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BIOMASS AND NUTRIENT DYNAMICS IN RESTORED WETLANDS ON THE OUTER COASTAL PLAIN OF MARYLAND, USA

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Abstract: A three-year study of aboveground biomass and nutrient dynamics in twelve restored depressional wetlands of different ages demonstrated significant annual variability among sites. Annual variations appeared to be 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 differences that are measured at individual wetland sites may be less important at the landscape level. Biomass decreased from the outer temporary to inner submersed zone, and there were few differences among wetlands when the temporary, seasonal, and submersed zones were compared. Nutrient concentrations in the plant biomass increased from the temporary zone to the submersed zone, resulting in few differences in nutrient standing crops across zones. Results from this study demonstrate that some measurements of restoration success (i.e., biomass production) should be used cautiously because they are likely to be highly variable among sites and across years and thus may be of limited use in post-restoration monitoring. Other ecosystem parameters (e.g., nutrient concentrations of biomass) are much more constant spatially and temporally, indicating that nutrient cycling processes in vegetation were established quickly following restoration. Nutrient characteristics of wetland vegetation thus may be a useful metric for evaluating restoration success or failure.

Key Words: restoration, Maryland, depressional wetlands, aboveground biomass, nutrient concentrations, nutrient standing stock, agricultural landscape

INTRODUCTION

Three general approaches are used in wetland restoration and creation projects (Mitsch and Wilson 1996, Stauffer and Brooks 1997, Middleton 1999). 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 (Middleton 1999, Zedler et al. 2001). 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 allowing vegetation development to occur naturally on the assumption that vegetation will rather quickly resemble the vegetation of natural wetlands (Mitsch et al. 1998). 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. Mitsch, however, did not indicate how many years it might take for convergence in structure and function to occur. In the scenario described by Mitsch, 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 (Mitsch and Gosselink 1993, Brown and Bedford 1997), but to date, there have been few multiple-year studies in which success of one method or the other has been thoroughly evaluated (e.g., Mitsch et al. 1998, Zedler et al. 2001).

Wetlands in Iowa, USA, for example, that had been restored using the self-design approach had vegetation that was only partially similar to vegetation in natural wetlands (Galatowitsch and van der Valk 1996a). Galatowitsch and van der Valk found that, after three years of self-design, 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. Galatowitsch and van der Valk suggested that the efficient community hypothesis (the self-design approach of Mitsch) needed to be modified so that seed/propagule dispersal 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) also noted the importance of seed dispersal in restoring vegetation in created wetlands. 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. Mitsch et al. (1998) found that many parameters (e.g., plant species diversity) were similar after three years in planted and unplanted constructed wetlands. Our objective in this paper is to report results of a three-year study of biomass and nutrient dynamics in twelve restored wetlands of different ages. We tested the assumption that biomass and nutrients standing crops would be greater in the oldest wetlands due to the replacement of annual and short-lived species with perennials that reproduce primarily by clonal propagation (e.g., *Typha* sp.).

STUDY SITES

The twelve restored wetlands are located on the Eastern Shore of Chesapeake Bay within the Inner Coastal Plain physiographic province (Figure 1). The approach used to restore the wetlands was similar to the self-design (Mitsch and Wilson 1996, Mitsch et al. 1998) and efficient community (Galatowitch and van der Valk 1996a) approaches. The study sites (Table 1) 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. With the exception of the three wetlands at the Eastern Neck Wildlife Refuge (Figure 1), the Chesapeake Wildlife Heritage (CWH) did restorations between 1986 and 1993 (Table 1). The basin topography at each site (Jordan et al. 1996) was similar to shallow, closed depressions typical of wetlands in the Prairie Pothole Region (Steward and Kantrud 1971, Galatowitsch and van der Valk 1996b) in the midwest and Carolina Bays along the Atlantic and Gulf Coastal Plains (Sharitz and Gibbons 1982, Lide et al. 1995, Kirkman et al. 2000).

PRECIPITATION AND HYDROLOGY

The long-term average precipitation at Chestertown, Maryland, USA, one of the nearest reporting weather stations, is 1112 mm. Precipitation was greater than the long-term average during the three years (1994–1996) of this study, 1138, 1175, and 1579 mm, respectively. Monthly patterns of precipitation were, however, different for the three years. Compared to 1994 and 1996, precipitation in 1995 was at or below normal for 7 of the first 9 months of the year, and the

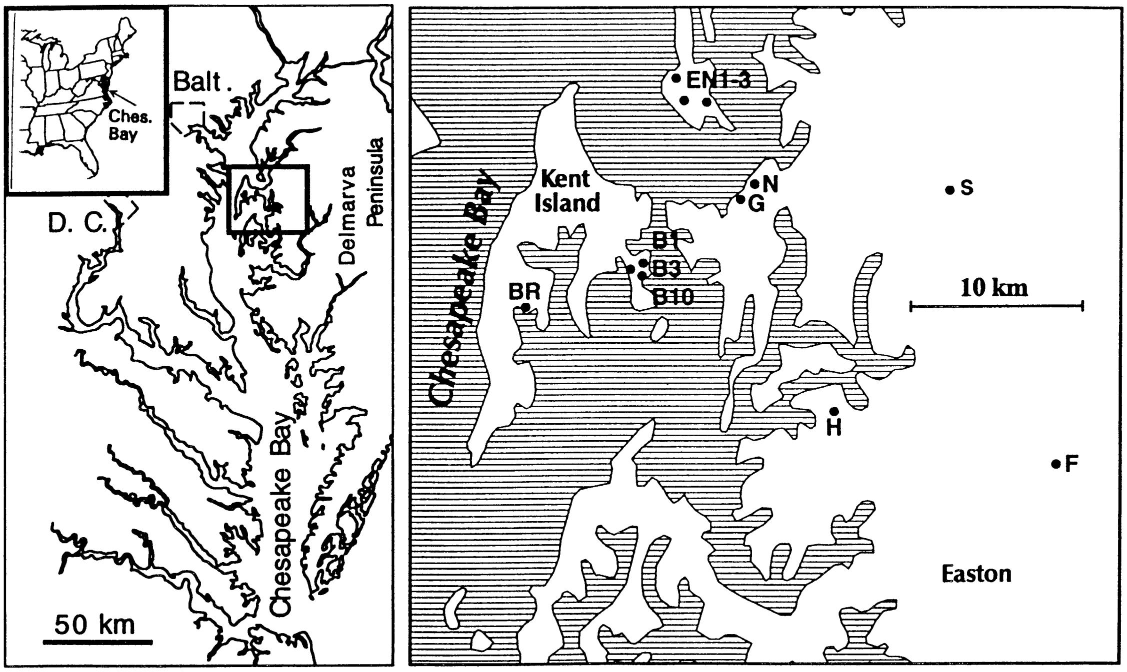

Figure 1. Map showing the location of the 12 study sites relative to the Chesapeake Bay. Abbreviations for the sites characterized in the text and in Table 1 are B1 = Barnstable 1; B3 = Barnstable 3; B10 = Barnstable 10; BR = Braun; EN 1–3 = Eastern Neck 1, 2, and 3; F = Foster; G = Gerber; H = Hope; N = Nesbit; S = Sultenfuss.

annual total was greater than the long-term average because of high rainfall in October (Figure 2). In contrast to 1995, 1994 and 1996 each had precipitation that was greater than the long-term average (Figure 2). Variations in precipitation during the summer months (Figure 2) had a large influence on water levels in the wetlands, as described in the next section.

Water levels were monitored weekly at all 12 sites from February 1994–November 1995. Measurements of water levels were made on staff gages that had been attached to the outlet structures at each wetland. Water levels varied seasonally in 1994, but the general patterns were similar at all sites, indicating that all of the study sites experienced similar hydrologic conditions (Figure 3). Continuous water-level-monitoring stations were installed at one site (Barnstable 1) in 1995 and at three other sites (Foster, Braun, Barnstable 10) in 1996 (Whigham et al. 1999). Data from the monitoring station at Barnstable 1 (Figure 4) demonstrate that water-level changes varied dramatically from year to year. Compared to 1994 (Figure 3), there was a decrease in water levels in 1995 that persisted for almost

Table 1. Characteristics of the 12 wetland study sites.

	Watershed			Wetland		Number of Plots		
Site	Hectares	Soils	% Crops	Hectares	Year Restored	Submersed	Emergent-Seasonal	Temporary
Barnstable 1	10.1	Mattapex/Elkton	85	0.4	1986	5	10	10
Barnstable 3	4.0	Elkton	55	1.2	1991	2	12	9
Barnstable 10	28.3	Mattapex/Elkton	70	4.0	1992	8	11	6
Braun	8.1	Mattapex	80	1.6	1992	8	7	7
Eastern Neck 1	~20	Mattapex/Othello	70	1.6	~1964	5	3	4
Eastern Neck 2	3.0	Mattapex/Othello	25	1.0	~1991	4	6	12
Eastern Neck 3	25.0	Mattapex/Othello	0	7.3	~1964	4	8	13
Foster	6.5	Falsington	60	0.4	1993	0	10	0
Gerber	4.0	Falsington	30	0.4	1990	6	9	9
Hope	8.0	Elkton	60	1.2	1993	5	10	10
Nesbit	10.1	Falsington/Sassafras	95	10.4	1989	4	12	7
Sultenfuss	20.2	Falsington	95	1.2	1992	0	10	10

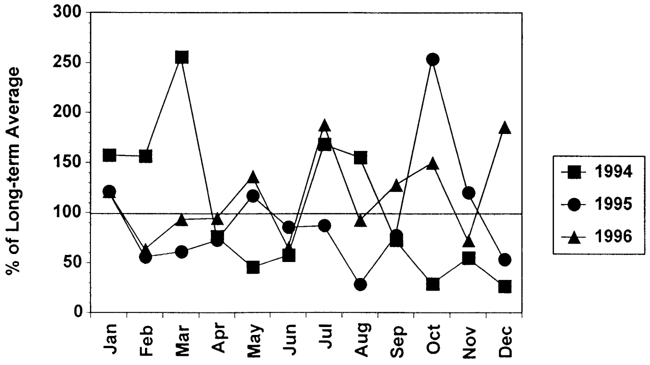

Figure 2. Precipitation data for Chestertown, MD, one of the closest weather stations to the study sites. Data are expressed as percent of the long-term monthly means (100%). Long-term annual average precipitation and yearly totals during the study are provided in the text.

all of the growing season (approximately from mid-May–late October). During 1996 and 1977, water levels were almost always above the weir V-notch at Barnstable 10 (Figure 4) and the other three sites with continuous monitoring stations (data for the latter not shown).

METHODS

In spring of 1994, 256 plots (each 2 X 2 m) were established in the 12 wetlands. Within each wetland, plots were distributed across three hydrologic zones, characterized as follows.

(1) The temporary zone was closest to adjacent uplands and was usually flooded only during the non-growing season months. Plant species in the temporary zone represented a range of wetland species from obligate upland to obligate wetland (Pepin and Whigham 1999).

(2) The emergent/seasonal zone was between the temporary zone and the portion of the wetland that was usually permanently flooded and dominated by submersed species. The amount of time that the emergent/seasonal zone was flooded or exposed depended on the annual rainfall pattern. In 1996, the year with the most precipitation (Figure 2), the emergent/seasonal zone in each wetland was flooded for the entire growing season. In 1995, the year with a summer drought (Figure 2), the emergent/seasonal zone in each wetland was exposed for almost all of the growing season. In 1994, the emergent/seasonal zones were flooded during the early part of the growing season and exposed during the summer. The emergent/seasonal zone supported mostly facultative and obligate emergent wetland species (Pepin and Whigham 1999).

(3) The submersed zone was flooded to the greatest depth and was dominated by submersed species, with few, if any, emergents (Pepin and Whigham 1999). Depth of flooding of the submersed zone varied within and between years. In 1994 and 1996, the zone was continuously inundated at all sites. In 1995, the submersed zone at several sites was exposed from mid-summer onward (Figure 4).

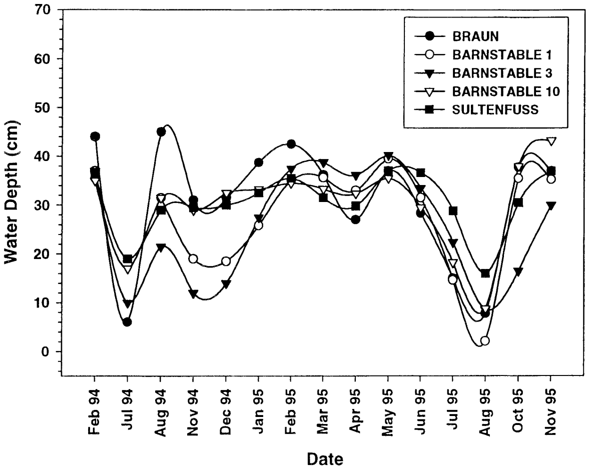

Figure 3. Depth of water in five representative wetlands between February 1994 and November 1995. Water levels in the other seven wetlands followed the same pattern but were not included in the figure for clarity of data presentation. Data were collected by making weekly observations on staff gauges (see Methods section for details).

Assignment of plots to zones within each wetland was based on relative water depth at the time they were established in 1994 and on a detailed elevation survey of each wetland that was conducted in 1995. In the 1995 survey, we used a Topcon CTS-2/2B total surveying station to determine the elevation of each plot relative to a fixed point established near the outlet of each wetland. The number of plots in each wetland and their distribution within zones are provided in Ta-

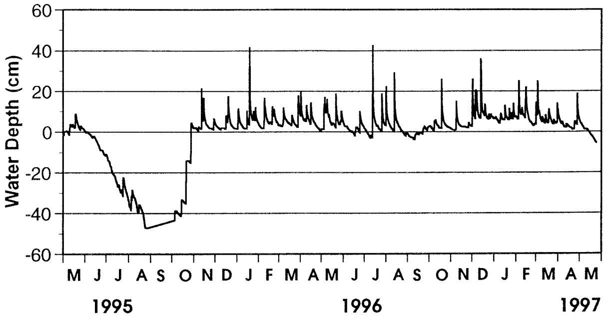

Figure 4. Water level at Barnstable 10 between April 1995 and May 1997. Data were collected at an automated station (see METHODS section for details). Positive and negative values represent water level above and below the bottom of the V-notch wier.

ble 1. In all but two wetlands (Foster and Sultenfuss), plots were established in each zone.

Each plot was divided into four 1 X 1 meter subplots. Three randomly chosen subplots were used to 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-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. The number of replicates per zone harvested each year for each wetland is shown in the three right-hand columns in Table 1. Harvested plant material was returned to the laboratory, gently washed to remove sediment, 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 Whigham et al. (1999).

The dried aboveground biomass samples from each year were analyzed for nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and sodium (Na) content. The carbon (C) content of biomass was only measured in 1995 and 1996. The biomass harvested from each plot was prepared for nutrient analyses by first grinding the dried material 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 concentrations. Nitrogen concentrations were determined by standard Kjeldahl procedures (Martin 1972). The other nutrients were analyzed on an individually coupled plasma emission (ICP) 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, while Ca, Mg, Na, and K were analyzed at Pennsylvania State University using ICP. Nutrient concentration and biomass data for each plot were combined to calculate nutrient standing stocks.

Biomass, nutrient concentration, and nutrient standing stock data were analyzed by analysis of variance (ANOVA) using SAS (SAS 1990) for main effects and interactions of year (1994, 1995, 1996), zone (submersed, emergent/seasonal, temporary), or wetland (12 wetland sites) differences. Multiple comparisons of the means were performed using the Tukey test. Percentage data for nutrients were arcsine-transformed before analysis with SAS. Statistical analyses of nutrient concentrations were performed only on data from plots that contained vascular plants. Statistical analyses of biomass and total nutrient standing stocks were performed on all plots, including those in which biomass and nutrient standing stocks were zero. Plant nomenclature follows Brown and Brown (1984).

RESULTS

There were highly significant differences between and within wetlands for almost all variables and significant differences between years for more than half (9 of 14) of the variables (Table 2). Overall, there were significant differences for 86.7% of the variables tested, demonstrating that biomass, nutrient concentrations, and nutrient standing stocks were highly variable within and between wetlands.

Aboveground biomass averaged 229.3 ± 9.1 g/m^2 for the three years, and there were no significant differences between years (Table 3). Biomass, however, varied widely among wetlands each year and, for almost all wetlands, biomass also varied from one year to another (Figure 5). The highest average biomass occurred at Braun (464.7 ± 93.2 g/m^2) in 1994, at Braun (285.3 ± 59.1 g/m^2), Eastern Neck 2 (330.7 ± 51.7 g/m^2), and Nesbit (328.1 ± 57.0 g/m^2) in 1995, and at Barnstable 3 (415.3 ± 50.8 g/m^2) in 1996. The greatest annual variation occurred at Barnstable 10, where average biomass was 244.7 ± 50.7 g/m^2 in 1994 and 9.4 ± 5.0 g/m^2 in 1996. In short, the biomass followed no consistent overall pattern among years or wetlands.

There was, however, a consistent pattern of biomass distribution across zones (Figure 6). Aboveground biomass was significantly lower in the submersed zone (range: 69.2 ± 13.4–137.8 ± 35.8 g/m^2), and within-zone biomass did not differ significantly among years. Average biomass in the seasonal/emergent zone was intermediate (range: 167.8 ± 23.6–232.3 ± 22.7 g/m^2), and biomass in 1996 was significantly less than in 1995 and 1994 (Figure 6). The temporary zone had significantly more biomass in each of the three years (range: 297.6 ± 23.5–358.6 ± 26.3 g/m^2), and there were no significant differences among years (Figure 6).

Except for Mg and Ca, percent nutrient concentrations in aboveground biomass differed significantly between years (Tables 2 and 3). Percent N concentrations were highest in 1996, significantly lower in 1995, and intermediate (1.23 ±. 0.06%) in 1994. Percent P was significantly lower in 1995 compared to 1994 and 1996. Potassium concentrations followed the same pattern as P, with a significantly lower %K average in 1995 compared to 1994 and 1996. Percent Ca was significantly lower in 1994 than in 1995 and 1996.

Table 2. Results of ANOVA tests for Years (Y), Wetland sites (S), Zones (Z), and interactions between Y, S, and Z for aboveground biomass, nutrient concentrations, and nutrient standing stocks. Values in the Tables are F values and probability levels. Degrees of freedom are provided with the F values.

Variable	Year (Y)	Site (S)	Zone (Z)	Y∗S	Y∗Z	S∗Z	Y∗S∗Z
Biomass	$F_{2} = 0.72$; $P = 0.4895$	$F_{11} = 4.03$; $P < 0.0001$	$F_{2} = 26.82$; $P < 0.0001$	$F_{22} = 4.73$; $P < 0.0001$	$F_{4} = 3.48$; $P = 0.0080$	$F_{18} = 4.90$; $P < 0.0001$	$F_{29} = 2.18$; $P = 0.0004$
%P	$F_{2} = 10.64$; $P < 0.0001$	$F_{11} = 18.94$; $P < 0.0001$	$F_{2} = 68.98$; $P < 0.0001$	$F_{22} = 5.04$; $P < 0.0001$	$F_{4} = 0.94$; $P = 0.4530$	$F_{18} = 5.13$; $P < 0.0001$	$F_{29} = 4.46$; $P < 0.0001$
Total P	$F_{2} = 17.48$; $P < 0.0001$	$F_{11} = 10.23$; $P < 0.0001$	$F_{2} = 7.97$; $P = 0.0004$	$F_{22} = 7.27$; $P < 0.0001$	$F_{4} = 4.58$; $P = 0.0012$	$F_{18} = 4.04$; $P < 0.0001$	$F_{29} = 2.92$; $P < 0.0001$
%N	$F_{2} = 2.85$; $P < 0.0589$	$F_{11} = 14.49$; $P < 0.0001$	$F_{2} = 77.32$; $P < 0.0001$	$F_{22} = 4.50$; $P < 0.0001$	$F_{4} = 9.01$; $P < 0.0001$	$F_{18} = 3.33$; $P < 0.0001$	$F_{29} = 2.61$; $P < 0.0001$
Total N	$F_{2} = 11.49$; $P < 0.0001$	$F_{11} = 7.84$; $P < 0.0001$	$F_{2} = 6.45$; $P = 0.0017$	$F_{22} = 6.21$; $P < 0.0001$	$F_{4} = 2.01$; $P = 0.0924$	$F_{18} = 4.80$; $P < 0.0001$	$F_{29} = 2.81$; $P < 0.0001$
%Ca	$F_{2} = 2.63$; $P = 0.0733$	$F_{11} = 16.68$; $P < 0.0001$	$F_{2} = 2.83$; $P = 0.0596$	$F_{22} = 3.10$; $P < 0.0001$	$F_{4} = 11.28$; $P < 0.0001$	$F_{18} = 4.36$; $P < 0.0001$	$F_{29} = 2.21$; $P = 0.0003$
Total Ca	$F_{2} = 3.67$; $P = 0.0261$	$F_{11} = 6.64$; $P < 0.0001$	$F_{2} = 22.17$; $P = 0.0556$	$F_{22} = 4.15$; $P < 0.0001$	$F_{4} = 1.53$; $P = 0.1933$	$F_{18} = 6.53$; $P < 0.0001$	$F_{29} = 1.73$; $P = 0.0115$
Mg	$F_{2} = 1.37$; $P = 0.2550$	$F_{11} = 12.38$; $P < 0.0001$	$F_{2} = 3.62$; $P = 0.0274$	$F_{22} = 5.68$; $P < 0.0001$	$F_{4} = 1.68$; $P = 0.1541$	$F_{18} = 4.07$; $P < 0.0001$	$F_{29} = 2.94$; $P < 0.0001$
Total Mg	$F_{2} = 1.41$; $P = 0.2475$	$F_{11} = 4.24$; $P < 0.0001$	$F_{2} = 30.02$; $P < 0.0001$	$F_{22} = 5.04$; $P < 0.0001$	$F_{4} = 1.46$; $P = 0.2142$	$F_{18} = 3.18$; $P < 0.0001$	$F_{29} = 1.89$; $P = 0.0038$
%K	$F_{2} = 29.32$; $P < 0.0001$	$F_{11} = 15.44$; $P < 0.0001$	$F_{2} = 53.11$; $P < 0.0001$	$F_{22} = 4.37$; $P < 0.0001$	$F_{4} = 1.73$; $P = 0.1410$	$F_{18} = 6.01$; $P < 0.0001$	$F_{29} = 2.74$; $P < 0.0001$
Total K	$F_{2} = 16.41$; $P < 0.0001$	$F_{11} = 10.46$; $P < 0.0001$	$F_{2} = 1.23$; $P = 0.2938$	$F_{22} = 6.31$; $P < 0.0001$	$F_{4} = 5.11$; $P = 0.0005$	$F_{18} = 4.33$; $P < 0.0001$	$F_{29} = 4.24$; $P < 0.0001$
%C	$F_{1} = 18.87$; $P < 0.0001$	$F_{11} = 8.51$; $P < 0.0001$	$F_{2} = 33.76$; $P < 0.0001$	$F_{11} = 8.28$; $P < 0.0001$	$F_{2} = 2.93$; $P = 0.0549$	$F_{17} = 3.16$; $P < 0.0001$	$F_{14} = 2.32$; $P = 0.0047$
Total C	$F_{1} = 0.77$; $P = 0.3831$	$F_{11} = 3.08$; $P < 0.0001$	$F_{2} = 9.64$; $P < 0.0001$	$F_{11} = 5.43$; $P < 0.0001$	$F_{2} = 0.33$; $P = 0.7181$	$F_{17} = 3.88$; $P < 0.0001$	$F_{14} = 2.00$; $P = 0.0176$
N : P	$F_{2} = 25.44$; $P < 0.0001$	$F_{11} = 16.32$; $P < 0.0001$	$F_{2} = 3.29$; $P = 0.4550$	$F_{22} = 3.88$; $P < 0.0001$	$F_{4} = 5.58$; $P = 0.0002$	$F_{18} = 1.17$; $P = 0.0034$	$F_{29} = 2.90$; $P = 0.0007$

Table 3. Comparisons of biomass, nutrient concentrations, and nutrient standing stocks in 1994, 1995, and 1996. Values are means and 1 standard error (Parentheses). Superscripts are used to show comparisons between years. Means with similar superscripts are not statistically different from each other at $P \leq 0.05$.

Measurement	1994	1995	1996
Biomass (g/m^{2})	249.1 (15.6)^{a}	224.2 (15.0)^{a}	214.3 (16.4)^{a}
% N	1.23 (0.6)^{ab}	1.17 (0.04)^{b}	1.32 (0.04)^{a}
Total N (g/m^{2})	2.14 (0.12)^{a}	2.08 (0.13)^{a}	2.49 (0.21)^{a}
% P	0.23 (0.009)^{a}	0.17 (0.008)^{b}	0.21 (0.007)^{a}
Total P (g/m^{2})	0.44 (0.026)^{a}	0.30 (0.020)^{b}	0.41 (0.033)^{a}
% Ca	0.49 (0.018)^{a}	0.55 (0.017)^{a}	0.57 (0.018)^{a}
Total Ca (g/m^{2})	1.10 (0.076)^{a}	1.21 (0.093)^{a}	1.18 (0.105)^{a}
% K	1.19 (0.005)^{a}	0.76 (0.040)^{b}	1.12 (0.043)^{a}
Total K (g/m^{2})	2.42 (0.153)^{a}	1.50 (0.115)^{b}	2.24 (0.185)^{a}
% C	—	39.97 (0.442)^{a}	37.64 (0.642)^{b}
Total C (g/m^{2})	—	93.96 (6.64)^{a}	87.55 (7.25)^{a}
% Mg	0.19 (0.005)^{a}	0.19 (0.004)^{a}	0.19 (0.005)^{a}
Total Mg (g/m^{2})	0.43 (0.024)^{a}	0.41 (0.028)^{a}	0.40 (0.032)^{a}
N : P	5.75 (0.16)^{a}	7.62 (0.21)^{b}	6.53 (0.16)^{c}

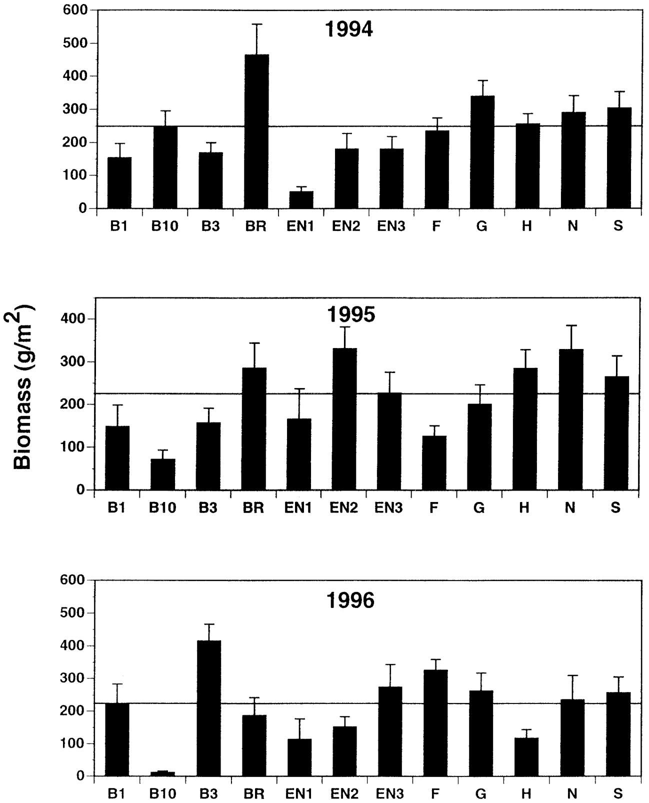

Figure 5. Mean annual biomass for each of the restored wetlands in 1994, 1995, and 1996. Values are means (g/m^2) ± 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in this analysis. None of the means are different from each other as indicated by similar letters above each bar at $P \leq 0.05$.

Carbon percentages of biomass differed significantly in the two years that it was measured.

Similar to the distribution of biomass within the wetlands, nutrient concentrations also differed among zones (Figure 7), but the general pattern was opposite the pattern for biomass, and it was more variable from year to year. In the majority of instances, nutrient concentrations increased from the temporary zone to the submersed zone. There were, however, several exceptions to this pattern. Carbon concentrations in 1996, % Mg in 1996, %Ca in 1995 and 1996, and %P in 1994 were lower in the submersed zone (Figure 7). Compared to the other two zones, the submersed zone had significantly higher nutrient concentrations in 1994, and with the exception of P, there were no significant differences between 1995 and 1996. There was no consistent pattern for nutrient concentrations in the seasonal/emergent zone. Comparing years, tissue nutrient concentrations were significantly lower in 1995 for %P and % K and significantly higher for % Ca in 1996, and there were no significant yearly differences for Mg and N concentrations. Carbon concentrations in the seasonal zone were significantly higher in 1995 (37.9 ± 0.80 %) than 1996 (34.4 ± 1.04 %).

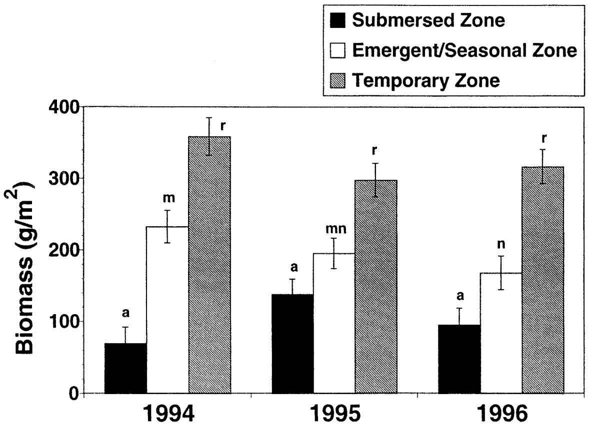

Figure 6. Mean annual biomass in each of the zones for all restored wetlands in 1994, 1995, and 1996. Values are means (g/m^2) ± 1 standard error. Statistical comparisons were made between years for each zone. There were no significant differences at $P \leq 0.05$ between years for the submersed and 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 different letters above the bars. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

Nutrient concentrations varied significantly among wetlands, and the wetland-year interactions were significant for all variables (Table 2). Examples of variations among wetlands and years are shown in Figures 8 and 9 for %N and %P, respectively. Percent N was more variable than %P among sites and years. Percent N was highly variable among sites in 1994 and less variable in 1995 and 1996 (Figure 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 (B10) in all three years and the lowest levels were found in plants at Eastern Neck 2 (EN 2).

N:P ratios in biomass were significantly different for each year of the study, significantly different between wetlands, but not significantly different between zones (Table 2). All interactions terms between the main effects variables were significantly different (Table 2). N:P ratios were lowest in the year with the lowest annual precipitation (1994 = 5.74 ± 0.16), intermediate in 1996 (6.54 ± 0.16), the year with an intermediate amount of precipitation, and highest in the wettest year (1995 = 7.6 ± 0.21). N:P ratios varied by a factor of almost 2X among wetlands (Figure 10).

Biomass and nutrient concentration data were combined to estimate total standing stocks of nutrients. There were significant differences among wetlands (Table 2) for all variables and the differences among

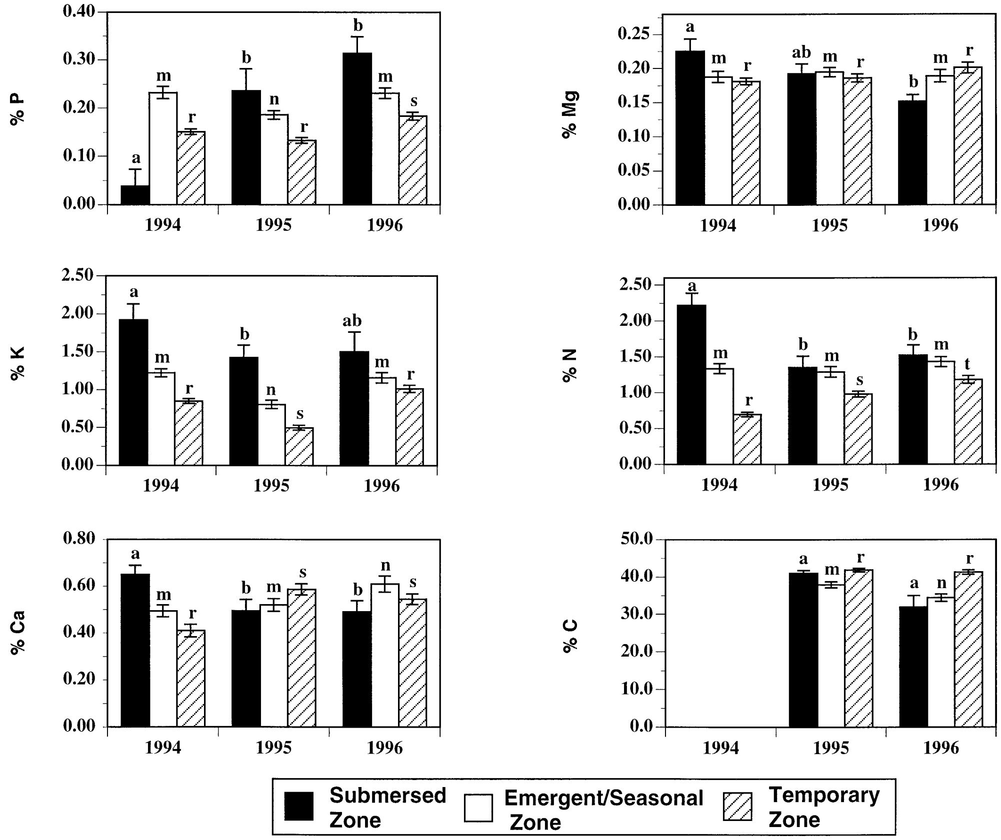

Figure 7. Mean concentrations (%) of Ca, K, P, C, N, and Mg in aboveground biomass in each of the zones for all restored wetlands in 1994, 1995, and 1996. Values are means ± 1 standard error. Statistical comparisons were made between years for each zone and the results, within zones, are indicated with letters above the bars at $P \leq 0.05$. There were significant differences between years for the submersed zone 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 that had vegetation were used in this analysis.

wetlands showed a pattern that was similar to the pattern for biomass (i.e., large differences among 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 Figures 11 and 12. Total N at two sites (EN1 and H) was less than average for all three years, and vegetation at Nesbit (N) and Sultenfuss (S) had higher than average Total N for all three years (Figure 11). Total N was highly variable among years at all other sites. Only Sultenfuss (S) had higher than average Total P in all three years (Figure 12). Four sites (B1, EN1, EN2, and H) had Total P standing stocks that were less than average for all three years. The other seven sites had Total P standing stocks that varied from above to below the average for all sites combined.

Average total nutrient stocks for all wetlands differed little among years, and significant differences were found only for K and P (Table 3). Total K and Total P were significantly lower in 1995. Total biomass distribution in the three zones also varied little between years. There were no significant differences in nutrient standing stocks for any nutrient in the submersed zone between years (Figure 13). In the emergent/seasonal and temporary zones, Total K and Total P were significantly lower in the emergent/seasonal and temporary zones in 1994. Total N was significantly different in all three years in the temporary zone.

DISCUSSION

There have been relatively few multiple year studies of biomass and nutrient changes of vegetation in restored wetlands, and we are not aware of any studies in which several wetlands have been measured for multiple years. Our results can, therefore, only be compared in a general manner with related studies. Comparisons with other studies are further limited because time and manpower limits did not enable us to attempt to estimate annual biomass production by sampling in-

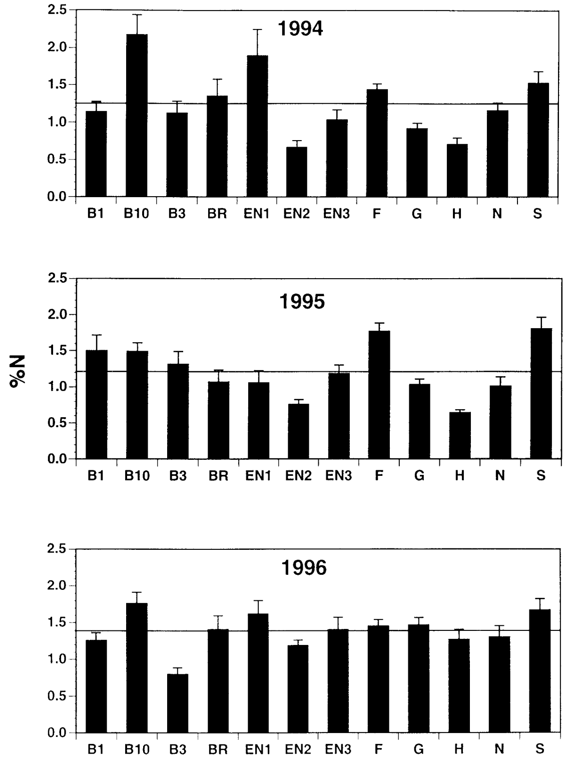

Figure 8. Mean nitrogen concentration of aboveground biomass for each of the restored wetlands in 1994, 1995, and 1996. Values are means ± 1 standard error. The horizontal line in each graph is the mean for all three years combined. Only subplots with aboveground biomass were used in this analysis.

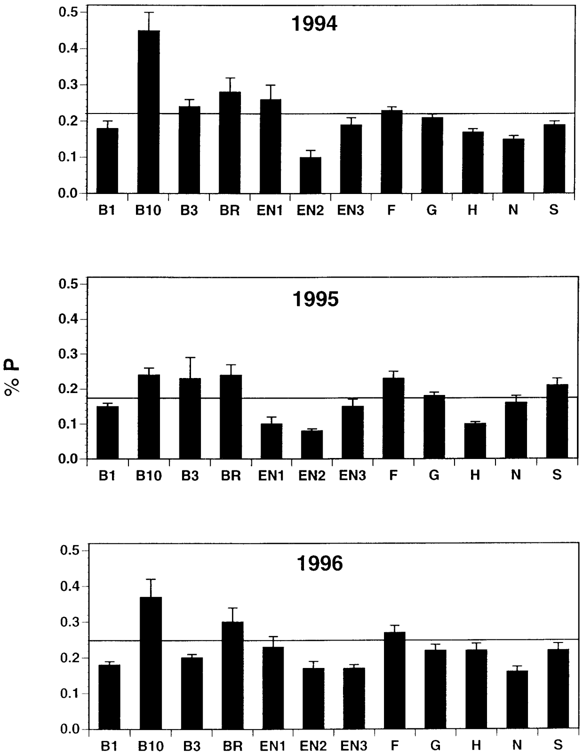

Figure 9. Mean phosphorus concentration of aboveground biomass for each of the restored wetlands in 1994, 1995, and 1996. Values are means ± 1 standard error. The horizontal line in each graph is the mean for all three years combined. Only subplots with aboveground biomass were used in this analysis.

dividual species when they were at peak biomass or by repeated measurements of shoot density and shoot size that could be used to estimate annual production. The approach that we used, measurements of biomass at the same time each year, was chosen to provide biomass and nutrient comparisons between and within sites.

Because we sampled only once per year and sampled later in the growing season, the measurements of aboveground biomass (e.g., Figure 5) represent underestimates of annual aboveground biomass production. Nutrient concentrations in biomass would also be less at that time of year, as nutrient levels in plant tissues decrease over the growing season as nutrients are allocated to reproductive structures and belowground biomass (e.g., Klopatek 1978, Bernard and Lauve 1995). As expected, biomass measured in this study was low compared to published data for nutrient-rich herb-dominated natural, restored, and constructed wetlands (Mitsch and Gosselink 1993, Vymazal et al. 1999). Biomass measured in this study was also at the lower end of range of annual production reported for emergent species in prairie pothole wetlands (Murkin 1989), wetlands that are most similar to those examined in this study. Biomass within the submersed zone was, however, similar to the range of values reported by Murkin (1989) and Grillas and Battedou (1998) for submersed macrophytes in prairie pothole wetlands and the Camargue in France, respectively.

Our principal objective was to evaluate the predic-

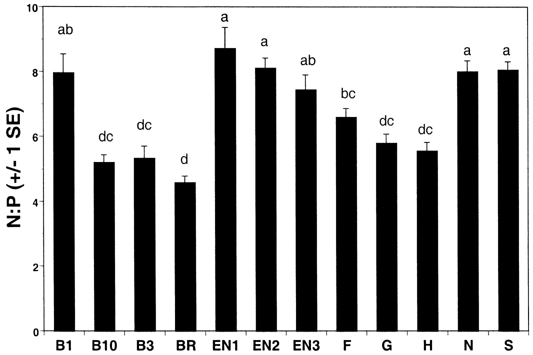

Figure 10. N:P ratios in biomass across the wetland study sites. Data for all zones and the three years are combined. Only plots that contained vegetation were used for this analysis. Values are means ± 1 standard error. Means that are not significantly different at P ≤ 0.05 from each other share the same letter above the bar.

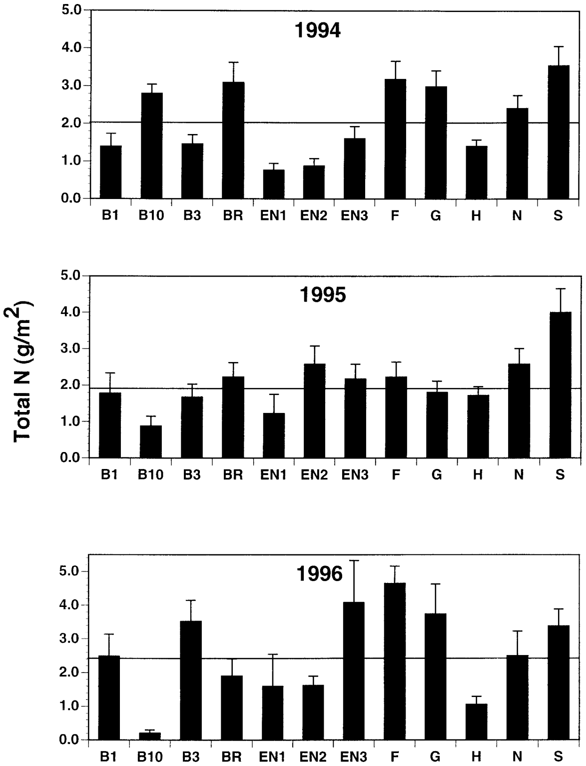

Figure 11. Mean Total N in aboveground biomass for each of the restored wetlands in 1994, 1995, and 1996. Values are means (g/m^2) ± 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

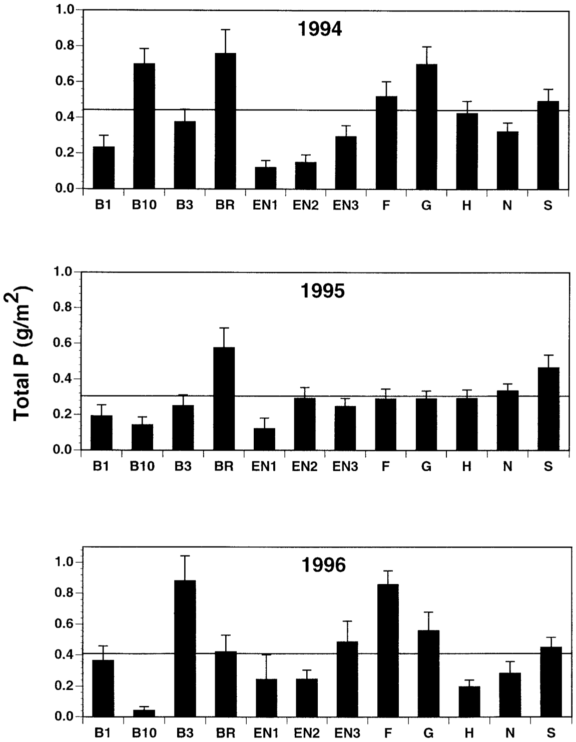

Figure 12. Mean Total P in aboveground biomass for each of the restored wetlands in 1994, 1995, and 1996. Values are means (g/m^2) ± 1 standard error. The horizontal line in each graph is the mean for all three years combined. All subplots (i.e., those with and without aboveground biomass) were used in this analysis.

tion that biomass would increase with time since restoration, primarily because long-lived perennials would replace shorter-lived species. We found that annual biomass measurements varied significantly among wetlands over the three years (Figure 5), and there was no pattern of increased biomass with time since restoration. For example, biomass at the four oldest sites (EN 1–3, B1) was more often less than the mean value for all sites combined (Figure 5). We can think of three explanations for the results that we obtained. First, we sampled the wetlands for three years, and considerably more time would be needed for the vegetation to develop and change in the predicted direction. We find no evidence to support this explanation. Two of the sites at the Eastern Neck National Wildlife Refuge (EN 1 and EN 3) were restored almost 30 years ago; yet, biomass at those sites was within the range of values measured at the much younger wetlands. One problem with this comparison, however, is that we do not know the management history (e.g., annual water-level manipulations) of the three sites at the Eastern Neck National Wildlife Refuge. The refuge is managed for wildlife, and the restored wetlands are resting and feeding sites for large numbers of wintering migratory waterfowl. It seems quite likely that waterfowl feeding would influence the amount of standing biomass and patterns of vegetation development (e.g., Cargill and Jerreries 1984, Van den Wyngaert 2001). Comparison of the three sites at Barnstable Hill (B1, B10, B3), however, offers further evidence that biomass, at most, increases very slowly with age since restoration. The three Barnstable wetlands occur on the same farm and were restored and managed in a similar manner by Chesapeake Wildlife Heritage. The B1 wetland was 5 and 6 years older than B3 and B1, respectively, at the time our study was initiated, but we found no consistent differences in biomass among the three wetlands.

The second explanation for the observed biomass pattern is that annual variations in hydrologic conditions strongly influence patterns of vegetation development in shallow depressional wetlands, resulting in no clear long-term pattern of vegetation development. Hydrologic control of vegetation development has been clearly shown for depressional wetlands in the prairie pothole region of the US (Seabloom et al. 2001). Potholes undergo vegetation cycles in response to water-level changes associated with wet and dry cy-

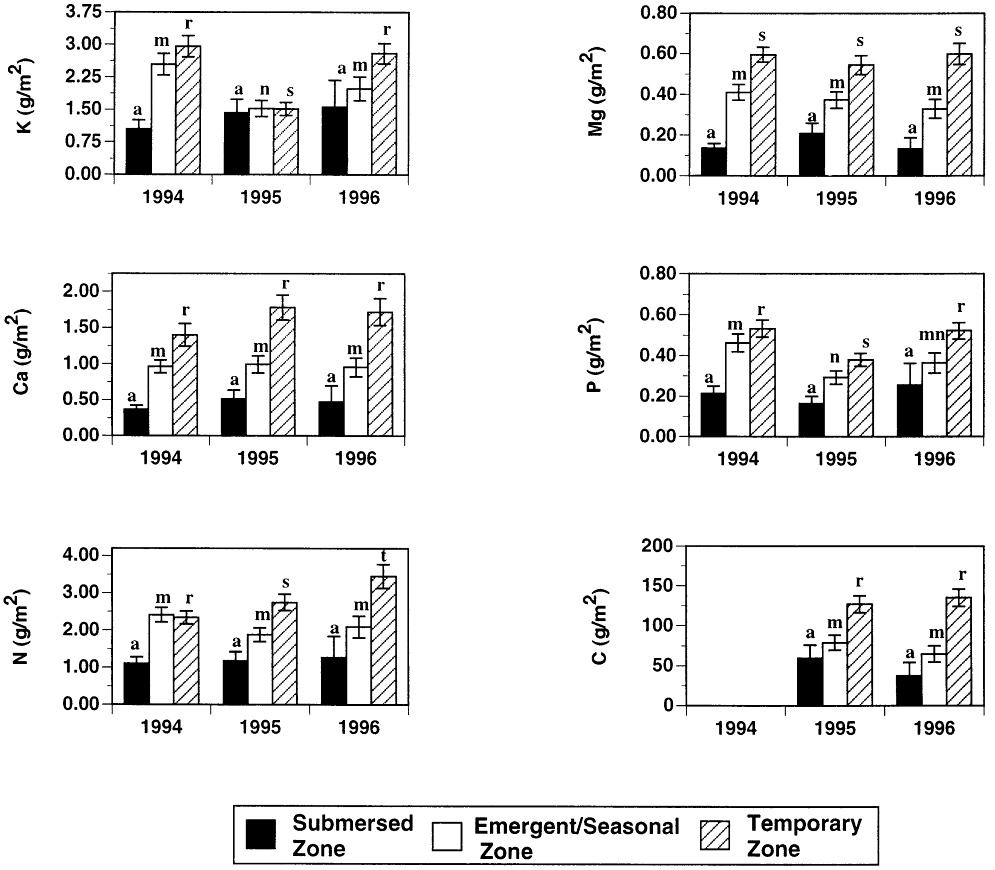

Figure 13. Mean total amounts of Ca, K, P, C, N, and Mg in aboveground biomass in each of the zones for all restored wetlands in 1994, 1995, and 1996. Values are means (g/m^2) ± 1 standard error. Statistical comparisons were made between years for each zone and the results, within zones, are indicated with letters above the bars for $P \leq 0.05$. There were no significant differences between years for the submersed zone. Significant differences between years in the emergent/seasonal zone were found K and P. Significant differences between years in the temporary zone were found for N, K, and P. All subplots were used in this analysis.

cles (Kantrud et al. 1989). During periods of high water, wetlands dominated by high biomass emergent perennial species deteriorate (called the 'degenerating stage') and change to an open water system dominated by submersed species that have lower biomass. During periods of low water, annuals followed by clonal perennials colonize wetlands, leading to dominance by emergent species (called the 'regenerating stage'). Similar patterns have been observed in depressional wetlands in the southeastern US (Kirkman et al. 1996, 2000). In South Carolina, vegetation in natural and restored herb-dominated depressional wetlands was relatively stable over more than four decades, due in part to varying hydrologic conditions (Kirkman et al. 1996). Kirkman and colleagues also found that variations in water levels, along with fire, had a strong impact on vegetation patterns in depressional wetlands in Georgia (Kirkman et al. 2000). It seems clear that vegetation in shallow depressional wetlands responds strongly to variations in hydrologic conditions (Seabloom et al. 2001), and annual variations in biomass were most likely the result of annual variations in precipitation that influenced water levels during the growing season. Herbivory and management activities, however, may have influenced biomass measurements.

Typha latifolia L., for example, was spreading rapidly by clonal propagation at the Hope (H) site, and in 1995, the site managers reduced that species by applying herbicides, thus resulting in lower biomass in 1996. Herbivores (e.g., muskrats) were also present at some of the sites, and we often saw direct evidence of plant consumption. Thus, at the level of individual wetlands, water-level variations from year to year, herbivore activity, and management all may have influenced biomass patterns. These results support the findings of Galatowitsch and van der Valk (1995) by demonstrating that annual variations in biomass in restored wetlands should be expected, especially in the early years following restoration. These conclusions are also supported by the results of recent modeling efforts of vegetation patterns following changes in hydrologic conditions in depressional wetlands (Seabloom et al. 2001) and patterns of annual biomass variation in playa wetlands (Pezzolesi et al. 1998).

Patterns of biomass and nutrient distribution within individual wetlands, however, were not as variable as patterns that were observed between wetlands. There were no significant differences between years in the pattern of biomass distribution within wetlands (Figure 6). Biomass decreased each year from the temporary to submersed zone, a pattern that was consistent with other studies of biomass distribution in depressional wetlands. However, considering all of the wetlands together at the landscape level, the variation among years is minimal for biomass, nutrient concentrations, and nutrient standing stocks (e.g., Table 3).

We also measured differences between years and between wetlands in the amounts of nutrients that are annually retained or released (Jordan et al. 1999). At the Barnstable 10 site, which we monitored continuously for three years, there were large annual differences in the amounts of nitrogen and phosphorus retained or released, further demonstrating the dynamic nature of these wetlands.

Finally, data on N:P ratios in the vegetation can be used to indicate whether or not there are nutrient controls on biomass production. Koerselman and Meuleman (1996) suggested that N:P ratios less than 14 are indicative of N-limiting conditions. Bedford et al. (1999) 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. We found that the range of N:P in biomass ranged from 5.7 ± 0.15 to 7.6 ± 0.20 over the three years. These results suggest that biomass production is N limited in these restored wetlands.

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 mostly due to annual variations in management and hydrologic conditions rather than any long-term pattern of vegetation development. 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 were small, suggesting that the overall levels of plant resources were relatively constant each year. The pattern of distribution of biomass within wetlands zones (i.e., decreasing biomass from the outside to inside of each wetland) was anticipated, 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.

Standing crop biomass did not increase 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 (Pepin and Whigham 1999), we agree with recent suggestions that the vegetation of restored wetlands may be quite dynamic for one or more decades (Malakoff 1998, Moore et al. 1999).

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