naturally with no seeding or planting, in the manner of prairie pothole restoration (Galatowitsch and van der Valk 1996b). All but one site (Braun) was restored on hydric soil. Despite years of row-cropping, a residual wetland seed bank was assumed to persist on the prior converted farmland on which these sites were restored.

Three wetlands at Eastern Neck National Wildlife Refuge (ENWR) were also included in the study (Table 1) but they differed from the other sites because they were not restored by CWH and thus their history was unknown. It is believed that they were allowed to re-vegetate naturally like the CWH sites. The two oldest and largest sites at ENWR had larger and deeper palustrine areas than the sites restored by CWH and they did not experience as pronounced a seasonal drawdown as the CWH sites.

Table 1. Characteristics of restored wetlands selected for this study and their watersheds.

Site	Wetland				Watershed		
	Site Code	Hectares	Built	No. Growing Seasons ¹	Hectares	Soils	Soil Type ²
Barnstable 1	B1	1.3	1986	8	14	Mattapex/Elkton	2
Barnstable 3	B3	1.3	May-91	4	4.0	Elkton	2
Barnstable 10	BX	3.7	Jul-92	3	19	Mattapex/Elkton	3
Braun	BR	2.3	Sep-92	2	12	Mattapex	1
Foster	F1	0.49	Oct-93	1	4.4	Falsington	3
Gerber	G1	0.41	Jul-90	5	3.6	Falsington	2
Hope	H1	0.88	May-93	2	3.2	Elkton	3
Nesbit	N1	0.39	Jul-89	6	10	Falsington/Sassafras	2
Sultenfuss	S1	1.4	Nov-92	2	19	Falsington	2
ENWR 1	E1	1.8	@1964	30	20	Mattapex/Othello	2
ENWR 2	E2	0.51	Aug-91	4	10	Mattapex/Othello	2
ENWR 3	E3	7.2	@1964	30	---	Mattapex/Othello	3

¹ refers to the number of growing seasons from time of restoration to outset of this study.

² refers to soil morphology and characteristics determined in the field. Silt loam soil, not hydric = 1, sandy loam soil, hydric = 2 and silt loam/clay soil, hydric = 3.

Methods

Data Collection

Two hundred permanent plots were established at the 9 CWH sites in 1994. An additional 57 plots were located at the 3 ENWR sites. The plots were each 2 X 2 m and they were divided into triangular 1 X 1 m subplots (van der Valk et al. 1994). Three of the subplots were used for biomass and nutrient analyses as described in the previous chapter. The fourth subplot was used to monitor vegetation dynamics. Within each wetland, the plots were distributed among three elevation zones representing different hydrologic regimes. The submersed zone is the deepest zone. While it is permanently flooded during most growing seasons, at times of extended summer drought (as in 1995), it could have little or no standing water. The emergent/seasonal zone lies between the submersed zone and the temporary zone that is usually flooded only during the non-growing season months. The emergent/seasonal zone experienced drawdown early in the summer and remained shallowly inundated (< 0.15 m) in years of normal precipitation. Depending on the amount of summer precipitation, the duration of inundation in the emergent/seasonal zone varied. It may be flooded for the entire growing season (as in 1996) or for only part of it (as in 1994 and 1995). The temporary zone is located at the highest elevations, closest to the adjacent uplands. It experiences an earlier and more pronounced drawdown than the emergent/seasonal zone. Drawdown in the temporary zone occurred by the onset of the growing season or shortly thereafter in a year of normal rainfall. Soil in the temporary zone was saturated for sufficient duration in the rooting zone during the growing season to support a predominance of hydrophytic vegetation. When the plots were established in

1994, they were assigned to one of the three zones based on their positions within the wetlands and relative water depth at the time they were established. Subsequently, plot elevation data and water level data were used to re-evaluate the original assignments given the plots in 1994. Where appropriate, plots were assigned to a different zone.

All emergent and submersed (SAV) vascular plants present within each permanent subplot were identified and their percent cover was estimated. The percentage of open water or bare ground was also estimated in each subplot. Cover was defined as the vertical crown or shoot-area projection per species in relation to the reference area (Mueller-Dombois and Ellenberg 1974). Sites were visited in the fall, during September and October, soon after the peak of aboveground biomass, at a time when most species were flowering or setting fruit which facilitated their identification. Data for the 9 CWH sites were collected in 1994-96. The 3 ENWR sites were only sampled during the 1995 and 1996 growing seasons. Taxonomic nomenclature follows Brown and Brown (1984).

Data Analysis

One-way ANOVA tests were used to analyze species richness and diversity data for the permanent subplots. Shannon diversity indices were calculated using PC-ORD (McCune and Mefford 1995). Pearson product-moment correlation coefficients were calculated with MINITAB (McKenzie et al. 1995) and used to evaluate patterns of species occurrence relative to year and vegetation zone. For significant factors, the Tukey's Test in MINITAB (McKenzie et al. 1995) was used to compare values.

Percent cover data were analyzed using TWINSpan (Two-Way Indicator Species Analysis) in PC-ORD (McCune and Mefford 1995) to construct a classification of plant communities and samples (Hill 1979). TWINSpan was selected as the classification technique because it is best suited for identifying groups at each extreme of a small number of environmental gradients (Gauch Jr. 1982, Jongman et al. 1987, van Groenewoud 1992, Belbin and McDonald 1993, Islebe et al. 1995, Vasquez and Norman 1995).

Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) in PC-ORD (McCune and Mefford 1995) was used to analyze heterogeneity of subplots and sites (Pirintsos et al. 1995) and for identifying relationships among plots (Motzkin 1994) and with environmental variables. DCA is indicated when detailed environmental data are not available (Kent and Coker 1992, McDonald et al. 1996). Prior to applying DCA, data were relativized using the double standardization of Bray and Curtis (1957). Austin and Greig-Smith (1968) found this technique for standardization gave more satisfactory results than raw data, sample relativization alone or species maximum adjustment alone. Using DCA with double standardization was selected as the "best ordination" for this data set in the sense of Kent and Coker (1992) as it enabled "a clear ecological interpretation (of the data) to be made."

For DCA analyses, substrate (i.e., soil) was classified as one of three types: silty clay loam hydric, sandy hydric or upland heavy clay loam soil (Table 1). Characteristics of the soil series for each wetland obtained from SCS county soil maps were confirmed by examination of the soil's morphology in the field. Changes in hydrologic regime are expressed most directly as elevation gradients in wetlands, with distinct plant communities found at particular elevation zones (Hammer 1992, Mitsch and Gosselink 1993, Padgett and Crow 1994). Therefore, the three vegetation zones were used as an environmental variable to describe each plot's hydrologic regime. By relating plot elevation to ancillary water level data, the effect of hydrology on vegetation was investigated. Relationships with other factors including size of wetland, age of wetland, year and size of watershed were also included in the analyses.

Results and Discussion

Occurrence of Species in Plots

Ninety-five (16.4%) of the permanent subplots contained no emergent or submersed vegetation when they were sampled. Sixty-nine (73%) of them were located in the submersed zone, 22 (23%) in the emergent zone and 4 (4%) in the temporary zone. While the number of subplots without any vegetation was greatest in 1996, the wettest year, it was not significantly different from years with normal and dry conditions, 1994 and 1995, respectively ($r = -0.323$, $p > 0.05$). Only 10 % ($r^2 = 0.104$) of the variation in the number of subplots without any vegetation was explained by year. However, the number of subplots without vegetation was significantly correlated with vegetation zone ($r = -0.876$, $p = 0.001$), with a significantly greater number of bare subplots in the deeper submersed zone. Vegetation zone explained 77% ($r^2 = 0.767$) of the variation in the number of subplots with no vegetation. Subplots with no vegetation were not used in any of the subsequent analyses to evaluate patterns of species distribution and abundance.

Occurrence of Species at Sites

Seventy-two species were observed at the 9 CWH sites during 1994-96 (Table 2). Of these, only 3 species (*Echinochloa crusgalli*, *Eleocharis obtusa* and *Ludwigia palustris*) were present at all of the sites but none of them were present during each of the three growing seasons that the subplots were sampled (Table 3). *Panicum virgatum* and *Typha latifolia* were found at all but one of the sites. *Eleocharis obtusa* was the most common species having been recorded at all sites except Braun in 1994. Thirty-two species (44%) were present only at one site (Table 3).

Frequency of Occurrence of Species

Eleocharis obtusa was also the most frequently sampled species, occurring in more than half the subplots in 1994 and 1995 (Table 3). Higher than usual water levels during 1996 likely resulted in the reduced number of subplots with *E. obtusa*. Nineteen species (26%) were observed in only one subplot during the three years and 4 species (6%) were observed in only two subplots. These "rare" species, indicated by an asterisk in Table 3, were not included in the subsequent ordinations. Only eleven species (15%), indicated in bold type in Table 3, occurred in 10% or more of the vegetated subplots.

Thirty seven of the species observed at CWH sites were also present at the ENWR sites (Table 4). Sixteen species, including tree species (*Acer rubrum*, *Liquidambar styraciflua* and *Platanus occidentalis*) were present at ENWR sites but not at CWH sites (Table 4). It is surprising that the three tree species were not found at the CWH sites because all of them have wind dispersed seeds and sources of propagules within close proximity of each of the wetlands. They are common species in other restored wetlands in the region (A. Pepin, personal observation).

Table 2. List of species observed in subplots at 9 Chesapeake Wildlife Heritage (CWH) sites and their wetland indicator status on a list developed by Reed (1988). The six-letter codes were used in coding species for data analysis and presentation.

SPECIES	STATUS	CODE	SPECIES	STATUS	CODE
<i>Acalypha rhomboidea</i>	FACU-	ACARHO	<i>Lespedeza striata</i>	FACU	LESSTR
<i>Agrostis alba</i>	FACW	AGRALB	<i>Lindernia anagallidea</i>	OBL	LINANA
<i>Agrostis tenuis</i>	UPL	AGR TEN	<i>Lonicera japonica</i>	FAC-	LONJAP
<i>Alisma plantago-aquatica</i>	OBL	ALIPLA	<i>Ludwigia alternifolia</i>	FACW+	LUDALT
<i>Ambrosia artemisiifolia</i>	FACU	AMBART	<i>Ludwigia palustris</i>	OBL	LUDPAL
<i>Ammannia coccinea</i>	OBL	AMMCOC	<i>Lycopus americanus</i>	OBL	LYCAME
<i>Asclepias incarnata</i>	OBL	ASCINC	<i>Oldenlandia uniflora</i>	FACW	OLDUNI
<i>Aster pilosus</i>	UPL	ASTPIL	<i>Panicum dichotomiflorum</i>	FACW-	PANDIC
<i>Aster subulatus</i>	OBL	ASTSUB	<i>Panicum virgatum</i>	FAC	PANVIR
<i>Aster vimineus</i>	FAC	ASTVIM	<i>Parthenocissus quinquefolia</i>	FACU	PARQUI
<i>Bidens frondosa</i>	FACW	BIDFRO	<i>Paspalum laeve</i>	FAC+	PASLAE
<i>Bidens polylepis</i>	FACW	BIDPOL	<i>Phragmites australis</i>	FACW	PHRAUS
<i>Bidens tripartita</i>	OBL	BIDTRI	<i>Pluchea purpurascens</i>	OBL	PLUPUR
<i>Boehmeria cylindrica</i>	FACW+	BOECYL	<i>Polygonum hydropiperoides</i>	OBL	POLHYD
<i>Campsis radicans</i>	FAC	CAMRAD	<i>Polygonum pensylvanicum</i>	FACW	POLPEN
<i>Cephalanthus occidentalis</i>	OBL	CEPOCC	<i>Polygonum persicaria</i>	FACW	POLPER
<i>Cyperus erythrorhizos</i>	FACW+	CYPERY	<i>Polygonum punctatum</i>	OBL	POLPUN
<i>Cyperus strigosus</i>	FACW	CYPSTR	<i>Potamogeton diversifolius</i>	OBL	POTDIV
<i>Digitaria ischaemum</i>	UPL	DIGISC	<i>Ranunculus sardous</i>	UPL	RANSAR
<i>Echinochloa crusgalli</i>	FACU	ECHCRU	<i>Rotala ramosior</i>	OBL	ROTRAM
<i>Eclipta alba</i>	FAC	ECLALB	<i>Rumex crispus</i>	FACU	RUMCRI
<i>Eleocharis obtusa</i>	OBL	ELEOBT	<i>Sagittaria latifolia</i>	OBL	SAGLAT
<i>Eleocharis palustris</i>	OBL	ELEPAL	<i>Salix nigra</i>	FACW+	SALNIG
<i>Eleocharis quadrangulata</i>	OBL	ELEQUA	<i>Scirpus americanus</i>	OBL	SCIAME
<i>Erigeron canadensis</i>	UPL	ERICAN	<i>Scirpus mucronatus</i>	OBL	SCIMUC
<i>Festuca pratensis</i>	FACU-	FESPRA	<i>Scirpus pungens</i>	FACW+	SCIPUN
<i>Fimbristylis autumnalis</i>	FACW+	FIMAUT	<i>Scirpus purshianus</i>	OBL	SCIPUR
<i>Galium obtusum</i>	FACW+	GALOBT	<i>Scirpus validus</i>	OBL	SCIVAL
<i>Hibiscus moscheutos</i>	OBL	HIBMOS	<i>Setaria faberi</i>	UPL	SETFAB
<i>Hypericum mutilum</i>	FACW	HYPMUT	<i>Setaria glauca</i>	FAC	SETGLA
<i>Ipomoea lacunosa</i>	FACW	IPO LAC	<i>Solidago altissima</i>	FACU-	SOLALT
<i>Juncus bufonius</i>	FACW	JUNBUF	<i>Taraxacum officinale</i>	FACU-	TAROFF
<i>Juncus canadensis</i>	OBL	JUNCAN	<i>Trifolium hybridum</i>	FACU-	TRIHYP
<i>Juncus effusus</i>	FACW+	JUNEFF	<i>Tripsacum dactyloides</i>	FACW	TRIDAC
<i>Juncus tenuis</i>	FAC-	JUNTEN	<i>Typha latifolia</i>	OBL	TYPLAT
<i>Leersia oryzoides</i>	OBL	LEEORY	<i>Xanthium strumarium</i>	FAC	XANSTR

Table 3. Frequency of species occurrence at 9 Chesapeake Wildlife Heritage (CWH) sites and percentage (by year and total) of vegetated subplots in which each species occurred. Total n = 481 subplots. Species in bold type occurred in 10% or more of vegetated subplots. "Rare" species, those occurring in <0.05% (1-2) subplots, are indicated by an asterisk. Species are arranged in decreasing order of abundance re: total # sites, then alphabetically. Species codes used in this table can be found in Table 2.

SPECIES CODE	TOTAL # SITES	# SITES 1994	# SITES 1995	# SITES 1996	% PLOTS 1994	% PLOTS 1995	% PLOTS 1996	% TOTAL PLOTS
ECHCRU	9	8	9	5	55.07	67.05	11.02	32.22
ELEOBT	9	8	9	9	94.04	82.06	50.02	50.94
LUDPAL	9	8	8	9	46.04	35.05	47.04	30.98
PANVIR	8	8	5	2	61.01	58.00	5.00	26.20
TYPLAT	8	6	8	6	24.00	28.01	41.00	19.75
ECLALB	6	5	6	2	17.00	38.00	4.00	12.27
ELEPAL	6	1	4	6	2.00	14.00	24.00	8.32
LEEORY	6	5	6	5	17.08	17.06	16.05	11.02
LINANA	6	4	4	1	23.00	11.00	1.00	7.28
POLPEN	6	6	3	2	11.00	4.00	5.00	4.16
POTDIV	6	6	3	3	23.04	3.04	12.09	13.31
SETGLA	6	4	5	3	20.00	13.00	6.00	8.11
XANSTR	6	5	6	2	30.00	46.00	4.00	16.63
ALIPLA	5	4	3	4	16.02	10.00	5.01	7.48
BIDPOL	5	5	4	2	25.00	30.00	13.00	14.14
HYPMUT	5	1	3	1	1.00	4.00	1.00	1.25
PANDIC	5	0	4	3	0.00	16.01	10.00	5.61
POLHYD	5	2	4	3	2.00	3.02	3.00	2.49
SETFAB	5	3	2	1	9.00	4.00	4.00	3.53
CYPSTR	4	2	3	1	7.00	7.00	2.00	3.33
DIGISC	4	3	3	1	17.00	21.00	6.00	9.15
LYCAME	4	4	3	2	5.02	5.01	3.00	3.53
ROTRAM	4	3	4	2	16.00	7.00	8.00	6.44
SALNIG	4	4	4	2	4.01	5.01	7.00	3.74
SCIMUC	4	4	4	4	40.02	17.01	36.01	20.79
SCIPUR	4	3	3	1	20.00	18.00	1.00	8.11
CYPERY	3	1	3	1	1.00	7.00	1.00	1.87
ELEQUA	3	0	1	3	0.00	1.00	8.00	1.87

Table 3. continued

SPECIES CODE	TOTAL # SITES	# SITES 1994	# SITES 1995	# SITES 1996	% PLOTS 1994	% PLOTS 1995	% PLOTS 1996	% TOTAL PLOTS
FIMAUT	3	1	3	1	1.00	8.00	1.00	2.08
JUNCAN	3	1	3	2	2.00	9.00	5.00	3.33
JUNTEN	3	0	3	1	0.00	9.00	7.00	3.33
ASTPIL	2	0	2	1	0.00	4.00	2.00	1.25
BIDFRO	2	0	1	1	0.00	3.00	1.00	0.83
BIDTRI	2	1	2	1	0.02	5.01	0.01	2.29
ERICAN*	2	0	2	0	0.00	2.00	0.00	0.42
GALOBT	2	1	2	1	1.00	4.01	4.00	2.08
HIBMOS	2	2	1	0	3.00	3.00	0.00	1.25
JUNEFF	2	1	2	2	0.03	4.04	3.04	5.20
PHRAUS	2	2	2	2	11.00	12.00	13.00	7.48
RUMCRI	2	2	0	1	4.00	0.00	1.00	1.04
ACARHO*	1	1	0	0	1.00	0.00	0.00	0.21
AGRALB*	1	1	0	0	1.00	0.00	0.00	0.21
AGR TEN*	1	0	0	1	0.00	0.00	1.00	0.21
AMBART*	1	0	1	0	0.00	1.00	0.00	0.21
AMMCOC	1	0	0	1	0.00	0.00	8.00	1.66
ASCINC*	1	0	0	1	0.00	0.00	1.00	0.21
ASTSUB*	1	0	0	1	0.00	0.00	1.00	0.21
ASTVIM	1	0	0	1	0.00	0.00	6.00	1.25
BOECYL*	1	0	0	1	0.00	0.00	1.00	0.21
CAMRAD*	1	0	1	0	0.00	1.00	0.00	0.21
CEPOCC*	1	0	0	1	0.00	0.00	1.00	0.21
FESPR	1	0	1	1	0.00	1.00	4.00	1.04
IPOLAC	1	0	1	0	0.00	1.00	0.00	0.21
JUNBUF*	1	0	1	0	0.00	1.00	0.00	0.21
LESSTR*	1	0	0	1	0.00	0.00	1.00	0.21
LONJAP*	1	1	0	0	1.00	0.00	0.00	0.21
LUDALT*	1	0	0	1	0.00	0.00	1.00	0.21
OLDUNI*	1	0	1	0	0.00	2.00	0.00	0.42
PARQUI*	1	0	1	0	0.00	1.00	0.00	0.21
PASLAE*	1	0	1	0	0.00	1.00	0.00	0.21
PLUPUR*	1	0	1	0	0.00	1.00	0.00	0.21
POLPER*	1	0	1	0	0.00	1.00	0.00	0.21

Table 3. continued

SPECIES	TOTAL	# SITES	# SITES	# SITES	% PLOTS	% PLOTS	% PLOTS	% TOTAL
CODE	# SITES	1994	1995	1996	1994	1995	1996	PLOTS
POLPUN	1	1	0	1	0.04	0.00	0.04	2.70
RANSAR*	1	0	1	0	0.00	1.00	0.00	0.21
SAGLAT	1	1	0	0	4.00	0.00	0.00	0.83
SCIAME*	1	1	0	0	1.00	0.00	0.00	0.21
SCIPUN	1	0	1	0	0.00	0.01	0.00	0.21
SCIVAL	1	1	0	0	7.00	0.00	0.00	1.46
SOLALT	1	0	1	1	0.00	1.00	3.00	0.83
TAROFF*	1	0	0	1	0.00	0.00	2.00	0.42
TRIDAC*	1	0	0	1	0.00	0.00	1.00	0.21
TRIHVB	1	0	1	1	0.00	2.00	5.00	1.46

Table 4. List of species observed in subplots at 3 Eastern Neck Wildlife Refuge (ENWR) sites and their wetland indicator status on a list developed by Reed (1988). The six-letter codes were used in coding species for data analysis and presentation. Species in bold type occurred at ENWR sites but not at Chesapeake Wildlife Heritage (CWH) sites.

SPECIES	STATUS	CODE	SPECIES	STATUS	CODE
<i>Acalypha rhomboidea</i>	FACU-	ACARHO	<i>Ludwigia alternifolia</i>	FACW+	LUDALT
<i>Acer rubrum</i>	FAC	ACERUB	<i>Ludwigia palustris</i>	OBL	LUDPAL
<i>Agrostis tenuis</i>	UPL	AGR TEN	<i>Lycopus americanus</i>	OBL	LYCAME
<i>Ambrosia artemisiifolia</i>	FACU	AMBART	<i>Mikania scandens</i>	FACW+	MIKSCA
<i>Asclepias incarnata</i>	OBL	ASCINC	<i>Panicum dichotomiflorum</i>	FACW-	PANDIC
<i>Bidens polylepis</i>	FACW	BIDPOL	<i>Panicum virgatum</i>	FAC	PANVIR
<i>Boehmeria cylindrica</i>	FACW+	BOECYL	<i>Phragmites australis</i>	FACW	PHRAUS
<i>Carex vulpinoidea</i>	OBL	CARVUL	<i>Plantago aristata</i>	UPL	PLAARI
<i>Cyperus erythrorhizos</i>	FACW+	CYPERY	<i>Platanus occidentalis</i>	FACW-	PLAOCC
<i>Decodon verticillatus</i>	OBL	DECVER	<i>Polygonum coccineum</i>	OBL	POLCOC
<i>Digitaria ischaemum</i>	UPL	DIGISC	<i>Polygonum hydropiperoides</i>	OBL	POLHYD
<i>Dulichium arundinaceum</i>	OBL	DULARU	<i>Polygonum pensylvanicum</i>	FACW	POLPEN
<i>Echinochloa crusgalli</i>	FACU	ECHCRU	<i>Polygonum persicaria</i>	FACW	POLPER
<i>Eclipta alba</i>	FAC	ECLALB	<i>Polygonum punctatum</i>	OBL	POLPUN
<i>Eleocharis obtusa</i>	OBL	ELEOBT	<i>Rosa multiflora</i>	FACU	ROSMUL
<i>Erechtites hieracifolia</i>	FACU	EREHIE	<i>Rotala ramosior</i>	OBL	ROTRAM
<i>Erigeron canadensis</i>	UPL	ERICAN	<i>Rubus argutus</i>	FACU	RUBARG
<i>Eupatorium pilosum</i>	FACW	EUPPIL	<i>Scirpus mucronatus</i>	OBL	SCIMUC
<i>Euthamia graminifolia</i>	FAC	EUTGRA	<i>Setaria faberi</i>	UPL	SETFAB
<i>Festuca pratensis</i>	FACU-	FESGRA	<i>Setaria glauca</i>	FAC	SETGLA
<i>Fimbristylis autumnalis</i>	FACW+	FIMAUT	<i>Trifolium arvense</i>	UPL	TRIARV
<i>Galium obtusum</i>	FACW+	GALOB	<i>Typha latifolia</i>	OBL	TYPLAT
<i>Hibiscus moscheutos</i>	OBL	HIBMOS	<i>Xanthium strumarium</i>	FAC	XANSTR
<i>Juncus canadensis</i>	OBL	JUNCAN			
<i>Juncus effusus</i>	FACW+	JUNEFF			
<i>Juncus tenuis</i>	FAC-	JUNTEN			
<i>Leersia oryzoides</i>	OBL	LEEORY			
<i>Leersia virginica</i>	FACW	LEEVIR			
<i>Liquidambar styraciflua</i>	FAC	LIQSTY			
<i>Lonicera japonica</i>	FAC-	LONJAP			

Annual Variations in Patterns of Species Occurrence

Patterns of species occurrence varied from year to year (Table 3) and they seemed to be related to differences in drawdown during the growing season. During the three years that subplots were sampled, drawdown conditions for individual sites varied quite dramatically, largely related to the amount of rainfall during the growing season. Water level data for Barnstable 1 (Fig. 1) are characteristic of those for the other restored sites. While rainfall was near normal during 1994 and 1995 at Chestertown, MD, the nearest reporting weather station (Fig. 2), field observations at the restored wetlands indicate conditions were much drier during 1995. One-way ANOVA for the number of subplots without standing water indicated a significant difference ($p < 0.001$) between years. There was a significantly greater number of subplots without standing water in 1995 than in 1994 or 1996, based on the Tukey's Test. Figure 1 indicates that Barnstable 1 experienced a pronounced drawdown from June - November 1995. Many of the submersed plots at this and the other sites lacked standing water when subplots were sampled in 1995. In contrast, 1996 was a very wet year during the growing season, particularly in June and July (Fig. 2). There was a much less pronounced drawdown at Barnstable 1 during 1996 than in the preceding drier year (Fig. 1). Rainfall during the growing season was near to slightly below normal in 1997 (Fig. 2). While water level data are not available for Barnstable 1 in 1994, it is likely the moderate level of drawdown that occurred in 1997 (Fig. 1) resembled that for 1994, since both years experienced similar near normal precipitation during the growing season (Fig. 2).

The abundance of some species was greatest in the dry year, while significantly less in the wet year (Table 3). Species exhibiting this pattern included: *Cyperus erythrorhizos*, *Fimbristylis autumnalis*, *Bidens polylepis*, *B. tripartita*, *B. frondosa*, *Polygonum pennsylvanicum*, *Panicum dichotomiflorum*, *Hypericum mutilum*, *Eclipta alba*, *Xanthium strumarium*, and *Echinochloa crusgalli*. *Cyperus strigosus*, *Panicum virgatum*, *Lindernia anagallidea*, *Setaria glauca* and *Digitaria ischaemum* were markedly less abundant in the wet year than in the other two years subplots were sampled. These species are all annuals and behaved like mud-flat species in the sense of van der Valk and Davis (1978). In their study of prairie marshes, *Bidens*, *Cyperus*, *Polygonum* and *Rumex* species were ephemerals whose seeds only germinated on exposed mud flats after drawdown, during periods when standing water was absent because of drought or water level manipulation. When the marshes re-flooded, these species were eliminated (In this study, there were mostly reductions in overall abundance rather than species elimination).

The emergent species found on the CWH sites exhibited two distinct patterns in response to seasonal fluctuations of water levels. The majority, including *Typha latifolia*, *Eleocharis palustris*, *E. quadrangulata*, and *Scirpus mucronatus* were most abundant in the wet year and less abundant in the dry year. These perennial species behaved like emergents in prairie marshes studied by van der Valk and Davis (1978) that germinated in very shallow water or on exposed mud flats and spread vegetatively in years when standing water persisted. However, not all emergent species were more abundant in the wet year. Another perennial species, *Eleocharis obtusa*, was markedly less abundant at 7 of 9 CWH sites in the wet year than in the other two years subplots were sampled. While the year with above normal precipitation would seem to favor this obligate emergent species, it did not. In a study of shallow marsh wetlands, Millar (1973) found that *Eleocharis palustris* became less abundant when greater than normal water depth was present at the start of this growing season. However, *Eleocharis obtusa* rather than *E. palustris* decreased in abundance due to high water levels at the CWH sites. Due to basin morphology, the shallow emergent zone of re-wetting favored by *Eleocharis obtusa* was narrower during the wet year and this may have resulted in its reduced abundance.

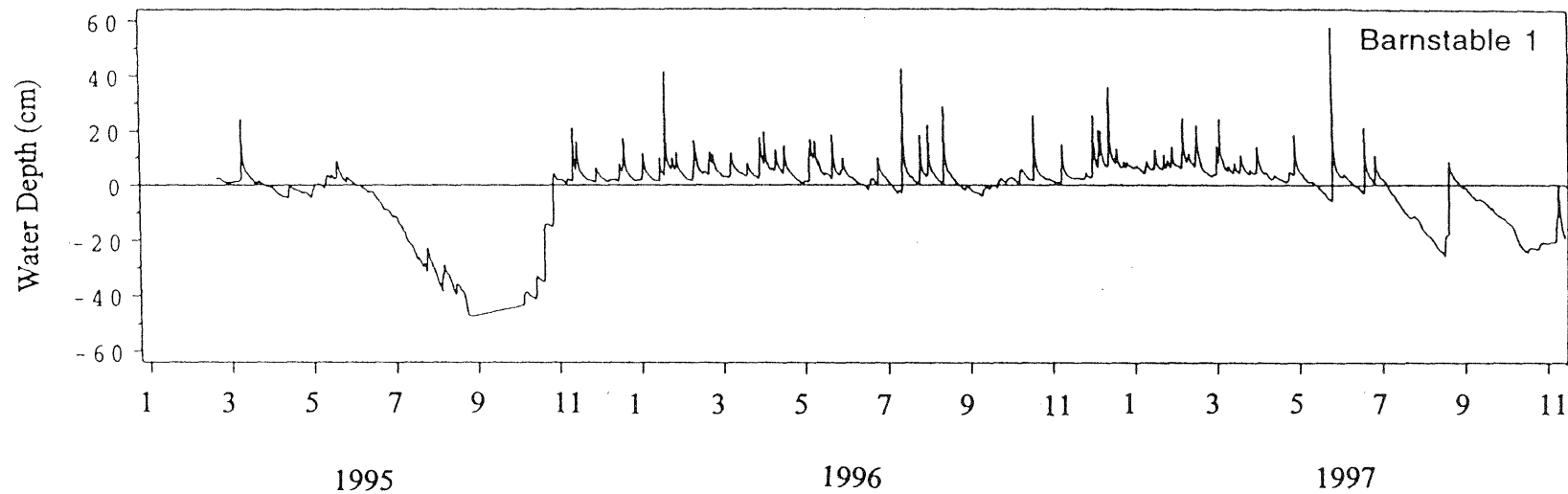


Figure 1. Water level data, in cm above (+) or below (-) the v-notch of the outlet weir, for Barnstable 1 from March 1995 - November 1997. Tick marks on the x-axis correspond to the first day of each month. Modified from Whigham et al. 1998.

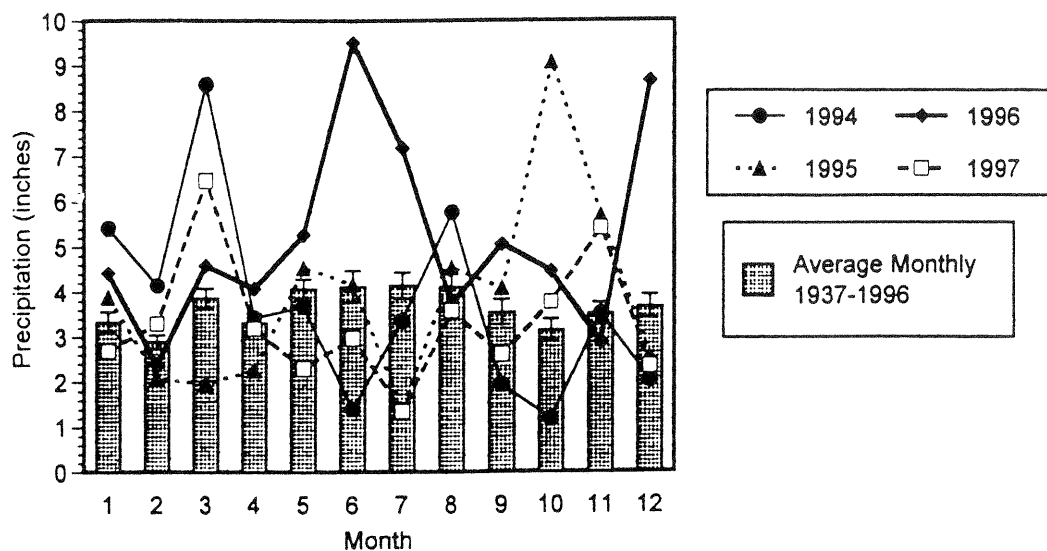


Figure 2. Precipitation data for Chestertown, Maryland, the nearest reporting weather station. The average monthly values are based on data from 1937-1996, omitting 1939, 1949 and 1950 when data were incomplete. Error bars represent the standard error. Monthly rainfall for 1994-1997 are overlaid on the average monthly values. Source: <http://www.ncdc.noaa.gov> and National Climatic Data Center, Asheville, NC.

Vegetation Development

The number of plots in which certain species were found each year increased in the emergent zone at individual sites, indicating vegetation development. *Leersia oryzoides* increased at Foster and Gerber, *Ludwigia palustris* at Foster, *Rotala ramosior* at Barnstable #3 and *Typha latifolia* at Braun, Gerber, Hope and Nesbit. *Salix nigra*, the only tree species observed at the CWH sites, increased in frequency of occurrence at Braun and Gerber.

One species, *Alisma plantago-aquatica* was characteristic of the most recently restored sites. For example, *A. plantago-aquatica* was present in all ten subplots at Foster during the first year following restoration and it then steadily declined during the second and third growing seasons. A similar pattern of decreased frequency of *Alisma plantago-aquatica* was also detected at Sultenfuss between years 2 to 4 following restoration. Of 36 subplots with *Alisma plantago-aquatica*, all but three were on sites during the first or second year following restoration.

Although their relative abundance across sites changed, the pattern of distribution within sites changed very little for some species. *Eleocharis obtusa* consistently occurred in the emergent zone subplots at Barnstable 1 and 3, Foster, Gerber and Nesbit. *Phragmites australis* was consistently found in subplots in the emergent zone at Nesbit. Species found in the same subplots each year in the temporary/seasonal zone included *Bidens polylepis* at Gerber, Hope and Nesbit and *Digitaria ischaemum* at Gerber and Hope.

Species Richness and Diversity

One-way ANOVAs for species richness at the 9 CWH sites found that there was no significant difference between the three years ($p > 0.115$) or for wetlands of different ages ($p > 0.589$). There was a significant difference in species richness between vegetation zones ($p < 0.001$), with richness increasing from 3.0 in the submersed zone to 9.1 in the emergent zone and 12.5 in the seasonal zone. The three zones differed significantly from each other based on the Tukey's Test.

Species diversity followed a similar pattern. While there was no significant difference in species diversity between the three years of the study ($p > 0.413$) or for wetlands of different ages ($p > 0.704$). There was a significant difference between vegetation zones and the zones were significantly different from each other. Species diversity increased from 0.59 for in the submersed zone to 1.61 for the emergent zone and 1.91 for the seasonal zone, respectively.

Species richness and diversity followed an expected pattern based on our understanding of the tolerances of wetland species to flooding (van der Valk and Pederson 1989, Merendino et al. 1990, van der Valk et al. 1994, Brown and Bedford 1997, Brown 1998). The submersed zone, with the most prolonged duration of flooding, had the fewest species and the lowest species diversity. *Potamogeton diversifolius*, the species of SAV found at the majority of these restored wetlands, was the most abundant species in the submersed zone. The emergent zone, with its fluctuating water level, had greater species richness and diversity than the submersed zone, but less than the seasonal zone. The seasonal zone, while possessing many of the same species as the emergent zone also included mud-flat annuals (van der Valk and Davis 1978). Mud-flat annuals are adapted to germinate quickly after drawdown for autumn flowering such as *Bidens*, *Cyperus* and *Polygonum* species. "Drier" species from the adjacent upland fields, such as species of *Aster* and *Setaria*, provided additional species richness and diversity to the seasonal zone.

Classification and Ordination of CWH Wetlands

Application of TWINSpan to data for the 456 vegetated subplots demonstrated a pattern of almost complete intermixing of species and samples. When data for all sites were divided into three vegetation zones (temporary, emergent, submersed) however, the TWINSpan output produced clearly defined clusters (Table 5). Mud-flat annuals (e.g., *Panicum virgatum*, *Bidens polylepis*, *Cyperus erythrorhizos*, *C. strigosus*, *Eclipta alba* and *Xanthium strumarium*) were found primarily in the temporary zone. Perennials such as *Scirpus mucronatus*, *Typha latifolia* and *Eleocharis palustris* were most abundant in the emergent zone while *Potamogeton diversifolius* was characteristic of the submersed zone.

In the TWINSpan output, species are clearly distributed into different vegetation zones based on their tolerances to inundation. While the permanent subplots are also mostly distributed into groups based on inundation, the species characterizations of individual subplots changed from year to year depending on the hydrologic regime, which varied greatly between years of high and low precipitation. Certain sites showed marked changes in emergent and temporary zone vegetation between years. For example, the emergent and temporary zones at Nesbit were separated into distinct clusters for 1994. In 1995, vegetation of both the emergent and temporary zone resembled and was clustered with that of the 1994 temporary zone (i.e., vegetation was "drier" overall with a larger percentage of mud-flat annuals). In 1996, the emergent and temporary zone vegetation resembled and was clustered with that of the 1994 emergent zone (i.e., vegetation was "wetter" with more abundant emergents). The submersed zone of some sites also showed changes from year to year depending on the hydrologic regime. For example, subplots in the submersed zone at Braun and Nesbit appeared with subplots in the temporary zone in 1995 which was the year with an early and extended drawdown. Thus, subplots that had no vegetation or only SAV during two years of the study, had vegetation during the dry year that was typically found in the temporary zone in other years.

The ordering of samples in the TWINSpan output (Table 5) indicated that the designation of subplots into zones showed a high degree of variation between sites. Despite an overall zone effect within wetlands due to the relative elevation of subplots, the degree of separation between zones varied from site to site. The emergent and temporary zones at Barnstable 3 showed little distinction and were found in the same cluster all three years. At other sites, the emergent and temporary zones were more dissimilar. For example, at Hope, the two zones were separated into distinct clusters each of the three years.

When DCA was applied to this data set, a well-defined gradient ($r = -0.52$) of plots based primarily on vegetation zone was obtained (Fig. 3). While Axis 1 was most strongly correlated with zone, Axis 2 was most strongly correlated with site ($r = -0.50$). As with the TWINSpan output, the species characterizations of subplots changed from year to year. For example, submersed zone plots appear with subplots in the temporary zone (lower left of Fig. 3). During 1995, when there was an early and extended drawdown, subplots in the submersed zone at Braun and Nesbit had vegetation that was typically found in the temporary zone in other years.

Differences Among Sites-- To further investigate the relative importance of vegetation zone and annual variations in the hydrologic regime on vegetation dynamics, vegetation data for each site were analyzed separately. In the TWINSpan output, there was a clear separation of subplots based on vegetation zone for some sites (Barnstable 3, Barnstable 10, Gerber, Hope, Nesbit and Sultenfuss). Vegetation zone was more strongly correlated with the primary axis than year for DCA applied to vegetation data for each of these six sites (Table 6). Annual hydrologic variations were more important than subplot elevations (i.e., vegetation zone) in explaining the vegetation dynamics at Braun, Barnstable 1 and Foster. When DCA was applied to the vegetation data for each of these

Table 5. TWINSpan output for vegetation data from 9 CWH sites combined into subgroups by vegetation zone (temporary, emergent and submersed). Site group codes are based on vegetation zone: 1) temporary; 2) emergent; and 3) submersed. Species group codes refer to vegetation zone and life history: I = mud-flat annuals; II = species found in both the emergent and temporary zones; III = emergent perennials; IV = submersed species. Species codes used in this table can be found in Table 2. Numbers within the table correspond to the following percent cover values: - = species absent, 1 = less than 2%; 2 = 2-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-50%; and, 6 = 51-100.

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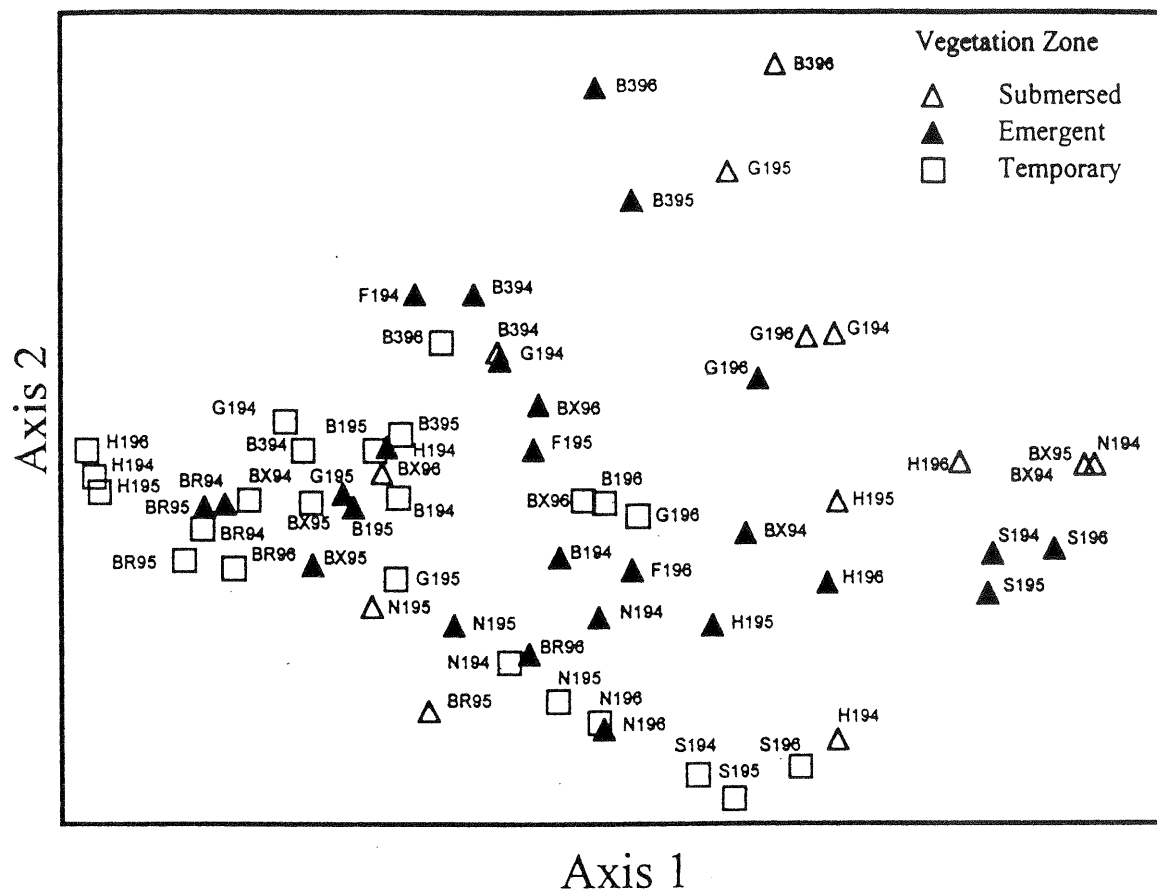


Figure 3. Ordination plot from DCA of CWH vegetation data divided into 3 zones.

Table 6. Pearson correlation coefficients with the primary axis for DCA applied to vegetation data for each of the CWH sites.

FACTOR		
Site	Year	Zone
Barnstable 1	-0.685	-0.442
Barnstable 3	-0.216	0.570
Barnstable 10	-0.545	-0.675
Braun	0.778	0.069
Foster	-0.843	N/A
Gerber	0.344	-0.550
Hope	0.278	-0.777
Nesbit	0.352	0.625
Sultenfuss	0.334	-0.900

three sites, the primary axes were more strongly correlated with year than with zone (Table 6). Braun, Barnstable 1 and Foster each responded differently to annual hydrologic variations. At Braun, the timing and extent of drawdown seemed to determine the overall nature of this site's vegetation from year to year. Figure 4 indicates how strongly vegetation varied from year to year at Braun. During 1994, this site's second growing season, vegetation in all subplots consisted primarily of *Panicum virgatum* and *Xanthium strumarium*, two mud-flat annual species. There were very low percent cover values for emergents and other mud-flat annuals in 1994. During 1995 and 1996, species diversity and richness increased at Braun. However, the character of the vegetation was markedly different for these years. In 1995, when there was an early and extended drawdown, vegetation in the submersed, emergent and temporary zone subplots was primarily mud-flat annuals, regardless of subplot elevation (Fig. 4). The above normal precipitation during the 1996 growing season resulted in higher than normal water levels at Braun, with perennial emergents present in most subplots, regardless of subplot elevation (Fig. 4). Subplots which in the previous "dry" year supported a predominance of mud-flat annuals were characterized by perennial emergents during the wetter than normal year. At Barnstable 1, yearly hydrologic changes were most important in explaining vegetation dynamics. However, zone was also strongly correlated with the primary axis for DCA (Table 6). In 1994, a temporary zone dominated by mud-flat annuals including *Echinochloa crusgalli*, *Panicum virgatum*, *Cyperus erythrorhizos*, *C. strigosus* and *Lindernia anagallidea* was present, with a shallowly flooded emergent zone vegetated with *Eleocharis palustris*, *E. obtusa*, *Typha latifolia*, *Hibiscus moscheutos* and *Phragmites australis* and a more deeply flooded emergent zone dominated by *Sagittaria latifolia* and *Scirpus validus* (Fig. 5). During the winter of 1994-1995, a muskrat eat-out changed the overall character of this site's vegetation. The deeply flooded emergent zone became even deeper as the result of muskrats digging up and feeding on tubers of *Sagittaria latifolia* and *Scirpus validus*. During 1995 and 1996, the formerly deeply flooded emergent subplots resembled those in the submersed zone and lacked vegetation. For the remaining undisturbed subplots, the vegetation dynamics followed a pattern identical to that at Braun, with a predominance of mud-flat annuals in 1995 and emergents in 1996 (Fig. 5), regardless of subplot elevation (i.e., zone). At Foster, only emergents subplots were present. While DCA (Table 6) indicated a strong year effect for vegetation at Foster, the changes in vegetation that were observed appear to be the result of the development of the emergent zone rather than due to annual hydrologic fluctuations. The majority of subplots for 1994, this site's first growing season, were clearly separated from those for 1995 and 1996 in the DCA ordination plot (Fig. 6). Early successional species such as *Echinochloa crusgalli*, *Rumex crispus*, *Lindernia anagallidea* and *Alisma plantago-aquatica*, that are frequently abundant in recently restored and created wetlands (A. Pepin, personal observation), dominated the subplots during 1994 and were much less abundant in 1995 and 1996. During 1995 and 1996, there was an increased abundance of emergent species, including *Ludwigia palustris*, *Leersia oryzoides*, *Polygonum hydropiperoides* and *Typha latifolia*, indicating the development of the emergent zone at Foster.

Site and Age Effects-- Two subgroups of data were analyzed to investigate the overall effects of zonation and variations in annual hydrologic pattern. Data were combined by vegetation zone and by year for each site to see whether these factors affected the vegetation dynamics of all CWH sites in a similar manner.

The effect of zonation was examined by combining data into vegetation zone subgroups for each site, while combining three years of data for each site's zones. It was expected that the TWINSpan analysis and DCA would separate species and subplots based on vegetation zones. In the TWINSpan output (Table 7) species groups are based on vegetation zone and life history. Review of the order of samples indicated that subplots were divided by age of the sites (or time since restoration) rather than by vegetation zone. Older sites (i.e., those that were 4-8 years old at the outset of this study) were separated

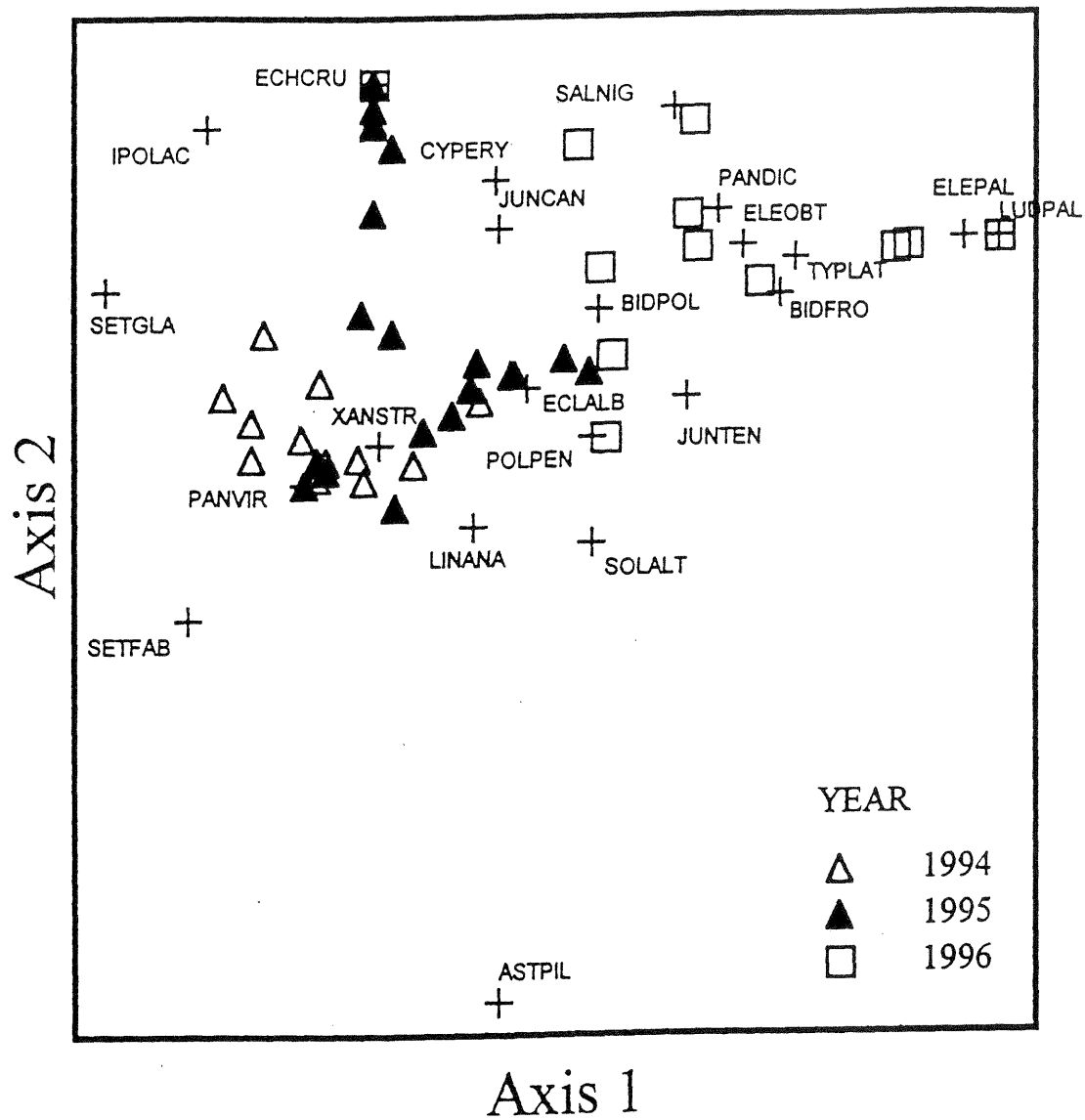


Figure 4. Ordination plot from DCA of vegetation data for Braun.

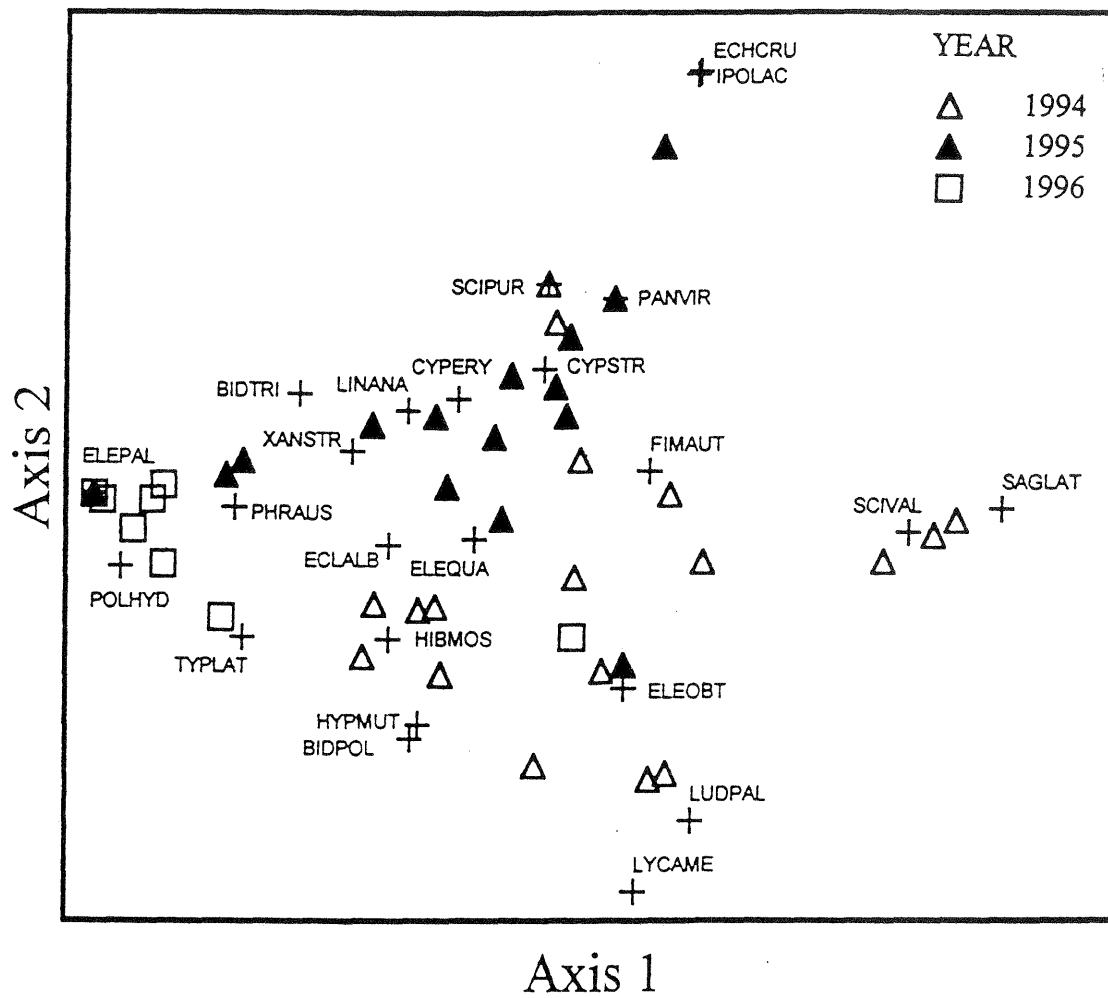


Figure 5. Ordination plot from DCA of vegetation data for Barnstable 1.

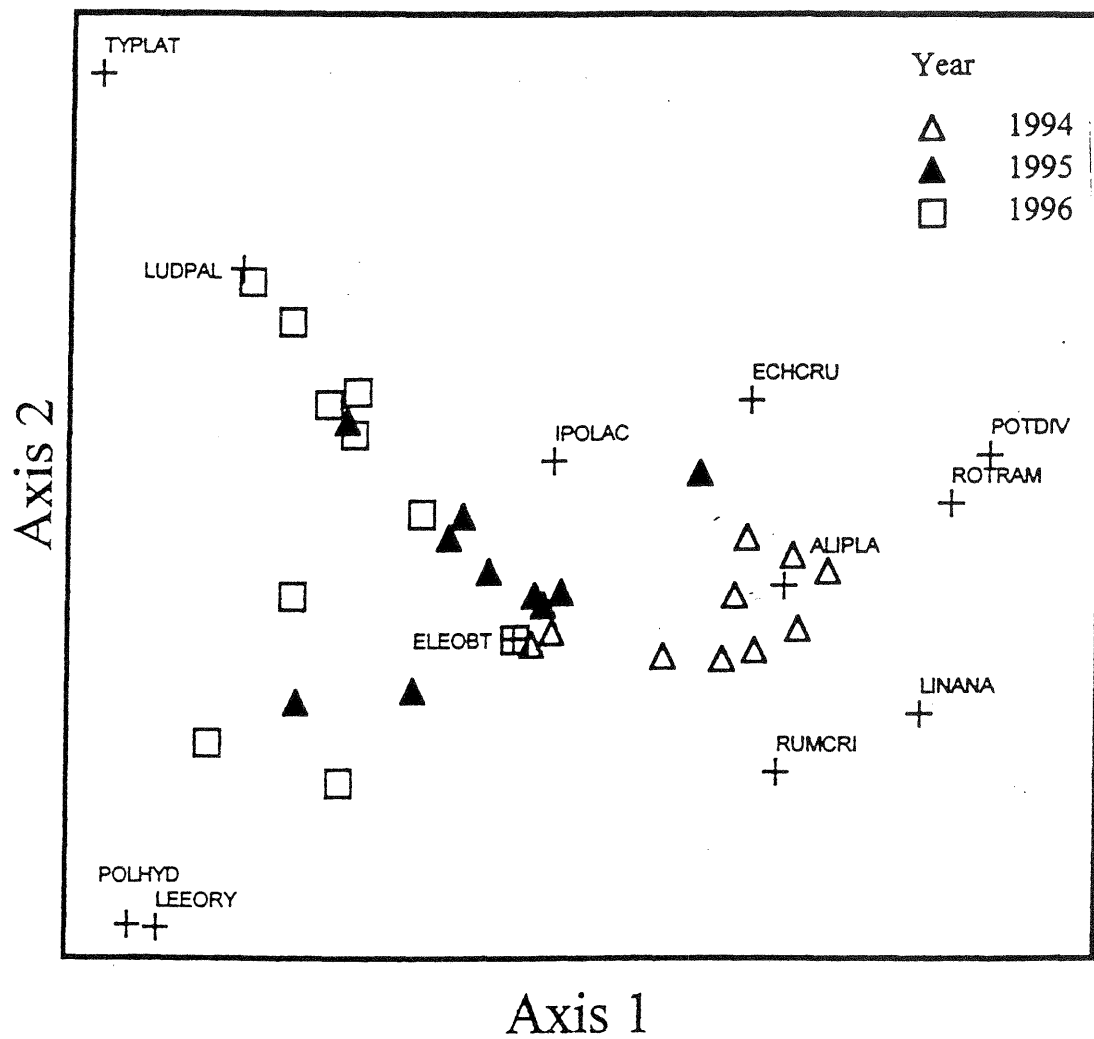


Figure 6. Ordination plot from DCA of vegetation data for Foster.

Table 7. TWINSpan output for vegetation data from 9 CWH sites divided by vegetation zone (temporary, emergent and submersed), while combining 3 years of data for each site's zones. Site group codes refer to number of years elapsed since restoration at the outset of this study: 1) 4-8; and 2) 1-3. Species group codes are based on vegetation zone and life history and are the same as those used in Table 5. Species codes used in this table can be found in Table 2. Numbers within the table correspond to the following percent cover values: - = species absent; 1 = less than 2%; 2 = 2-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-50%; and, 6 = 51-100%.

SPECIES CODE	SITE GROUP CODE		SPECIES GROUP CODE
	1	2	
GALOB	- - - - - 1 2	- - - - - 1 -	III
SCIMUC	- - 5 3 5 2 3 2	- - - - - 1 2	
SCIPUN	- - - - - 2 -	- - - - - 1 -	
BIDTRI	1 2 - - - - -	- - - - - 1 -	
LYCAME	1 1 - - - 1 1	- - - - - 1 -	
AMMCOC	- - 2 1 - - -	- - - - - - -	
PHRAUS	- 1 - - - 4 4	- - - - - - -	
CYPSTR	1 1 - 1 1 1 - 1	- - - - - - -	
ELEQUA	2 2 - - 1 1 - 1	- - - - - - -	
FIMAUT	1 3 2 1 1 - -	- - - - - - -	
HIBMOS	1 1 - - - - 1	- - - - - - -	
SAGLAT	3 1 - - - - -	- - - - - - -	
SCIPUR	4 2 1 - 3 1 3 1	- - - - - - -	
SCVAL	4 1 - - - - -	- - - - - - -	
CYPERY	1 1 - - 1 - 1 -	- - - - - 1 - -	
ELEPAL	3 5 2 4 - - - 4	- 2 1 1 2 - 1 -	
LINANA	1 2 1 1 1 2 1 -	1 - 1 - - 1 - -	
ROTRAM	- - 2 2 1 2 - -	2 - - - - - -	
XANSTR	4 3 - 1 1 2 3 3	- - 3 - 2 3 - -	
BIDFRO	- - - - - 1 1	- - 1 - - - -	I
DIGISC	- - - 1 2 4 2 1	- - - - - 5 - -	
BIDPOL	- 2 - - 1 2 1 2	- 1 1 - 1 4 4 -	
ECLALB	1 1 - - 1 1 1 1	- 3 2 2 2 1 -	
HYPMUT	- 1 - 1 1 - - -	- - - 1 - 1 -	
IPOAC	- 1 - - - - -	1 - 1 - - - -	
JUNCAN	- - - - - 1 2	- 2 - - - 1 1 -	
POLPEN	- - - 1 - 1 - 1	- 1 - 1 1 1 -	
SETGLA	- - - 1 1 1 1 -	- 1 1 1 1 2 -	
ASTPIL	- - - - - - -	- - - - 1 1 -	
ASTVIM	- - - - - - -	- - - - 1 - -	
FESPRA	- - - - - - -	- - - - 2 - -	
JUNTEN	- - - - - - -	- - - 2 1 2 -	
RUMCRI	- - - - - - -	1 1 - - - 1 -	
SETFAB	- - - 1 1 - - -	- - - 1 1 2 -	
SOLALT	- - - - - - -	- - - - 2 - -	
TRIHYP	- - - - - - -	- - - - 1 - -	
PANVR	4 2 2 5 4 1 1 -	- 4 5 4 5 5 5 - 1	
ALIPLA	- - - - - 1 - -	3 2 - 1 2 - - - 1	II
ELEOBT	4 4 5 4 5 5 4 4	5 4 2 4 5 3 2 1 3	
PANDIC	- - 1 4 - - 1 1	- 1 1 - - 1 3 - 1	
TYPLAT	1 3 - - 3 2 1 4	1 5 1 1 1 1 2 1 2	
ECHCRU	1 1 1 3 2 2 5 2	2 3 3 5 3 4 1 1 4	
LEEORY	- - - 3 3 1 1	3 3 - - 1 - 1 5	
LUDPAL	3 2 - 2 4 4 4 4	5 3 4 3 4 1 1 1 5	
SALNIG	- - - - - 1 1 1	- - - - - 3 - 1 -	
JUNEFF	- - - - - - -	- - - - - 1 4 2	
POLHYD	- 1 - - - - -	1 1 - 1 - 1 - 2	
POLPUN	- - - - - - -	- - - - - 1 2	IV
POTDIV	- - - - 1 - - 1	1 2 - 5 - - 5 2	

from younger sites (i. e. those that were 1-3 years old when the study began). When DCA was performed on these data, Axis 1 (Fig. 7) was most strongly correlated with age of site ($r = -0.68$) and site ($r = 0.67$) and weakly correlated with vegetation zone ($r = 0.13$). The vectors in Figure 7 indicate that the degree of separation between zones varied with site. While the emergent and temporary zones (labeled as B and C, respectively) for the older sites (Barnstable 1, Nesbit and Gerber) resembled each other (as indicated by the short vectors between zones), the emergent and temporary zones for the younger sites (Barnstable 10, Hope and Sultenfuss) tended to be more dissimilar (as indicated by the longer vectors between zones).

The effect of variations in annual hydrologic pattern was investigated by combining the data into subgroups for each of the three years, while combining data for each site's vegetation zones. If there had been a consistent overall effect across sites in response to hydrologic variations, the primary axis was expected to be strongly correlated with year and the vectors in Figure 8 should all have followed a similar pattern. Instead, Axis 1 was most strongly correlated with age of site ($r = -0.66$) and site ($r = .62$) and only weakly correlated with year ($r = 0.04$). The vectors in Figure 8 varied in direction of change and length from site to site, indicating that each site responded in a unique manner to annual changes in hydrology.

The effect of age of site on vegetation was clearest when the data were analyzed in subgroups for each wetland. In the TWINSpan output (Table 8), Barnstable 1, Barnstable 3, Gerber and Nesbit formed a group of sites that ranged in age between 4 and 8 years at the beginning of the study. Braun, Barnstable 10 and Hope formed a group of sites that were between 2 and 3 years old. Foster and Sultenfuss represented the youngest sites (1-2 years). When DCA was applied to these data, a well-defined gradient ($r = 0.87$) from younger to older sites was found on Axis 1. Clusters of species were based primarily on the age of the site rather than to tolerance to inundation. Certain species were most characteristic of older sites. For example, emergents including *Eleocharis palustris*, *E. quadrangulata*, *Sagittaria latifolia*, *Scirpus mucronatus* and *S. purshianus* and mud-flat annuals such as *Cyperus erythrorhizos*, *C. strigosus*, *Fimbristylis autumnalis* and *Xanthium strumarium* were most strongly associated with Barnstable 1 and 3, Nesbit and Gerber, sites ranging in age from 4-8 years at the beginning of this study (Fig. 9). Different species were most strongly associated with younger sites. Mud-flat annuals including *Bidens polylepis*, *Polygonum pennsylvanicum*, *P. hydropiperoides*, *Digitaria ischaemum* and *Eclipta alba* were characteristic of Braun, Sultenfuss, Hope and Barnstable 10, sites aged 2-4 years at the study's outset (Fig. 9). Fewer emergent species, primarily *Juncus effusus* and *Leersia oryzoides*, were associated with young sites, indicating a less, well-developed emergent zone at younger sites (Fig. 9).

Soil Effects-- When DCA was applied to subgroups of data for the 9 CWH sites (Fig. 9), a relatively strong correlation with soil type ($r = 0.41$) was noted for the first axis. Similarly, when data were divided into vegetation zone subgroups for each site, the second axis (Fig. 7) was most strongly correlated ($r = -0.39$) with soil.

To further investigate the relative importance of soil type on the vegetation dynamics of these restored wetlands, data were analyzed for four sites (Foster, Hope, Braun and Sultenfuss) of similar age (1-2 years) that were restored on 3 different soil types. Foster and Hope were restored on a silt loam hydric soil, Braun was restored on a silt loam upland soil and Sultenfuss on a sandy loam hydric soil. When DCA was performed on these data, Axis 1 (Fig. 10) was most strongly correlated with site and soil type ($r = 0.66$ and 0.46 , respectively), while Axis 2 was most strongly correlated with soil ($r = 0.57$). Soil type explains 21% ($r^2 = 0.212$) and 33% ($r^2 = 0.325$) of the variation in the primary and secondary axes, indicating that soil type plays a role in the establishment of different plant communities on sites of similar ages with similar hydrology.

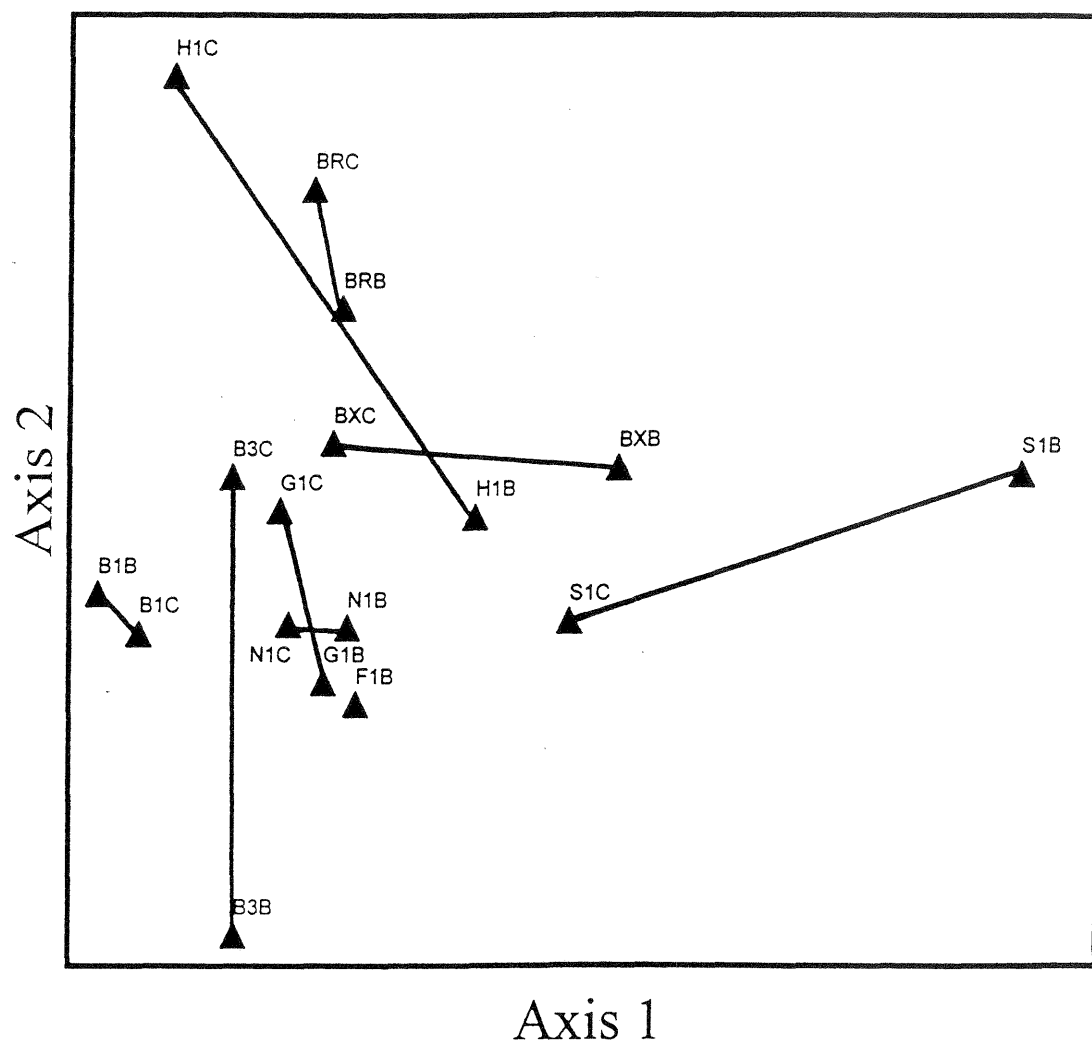


Figure 7. Ordination plot from DCA of CWH vegetation data combined into vegetation subgroups for each site. B refers to the emergent zone while C refers to the temporary zone. Relative length of vectors indicates the degree of difference between vegetation present in the emergent and temporary zones for a particular site.

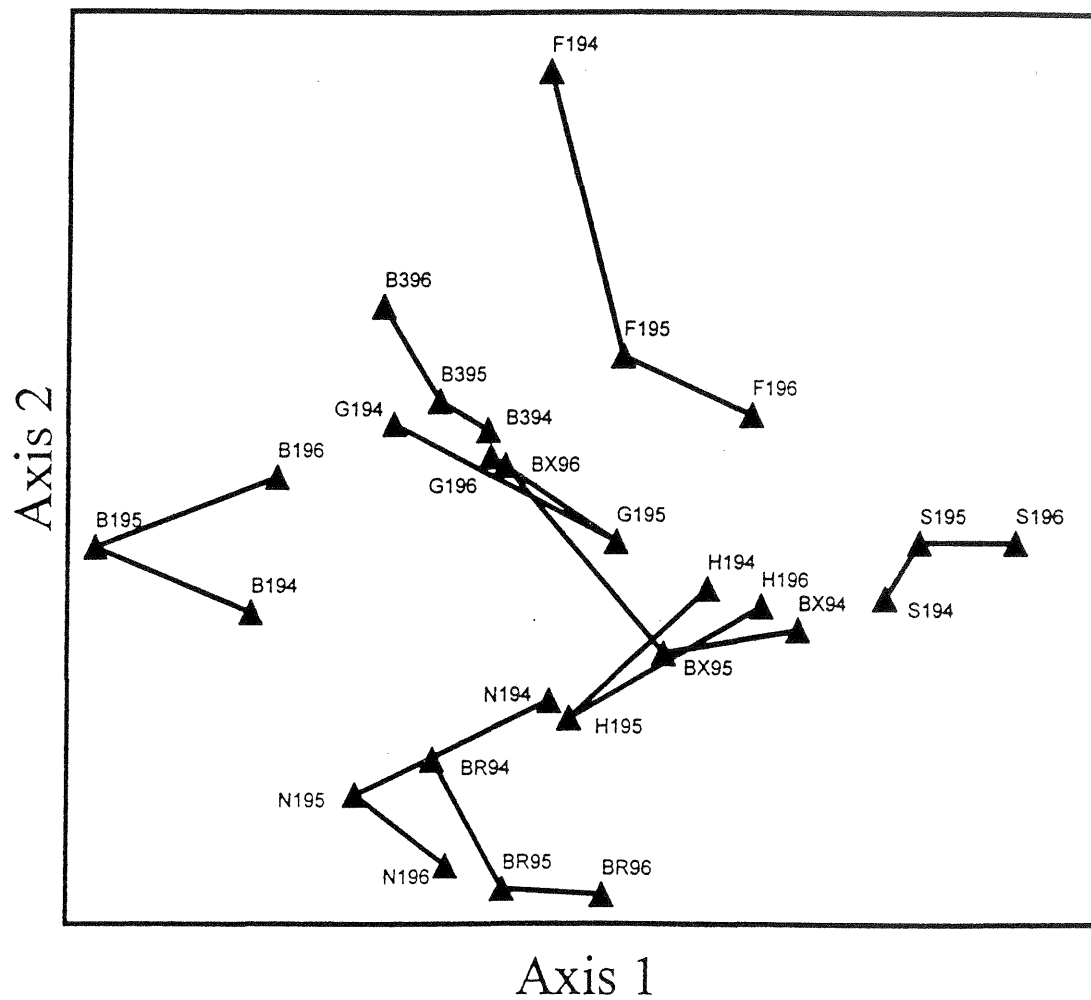


Figure 8. Time series ordination plot from DCA of CWH vegetation data, showing trajectories representing change in communities for each site from 1994 to 1995 and 1996. Note the strong site effect and the lack of one consistent pattern of change between years.

Table 8. TWINSpan output for vegetation data from 9 CWH sites combined into subgroups for each wetland. Site group codes refer to number of years elapsed since restoration at the outset of this study: 1) 4-8; 2) 2-3; and 3) 1-2. Species codes used in this table can be found in Table 2. Numbers within the table correspond to the following percent cover values: - = species absent, 1 = less than 2%; 2 = 2-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-50%; and, 6 = 51-100%.

SPECIES CODE	SITE GROUP CODE		
	1	2	3
SCIVAL	5 - - -	- - - -	- -
SCIPUR	5 1 5 5	- - - -	- -
SAGLAT	5 - - -	- - - -	- -
PHRAUS	1 - - 5	- - - -	- -
HIBMOS	5 - - 4	- - - -	- -
FIMAUT	5 4 1 1	- - - -	- -
ELEQUA	5 - 5 3	- - - -	- -
CYPSTR	5 4 5 5	- - - -	- -
SCIMUC	- 5 5 4	- - - -	3
ROTRAM	- 5 5 1	- - - -	5 -
LYCAME	4 - 4 5	- - - -	5
LINANA	5 5 5 5	3 - - -	5 -
XANSTR	5 3 5 5	5 3 - -	- -
ELEPAL	5 5 - 5	1 3 3 -	- -
CYPERY	5 - 4 5	5 - - -	- -
HYPMUT	3 4 3 -	- 5 2 -	- -
GALOBT	- - - 5	- - - -	3
ELEOBT	5 5 5 5	3 5 4 5	4
DIGISC	- 1 5 3	- - 5 -	- -
SCIPUN	- - 5 -	- - - -	4
BIDTRI	5 - - -	- - - -	5
POLPEN	- 4 4 5	5 5 3 -	- -
PANVIR	4 5 4 1	5 5 5 -	1
BIDPOL	4 - 4 4	5 2 5 -	- -
BIDFRO	- - - 5	5 - - -	- -
TYPLAT	5 - 5 5	2 3 5 3	4
PANDIC	- 5 - 2	4 - 5 -	2
LUDPAL	5 3 5 5	5 5 3 5	5
ECHCRU	3 5 5 5	5 5 5 4	5
SALNIG	- - 3 2	5 - - -	4
IPOLAC	5 - - -	5 - - -	4 -
SETFAB	- 2 4 -	3 2 5 -	- -
JUNCAN	- - - 5	2 - 5 -	- -
ECLALB	3 - 4 4	5 5 2 -	- -
POTDIV	- - 4 3	- 5 3 1	5
LEEORY	- - 5 3	- 1 5 5	5
RUMCRI	- - - -	- - 5 5	-
POLHYD	1 - - -	- 5 4 4	5
POLPUN	- - - -	- - - -	5
JUNEFF	- - - -	- - 4 -	5
ALIPLA	- - 1 -	- 3 3 5	3
SETGLA	- 1 4 2	5 4 5 -	- -
TRIHYP	- - - -	- - 5 -	- -
SOLALT	- - - -	5 - - -	- -
JUNTEN	- - - -	4 5 5 -	- -
FESPRA	- - - -	- - 5 -	- -
ASTVIM	- - - -	- - 5 -	- -
STPIL	- - - -	5 - 5 -	- -

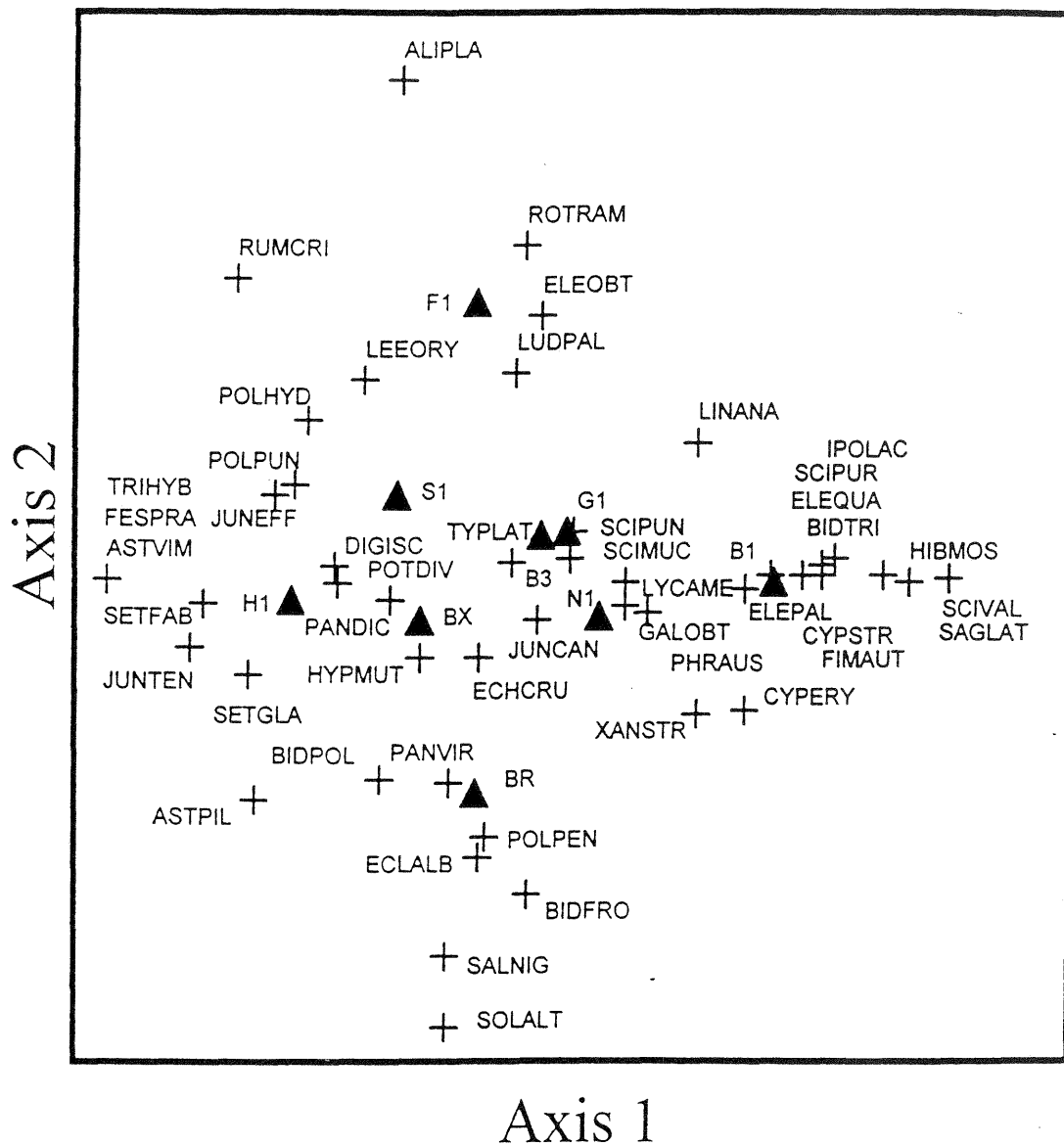


Figure 9. Ordination plot from DCA of CWH vegetation data combined into subgroups by site.

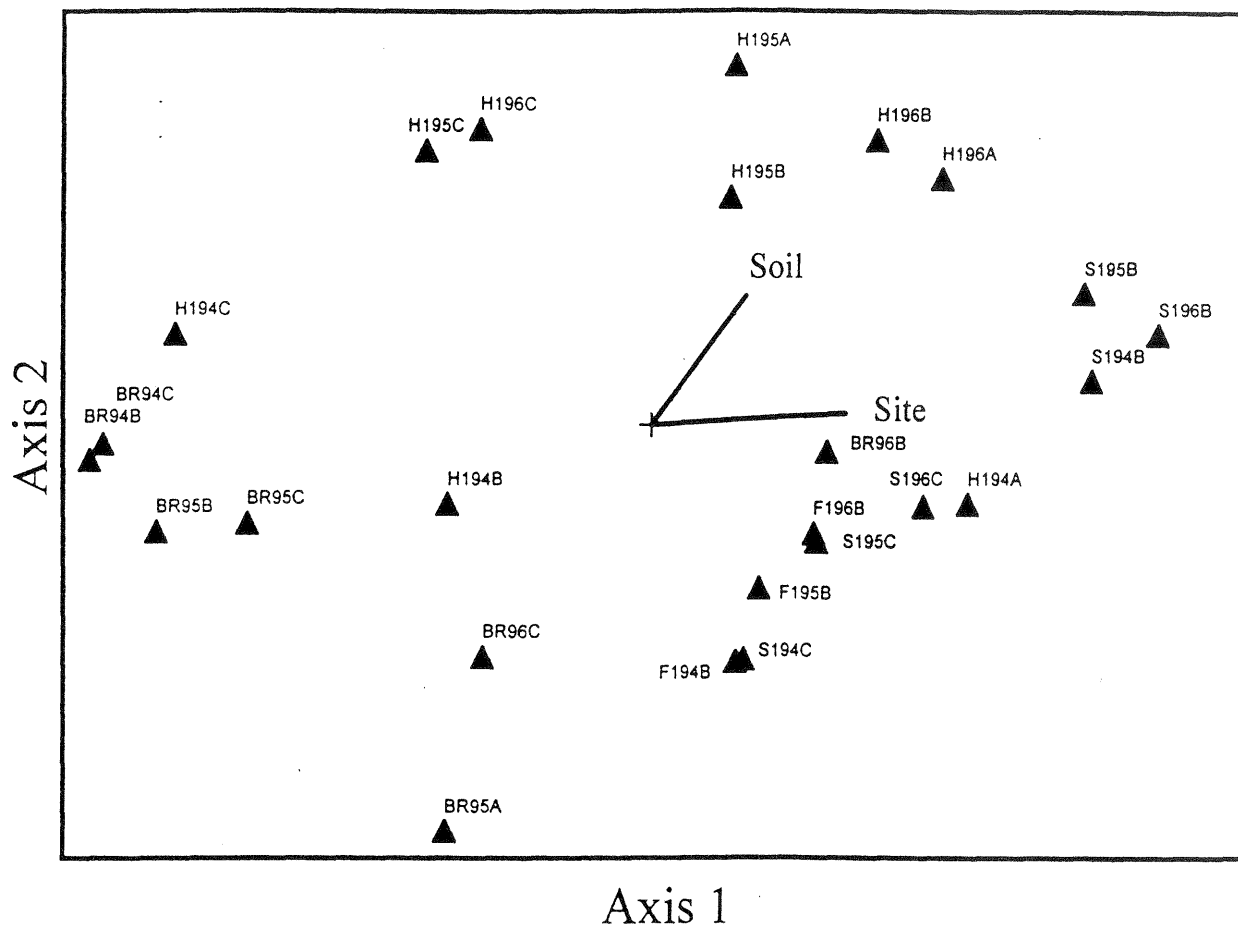


Figure 10. Ordination plot from DCA of vegetation data for 4 sites (Foster, Hope, Braun and Sultenfuss) of similar age (1-2 years at the outset of this study). A refers to the submersed zone, B refers to the emergent zone and C refers to the temporary zone. Axis 1 is most strongly correlated with site ($r = 0.659$) and soil ($r = 0.460$), while Axis 2 is most strongly correlated with soil ($r = 0.601$).

Classification and Ordination of ENWR Wetlands

Given the significant effect of age of site (or time elapsed since restoration) on the vegetation dynamics of the 9 CWH sites, it was expected that the two older ENWR sites would possess vegetation communities that were quite different from the relatively younger CWH sites. When DCA was applied to data for the 9 CWH and the 3 ENWR sites, subdivided by site, the primary axis (Fig. 11) was most strongly correlated with site and age of site ($r = 0.79$ and 0.72 , respectively). The secondary axis of the DCA (Fig. 11) was most strongly correlated with soil type ($r = -0.52$), providing additional evidence that soil type affects the vegetation dynamics of these restored sites. In reviewing the ordination plot (Fig. 11), four distinct age groups are present. Two ENWR sites (E1 and E3) are more than 30 years old and were located on the far right of the ordination plot and were clearly separated from the younger sites. The other ENWR site (E2) was 4 years old at the time the study began. It was located closer to the CWH sites and is part of a group of sites ranging in age from 2-4 years (including also Sultenfuss, Braun, Barnstable 10 and Hope). The oldest CWH sites (4-8 years) form a separate group to the upper left (including Nesbit, Barnstable 1, Gerber and Barnstable 3) while the youngest CWH site, Foster (F1) is found in the lower left of Figure 11.

Conclusions

The Effect of Hydrology

The results of this study indicate that hydrology, as expressed by vegetation zone (i.e., the relative elevation of subplots) is the primary controlling factor in the vegetation dynamics of these restored wetlands, across sites and within sites. The submersed zone, the deepest zone that was permanently flooded during most growing seasons, was characterized by open water or submersed vegetation (*Potamogeton diversifolius*) in years with normal or above normal rainfall during the growing season. The emergent zone, which lies between the submersed zone and the temporary zone, experienced drawdown early in the summer and remained shallowly inundated (< 0.15 m) during the growing season in years of normal or greater precipitation. Perennials such as *Scirpus mucronatus*, *Typha latifolia* and *Eleocharis palustris* were most abundant in the emergent zone. The temporary zone, located at the highest elevations closest to the adjacent uplands, experienced a more pronounced drawdown, usually by the onset of the growing season or shortly thereafter. Mud-flat annuals including *Cyperus erythrorhizos*, *C. strigosus*, *Bidens polylepis*, *Eclipta alba*, *Panicum virgatum* and *Xanthium strumarium* were found primarily in the temporary zone.

These findings are consistent with other studies that support the importance of hydrologic regime (i.e., timing of drawdown) in the vegetation dynamics of freshwater wetlands (Naim 1987, van der Valk and Pederson 1989, van der Valk et al. 1992), including field studies at the Delta Marsh (Welling et al. 1988a, b, Merendino et al. 1990). Seedling and shoot density of emergents was greatest where soil moisture was highest and drawdown was later or where plots remained shallowly flooded, while annuals were favored where soil moisture was lower and drawdown occurred earlier (Welling et al. 1988a, b, van der Valk and Pederson 1989, Merendino et al. 1990, van der Valk et al. 1992).

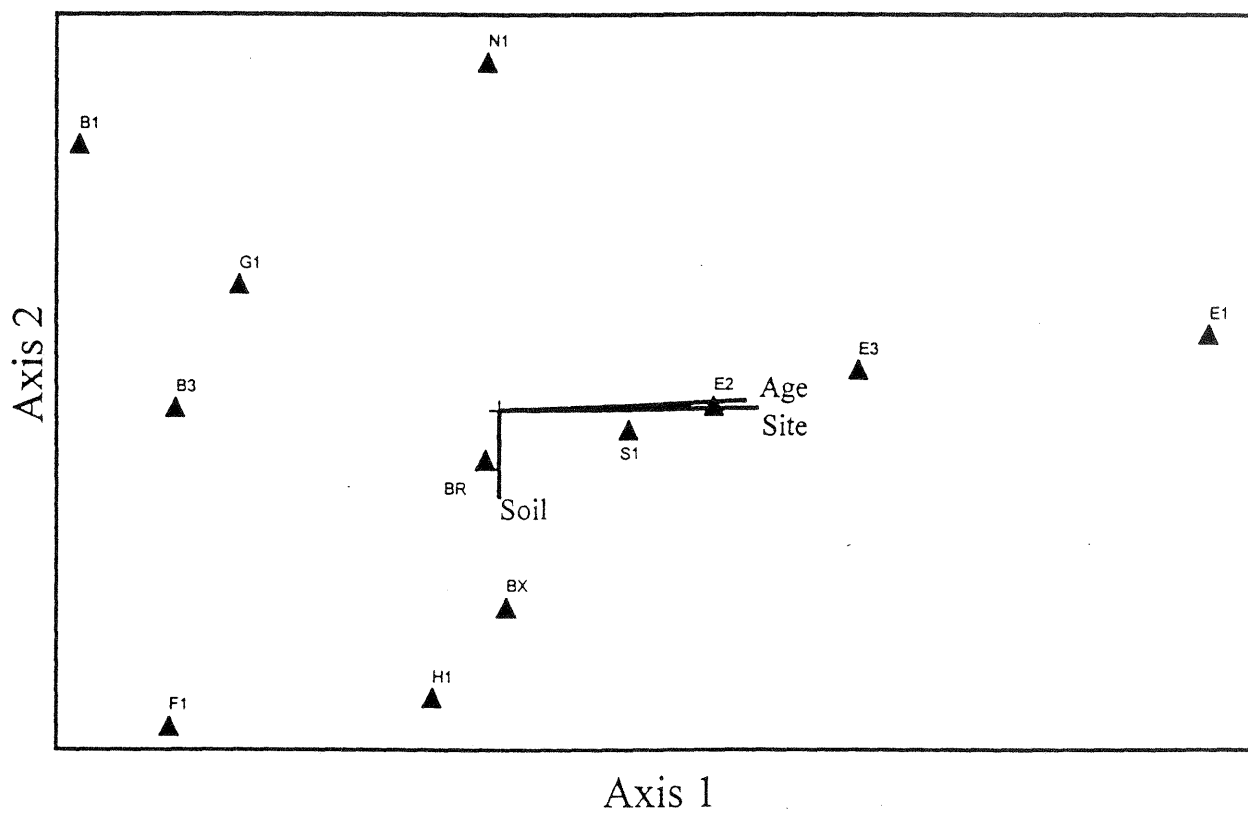


Figure 11. Ordination plot from DCA of vegetation data for 9 CWH and 3 ENWR sites combined into subgroups by site. Axis 1 is most strongly correlated with site ($r = 0.786$) and age of site ($r = 0.718$), while Axis 2 is most strongly correlated with soil type ($r = -0.519$).

Seasonal Variation

The stability of vegetation within the wetlands was strongly influenced by seasonal variations in water level. Annual hydrologic changes affected the overall character of vegetation across sites and of vegetation zones within sites by determining individual species distributions. The abundance of mud-flat annuals at all sites and in all vegetation zones was greatest in the dry year (with an earlier drawdown), while significantly less in the wet year (with a latter, less pronounced drawdown). The majority of emergents displayed the opposite pattern - they were most abundant in the wet year and relatively less abundant in the dry year. This fluctuating abundance of mud-flat annuals and emergent perennials in response to changes in hydrology resembles the pattern of prairie marshes (Kadlec 1962, Harris and Marshall 1963, Meeks 1969, Merendino et al. 1990) where the timing and extent of drawdown determine which plant species become established and survive.

Site Age

The amount of time elapsed since restoration was also shown to affect the vegetation. It was assumed that the vegetation would be more dynamic in young wetlands (i.e., 1-3 years following restoration). The vegetation of the emergent and temporary zones (Fig. 7) indicates that the younger sites (Barnstable 10, Braun, Hope, Foster and Sultenfuss) were more dissimilar from each while the older sites (Barnstable 1 and 3, Nesbit and Gerber) resembled each other. While younger sites were more different from each other than were older sites, vegetation was quite dynamic, regardless of age. The relative degree of change in vegetation between years (as indicated by relative length of vectors in Figure 8) exhibited no consistent age-related pattern. Older sites such as Barnstable 1 and Nesbit (6 and 8 years) possessed vectors as long or longer than younger sites such as Foster and Hope (1 and 2 years). Sultenfuss and Barnstable 3 (2 and 4 years) showed the least change (i.e., shortest vectors) between years (Fig. 8).

There did appear to be a pattern of species distribution related to age. Certain species were most strongly correlated with older sites, while other species were most abundant at younger sites. Mud-flat annuals including *Cyperus erythrorhizos*, *C. strigosus*, *Fimbristylis autumnalis*, *Xanthium strumarium* and emergent perennials such as *Eleocharis palustris*, *E. quadrangulata*, *Scirpus mucronatus* and *S. purshianus* were most abundant at sites ranging in age from 4-8 years at the outset of this study (Table 7, Fig. 9). Other mud-flat annual species such as *Bidens polylepis*, *Panicum virgatum*, *Eclipta alba*, *Rumex crispus* and *Digitaria ischaemum* and emergent perennials including *Juncus effusus*, *Polygonum pensylvanicum*, *P. hydropiperoides* and *Leersia oryzoides* were associated with younger sites (1-2 years) (Table 7, Fig. 9). While Reinartz and Warne (1993) reported a higher species richness and diversity of native wetland species at older created sites, they did not note any particular age-related patterns of species occurrence. One possibility, suggested by Galatowitsch and van der Valk (1995), is that species present at young sites (i.e., the "initial invaders") are environmental generalists, while those present on older sites, and not colonizing recently flooded basins, are specialists with specific environmental requirements. Patterns of recolonization by species in prairie marshes have also been found to be related to dispersal ability and method (Galatowitsch and van der Valk 1996b, c). Future studies will determine whether the abundance of species at CWH sites changes over time, with the vegetation at younger sites coming to resemble that found during this study at older sites, or if particular species will remain characteristic of certain sites regardless of age.

Effect of Soil Type

Vegetation patterns were found to be correlated with soil type, with different vegetation present on sites of similar age but different soil type (Fig. 10). Other investigators (e.g., Harris and Marshall 1963, Galatowitsch and van der Valk 1996a) observed that the nature of the substrate (i.e., soil type) affected the character of prairie marsh vegetation. Organic matter amendments, that helped to retain soil moisture and provided nutrients, enhanced the survivorship of hand-planted *Carex* in created wetlands in Pennsylvania (Stauffer and Brooks 1997). How soil type affects the vegetation dynamics of restored and created wetlands needs to be studied directly.

Differences Among Sites

While there were overall effects on vegetation of these restored sites due to vegetation zone (i.e., relative elevation of subplots), time elapsed since restoration and soil type, the vegetation dynamics of individual restored sites varied significantly. For example, seasonal changes did not affect all sites in a similar manner (Fig. 8) and the character of the emergent and temporary zones varied from site to site (Fig. 7).

Individual sites, seemed to be to a large extent, unique in how they responded to environmental factors. These findings support Niering (1990) who suggested that "No two sites, even though similar, will support exactly the same plant association." Differences in seed bank could in part explain the strong site effect observed in this study. Galatowitsch and van der Valk (1996b) found the seed banks of restored prairie wetlands were highly variable and that there was no certainty that species capable of becoming established in a particular wetland will ever do so given the random nature of dispersal. Differences between site based on size of watershed, size of wetland, basin morphology, soil type and other environmental variables that were not measured, in all likelihood, also affected the make-up of the vegetation of these restored wetlands. Recent experimental work on constructed wetlands in New Jersey (Vivian-Smith and Handel 1996) and previous work on freshwater wetlands (Galinato and van der Valk 1986, van der Valk and Pederson 1989, van der Valk et al. 1992) found that recruitment from the soil seed bank in developing wetlands was strongly affected by small environmental changes (including soil moisture, temperature, salinity and pH). The between site differences in vegetation observed in this study generally corroborate Niering's (1990) suggestion that vegetation "change in wetlands is usually not directional and generally not predictable since fluctuating water levels, chance, and catastrophe are constantly interacting."

Overview of Factors Affecting Vegetation Development

The vegetation development of these restored sites appears to be the result of a combination of many factors. Comparison of vegetation patterns across sites, both within and between hydrologic zones, indicated that hydrologic regime, as expressed by relative plot elevation, was the most important factor controlling the vegetation dynamics of these restored sites. At the landscape level, the relative elevation of plots results in three distinct vegetation zones: submersed, emergent and temporary. Within sites, variations in the extent and composition of these vegetation zones were modulated by annual changes in the hydrologic regime.

The differences in vegetation community observed at the landscape level and within sites (for different years) were the result of hydrology operating on the soil seed bank of the restored wetlands. While not assessed as part of this study, the soil seed bank undoubtedly varied between sites, since differences in agricultural history and the nature of drainage prior to restoration have been found to significantly affect soil seed banks (Galatowitsch and van der Valk 1994). Even with identical seed banks, small changes in

environmental conditions present during the colonization phase significantly affect the community composition of developing wetlands (Vivian-Smith and Handel 1996).

While no significant effects due to size of wetland or watershed were detected, the age of site and soil type significantly affected the vegetation composition of these restored wetlands. These factors acted as modifiers to the overall effects of hydrology. As sites aged, their vegetation tended to become more similar, while vegetation at younger sites was more dynamic and dissimilar. Younger sites were found to have less well-developed emergent zones. As young sites aged, emergent species became more diverse and numerous, particularly at Foster and Braun. Soil type also affected community composition, with significant differences between sites of the same age that were restored on different soils. While previous investigators suggested that soil texture and organic matter content affected the soil moisture regime (Bartoldus and Heliotis 1989) and nutrient availability (Allen et al. 1989, Stauffer and Brooks 1997), the manner in which soil type affects the vegetation dynamics of developing wetlands needs further study.

While not one of this study's objectives, observations indicate that wildlife, in all likelihood, have contributed to the plant species diversity of these restored wetlands. Numerous avian species, including various herons, egrets, shorebirds, raptors, waterfowl and passerines, were observed utilizing these restored wetlands, particularly during spring and fall migration (A. Pepin, personal observation). One plant species that was, in all likelihood, dispersed to these isolated restored sites by migrating waterfowl is a bulrush, *Scirpus mucronatus*. A native of Europe, this species has been collected as a waif on ballast at Camden, New Jersey, according to Gleason (1952). While not listed in Brown and Brown's (1984) "Herbaceous Plants of Maryland," *Scirpus mucronatus* grew on 4 of the 9 CWH sites and was the fifth most abundant species, present in nearly 21% of the total vegetated subplots (Table 3). With large bristled achenes ripening in the fall, the fruits of *Scirpus mucronatus* appear well-suited for long-distance dispersal that is characteristic of plants that occupy patchy environments (Barbour et al. 1987). These restored wetlands provide important habitat for both flora and fauna and significantly increase the biodiversity of this largely agricultural area.

Future Vegetation Development

What predictions can be made about the future vegetation dynamics of the 9 CWH restored wetlands based on this three-year study? Reinartz and Warne (1993) proposed two possible scenarios for the long-term development of similar isolated marshes supplied primarily by surface water and experiencing large fluctuations in water level both seasonally and long-term. One scenario, based on van der Valk and Davis (1978) and van der Valk (1981), suggested that a "resilience of vegetation will develop due to a dynamic balancing of species" as water levels fluctuate through wet and dry years. Plant species diversity will lead to stability and persistence of wetland communities over a wide range of hydrologic changes (Willard and Hiller 1990). In this first scenario (Reinartz and Warne 1993), there are "dynamic movements of vegetation driven by changing water levels." In the second scenario (Reinartz and Warne 1993), fluctuating water levels favor species that can tolerate a wide range of water levels (e.g., species of *Typha* and *Phragmites*) and eliminate those that cannot.

In the temporal scale of this study, observations indicate that the vegetation dynamics of the 9 CWH restored wetlands most closely resemble van der Valk's (1981) Gleasonian model of succession in freshwater wetlands. These sites were found to exhibit dynamic changes in vegetation due to fluctuating water levels (from drought or water level manipulations to maintain waterfowl habitat).

No evidence for succession to a forested wetland was observed during this study (except for *Salix nigra*, no tree species were present on these sites from 3-10 years after restoration). Kirkman et al. (1996) found that herb-dominated depression wetlands in South Carolina did not necessarily represent a step in a successional continuum towards an

eventual forested wetland. Many of the depression wetlands in their study remained herbaceous for over 40 years. The dominance of herbaceous vegetation was controlled primarily by hydrologic conditions (Kirkman et al. 1996). This would seem to be the case for the CWH restored wetlands. If hardwoods (such as *Acer rubrum* or *Liquidambar styraciflua*) commonly found in palustrine forested wetlands adjacent to the CWH sites do become established during drought periods, subsequent re-flooding each winter will likely result in their death, unless seedlings are old enough to survive seasonal inundation. Due to fluctuating water levels (from drought or water level manipulations to maintain waterfowl habitat), vegetation at the CWH sites, in all likelihood, will persist as herbaceous-dominated depression wetlands. Long-term studies will provide additional insights into the vegetation dynamics and path of succession for these restored wetlands.

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