

The Influence of Microtopography on Soil Nutrients in Created Mitigation Wetlands

Kurt F. Moser,¹ Changwoo Ahn,^{1,2} and Gregory B. Noe³

Abstract

This study explores the relationship between microtopography and soil nutrients (and trace elements), comparing results for created and reference wetlands in Virginia, and examining the effects of disking during wetland creation. Replicate multiscale tangentially conjoined circular transects were used to quantify microtopography both in terms of elevation and by two microtopographic indices. Corresponding soil samples were analyzed for moisture content, total C and N, KCl-extractable $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, and Mehlich-3 extractable P, Ca, Mg, K, Al, Fe, and Mn. Means and variances of soil nutrient/element concentrations were compared between created and natural wetlands and between disked and nondisked created wetlands. Natural sites had higher and more variable soil moisture, higher extractable P and Fe, lower Mn than created wetlands, and comparatively high variability in nutrient concentrations. Disked sites had higher soil moisture,

$\text{NH}_4\text{-N}$, Fe, and Mn than did nondisked sites. Consistently low variances (Levene test for inequality) suggested that nondisked sites had minimal nutrient heterogeneity. Across sites, low P availability was inferred by the molar ratio (Mehlich-3 $[\text{P}/(\text{Al} + \text{Fe})] < 0.06$); strong intercorrelations among total C, total N, and extractable Fe, Al, and P suggested that humic-metal-P complexes may be important for P retention and availability. Correlations between nutrient/element concentrations and microtopographic indices suggested increased Mn and decreased K and Al availability with increased surface roughness. Disking appears to enhance water and nutrient retention, as well as nutrient heterogeneity otherwise absent from created wetlands, thus potentially promoting ecosystem development.

Key words: created wetland, disking, microtopography, soil nutrients, surface roughness, wetland mitigation.

Introduction

Plant-scale topographic variability, or microtopography, may influence wetland hydrology and physicochemistry, thus affecting the balance of plant nutrients in soil. Wetland plants vary in nutrient demands (McJannet et al. 1995; Güsewell & Koerselman 2002) and in adaptations to flooded soil conditions (Kozlowski 1984). Plants also differ in morphology and in their ability to exploit nutrients (Crick & Grime 1987; Hinsinger 2001). Individual species-level responses to soil conditions may determine community composition, richness, and diversity (Bedford et al. 1999; Güsewell et al. 2005), ultimately determining ecosystem functions.

The use of heavy machinery for grading during wetland creation tends to reduce the microtopographic variability commonly found in natural settings (Stolt et al. 2000). Created wetlands also tend to lack the spatial variability of nutrients and biogeochemical processes found in natural wetlands (Bruland et al. 2006). In spite of these characteristic failings, created wetlands are increasingly used to

mitigate the loss of natural wetlands. An area of concern for mitigation is the extent to which uniformity of physicochemical conditions may lead to the predominance of few species, thus to a paucity of ecosystem functions (Hooper et al. 2002). In theory, greater variability in localized (plant scale) nutrient or hydrologic/redoximorphic conditions should support greater plant diversity generally (Tilman 1997; Larkin et al. 2006), greater diversity of functional vegetation types and associated biota (Boutin & Keddy 1993; Grime et al. 1997), and greater ecosystem stability to disturbance (Hooper et al. 2002). Induced microtopography during the restoration or creation of wetlands may enhance such variability and benefit ecosystem development.

Substantial chemical heterogeneity exists at small (1.5-cm interval) vertical scales in wetland soils (Hunt et al. 1997), indicating that even small-scale variations in relief may meaningfully affect soil nutrients. Gradients of increasing moisture, substrate pH and exchangeable Ca and Mg, and decreasing inorganic N and total P have been shown associated with a microtopographic gradient from higher to lower elevations (Karlin & Bliss 1984; Stoeckel & Miller-Goodman 2001; Bruland & Richardson 2005). Vertical relief may also affect the flux of nutrients with Mn, Fe, and P complexed to Fe accumulating above the water table in microhigh soils, a net upward translocation (Fiedler et al. 2004).

¹ Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030, U.S.A.

² Address correspondence to C. Ahn, email cahn@gmu.edu

³ U.S. Geological Survey, Reston, VA 20192, U.S.A.

The relationship between microtopography and nutrient distribution is commonly explained in terms of hydrologic/redoximorphic regimes. For instance, in wetland soils, iron plays an important role in phosphorus adsorption, retention, and release (Patrick & Khalid 1974; Baldwin & Mitchell 2000; Aldous et al. 2005); aluminum can likewise affect P availability (Richardson 1985; Axt & Walbridge 1999; Darke & Walbridge 2000). Although availability of aluminum-bound phosphate is unaffected by redox status, iron-bound phosphate becomes soluble and available under anaerobic conditions. Consequently, the redox status of Fe in flooded soils may determine P availability (Aldous et al. 2005). Microtopographic elevation affects the frequency, duration, and spatial variability of flooding (Pollock et al. 1998; Fiedler et al. 2004), so it may affect redox conditions and availability of redox-sensitive nutrients. Microtopography may also enhance water retention and soil moisture through increased depression storage (Kamphorst et al. 2000). Thus, roughing the surface (as by disking, the use of tractor-drawn offset disk, or disk harrower) may help establish wetland hydrology, in addition to promoting redoximorphic variability. Field experiments show higher water retention and water table levels for disked than for nondisked wetland restoration plots (Tweedy et al. 2001).

Within the time frame legally mandated for monitoring at mitigation sites, created wetlands show little evidence of ecosystem development comparable to that of natural wetlands and many fail to meet basic success criteria (National Research Council 2001; Spieles 2005). Our hope is that wetland creation methods might be refined to enhance wetland ecosystem development and functional diversity, increasing the probability that lost wetland ecosystem services are actually replaced, as well as legally mitigated. This study examines the effects of artificially induced microtopography on soil nutrients in nontidal freshwater mitigation wetlands, supplementing a study that suggests disking quantitatively enhances created wetland microtopography and plant diversity (Moser et al. 2007). We investigate major limiting nutrients (N, P, and K) and macronutrients (Ca and Mg) as well as micronutrients/trace elements involved in toxicity and P availability (Fe, Mn, and Al). Broadly stated, our questions are (1) How do created and natural wetlands differ in terms of soil nutrients/elements? (2) How do disked and nondisked created wetlands differ in terms of these nutrients/elements? and (3) How does microtopography relate to the distribution/abundance of soil nutrients?

Methods

Site Details

Field research was carried out in summer 2005 at 12 study sites in created and natural nontidal freshwater wetlands in Virginia, U.S.A. Created wetlands were North Fork (lat 38°49.4'N, long 77°40.2'W) and Cedar Run (lat 38°37.6'N,

long 77°33.6'W) mitigation banks in Prince William County; natural wetlands were at Huntley Meadows Park (lat 38°45.0'N, long 77°06.8'W) in Fairfax County. Although all study wetlands are located within 30 km of Fairfax, Virginia, the created wetlands are located in the Piedmont physiogeographic province, generally characterized by rolling terrain underlain by igneous and metamorphic rock, whereas the natural wetlands were in the Coastal Plain, comparatively flat and underlain by unconsolidated sediment. Although portions of the created wetlands were intended to mitigate the loss of palustrine forested wetlands, all planted trees were small saplings at the time of the study, and these wetlands could best be characterized as palustrine emergent, comparable to the natural wetlands.

North Fork is a 125-acre wetland/upland complex created in 1999–2000 on land formerly used as cattle pasture. Soils are generally silt loams and silty clay loams over Newark Supergroup basalt and sandstone/siltstone formations of the Culpeper Basin. Four study sites were located in a 51-acre wetland area surrounding open water, with vegetation in its fifth growing season following disked wetland creation. Cedar Run is a large multiple-wetland complex developed on land formerly used for agriculture. Soils are primarily silt loams over Newark Supergroup interbedded sandstone/siltstone/shale. Two study sites were located in a 67-acre wetland complex created and disked in 2004–2005, whereas two sites were in a smaller adjacent wetland that was regraded without disking and seeded in late 2004. All Cedar Run sites were thus in their first growing season. The 1,425-acre Huntley Meadows Park prominently features beaver-engineered wetlands in an urbanized watershed. Soils are derived from gravel, sand, silt, and clay of the Shirley Formation, Pleistocene Epoch deposits of the Potomac River. Two study sites were in a mature (>30 years old) emergent wetland, whereas two sites were in an emergent wetland adjacent to a more recently established (approximately 10 years old) beaver pond.

Microtopography

Each of the 12 study sites was examined using a single set of tangentially conjoined circular transects, with field measurements and samples taken at regular intervals along the circular paths (Fig. 1). The circular transect is an approach designed to be directionally unbiased; any confounding directional effects of disking orientation, wind, direction of hydrologic flows, orientation of incident sunlight, and so forth are thus minimized. Transects were laid out as 0.5-, 1-, and 4-m-diameter circles using polyethylene tubing hoops. Within each wetland, sites were randomly selected, although for created wetlands where marked survey locations had been previously established, a survey marker was randomly selected and the study site established 3 m to the north.

Each soil sampling location was associated with three microtopographic parameters determined from fine-scale

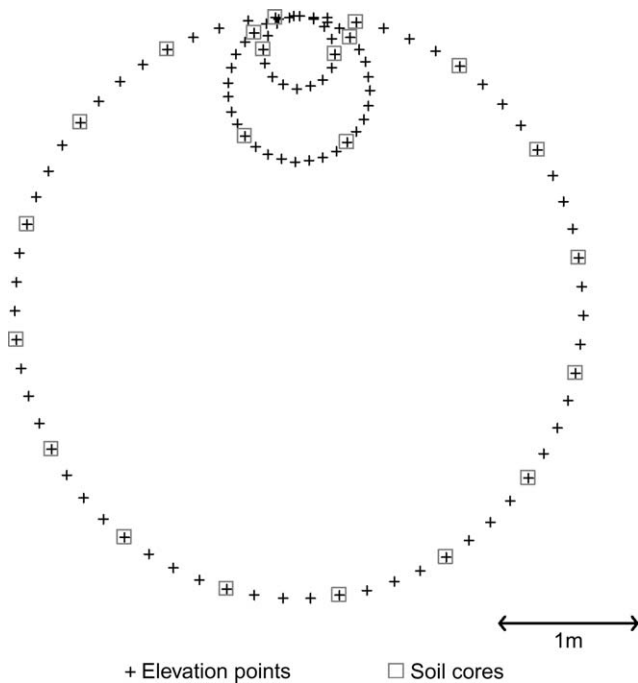


Figure 1. Multiscale circular transects. Microtopographic elevation data point intervals are 10 cm for 0.5- and 1-m transects and 20 cm for the 4-m transects. Soil sampling locations are at 80-cm intervals.

survey of transect elevations (10- to 20-cm interval; Fig. 1). These were the indices tortuosity (Kamphorst et al. 2000), limiting elevation difference (Linden & Van Doren 1986), and elevation relative to the mean multi-scale transect elevation. Whereas tortuosity is an overall measure of roughness akin to surface area, limiting elevation difference reflects the degree of topographic relief. Index measures were calculated for each soil sampling location based on transect data for near-neighbor data points (points within 30–60 cm, depending on the transect scale) using a methodology developed for evaluating wetland microtopography (Moser et al. 2007). Subsets of the data from that study, these indices characterize the immediate surrounding microtopography and are referred to as proximal tortuosity (pT) and proximal limiting elevation difference (pLD).

Soil Sampling and Analysis

Soil samples were collected at 80-cm intervals along 0.5-, 1-, and 4-m-diameter transects (162 samples total; Fig. 1) between 26 July and 2 August 2005 at peak vegetation growth. A soil probe/auger (1.8-cm inner diameter) was used to collect the top 10 cm of soil, excluding surface litter. Samples were stored in polyethylene bags and transported on ice, then stored in the lab at -15°C pending analysis. Samples were thawed and homogenized by hand, with roots, and recognizable plant material and coarse gravel removed. Subsamples were oven-dried at 105°C for

48 hours and used to determine moisture content for each sample (calculated as [wet weight – dry weight]/dry weight, expressed as a percentage). Dried subsamples were passed through a 2-mm sieve and ground with a mortar and pestle before analysis for total C and N (percent dry weight) using a Perkin-Elmer 2400 Series II CHNS/O analyzer (Perkin-Elmer Corporation, Norwalk, CT, U.S.A.). KCl extraction (Mulvaney 1996) was performed on field-moist samples to quantify available inorganic nitrogen ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, expressed as $\mu\text{g N/g}$ dry weight), with 40 mL of 1M KCl added to 4 g dry weight equivalent soil, the mixture shaken at room temperature for 60 minutes on a reciprocating shaker table and allowed to settle for 30 minutes, and the supernatant passed through a 1.2- μm glass fiber filter, followed by colorimetric analysis using an Astoria-Pacific segmented flow analyzer (Astoria-Pacific International, Clackamas, OR, U.S.A.). Mehlich-3 extraction (Mehlich 1984) was performed for field-moist samples to quantify available Al, Fe, P, Ca, Mg, Mn, and K, with 20 mL of Mehlich-3 extractant added to 2 g dry weight equivalent of soil, the mixture shaken at room temperature for 5 minutes on a reciprocating shaker table and allowed to settle for 1 minute, then passed through a 0.45- μm polyethersulfone filter. A ratio of 1:10 (v:v) dilutions were analyzed by inductively coupled plasma optical emission spectroscopy (ICP-OES) using a Perkin-Elmer Optima 4300 DV analyzer (Perkin-Elmer Corporation) and also analyzed for inorganic P by colorimetry using a Technicon II Autoanalyzer (Bran + Luebbe GmbH, Norderstedt, Germany). Because P availability depends to a great extent on both Al and Fe, the molar ratio $[\text{P}/(\text{Al} + \text{Fe})]$ for Mehlich-3 extraction was used as a measure to predict P saturation (Kleinman & Sharpley 2002; Sims et al. 2002). Soil inorganic N:P (designated iN:iP) ratios $[(\text{NO}_3\text{-N} + \text{NH}_4\text{-N})/\text{ortho-P}]$, pertaining to the forms of N and P most available to plants, were also used to determine N or P limitation (Wassen et al. 1995; Koerselman & Meuleman 1996; Bedford et al. 1999). N limitation was inferred for iN:iP less than 14, P limitation for iN:iP greater than 16, and colimitation for ratios in between.

Statistical Analysis

Because the hydrogeomorphic settings differed among study localities, our analysis treats soil moisture as a covariate reflecting differences in both soil pore space attributable to soil composition and proximity to the water table (i.e., concentrations of mobile/water-soluble nutrients were expected to reflect water volume). Moreover, our analysis also stresses comparison of group variances, a necessity because topographic variability may influence nutrient distribution irrespective of nutrient abundance (i.e., group means). Our data conformed poorly to the implicit assumptions of multivariate analysis of variance and covariance, so univariate analysis of covariance (ANCOVA) was carried out separately for each nutrient

variable. Where the covariate was not significant ($\alpha = 0.05$) or the assumption of homogeneity of regression slopes could not be met, univariate analysis of variance (ANOVA) was performed. Data were categorized into four wetland groups for ANOVA/ANCOVA: (1) disked, North Fork ($n = 52$); (2) disked Cedar Run ($n = 26$); (3) nondisked Cedar Run ($n = 28$); and (4) natural, Huntley Meadows ($n = 52$). ANOVA/ANCOVA analyses were nested two-factor analyses (site nested within wetland group) using type III sums of squares and an alpha level of 0.05. Post hoc Dunnett's T3 pairwise comparisons were performed for ANOVA; because this test is not appropriate for ANCOVA, Bonferroni adjustment was applied for ANCOVA pairwise comparisons. Comparisons of means for microtopographic index measures have previously been reported for the parent dataset (Moser et al. 2007), so microtopographic index parameters were not compared here. The Levene test of equality of variance (commonly used to test the ANOVA/ANCOVA equality of variance assumption) was used as a more robust alternative to Bartlett's two-sample test for comparing group variances ($\alpha = 0.05$); Bonferroni adjustment was applied for pairwise comparisons. Correlations among microtopographic indices and nutrient variables for each soil sample location were examined using nonparametric Spearman rank correlation coefficients, using untransformed variables. ANOVA/ANCOVA and Spearman correlation analyses were performed using SPSS (SPSS, Inc. 2004). Correlation-based principal components analysis (PCA, conducted using normalized variables) was also performed to reduce the number of nutrient variables to a small number of factors, using PRIMER (PRIMER-E Ltd. 2006). To better conform to the assumptions of ANOVA/ANCOVA and PCA, natural log transformations were applied for Ca, Mg, Mn, and $\text{NO}_3\text{-N}$. For log-transformed variables, reported values are converted back to original units.

Results

The microtopographic data supported the notion that though the microtopography of disked created wetlands is generally comparable to that of the natural wetlands at the extent and resolution examined, disked sites have more pronounced microtopography than do nondisked created wetland sites. pLD index means clearly distinguished disked and nondisked created wetland microtopography, with minimal relief evident in nondisked sites (Table 1); pT likewise showed nondisked sites to be comparatively low in microtopography (Table 1). Although pLD and pT means for the natural sites were intermediate, their overall ranges encompassed the corresponding ranges of both disked and nondisked sites.

Soil moisture content, with an overall range between 12 and 44% (Table 1), correlated positively, but weakly, with the pLD index but not with the pT index or relative elevation (Table 2). Soil moisture differed significantly among wetlands ($F_{[3,8,2]} = 8.77$, $p = 0.006$; Fig. 2), and it corre-

Table 1. Proximal microtopographic indices ($\bar{X} \pm 1$ SE) for pT, pLD, and soil moisture content.

	pT	pLD (cm)	Moisture (%)
North Fork (disked)	1.013 \pm 0.002	5.0 \pm 0.8	26.5 \pm 0.5
Cedar Run (disked)	1.012 \pm 0.001	6.1 \pm 0.9	22.8 \pm 0.8
Cedar Run (nondisked)	1.003 \pm <0.001	1.6 \pm 0.2	16.8 \pm 0.7
Huntley Meadows (natural)	1.011 \pm 0.003	4.3 \pm 0.7	32.4 \pm 0.5

lated significantly with most parameters (Table 2). Soil moisture was weakly/positively correlated with extractable Ca, Al, Fe, total P, ortho-P, $\text{NO}_3\text{-N}$, and $\text{NH}_4\text{-N}$, and weakly/negatively with Mn. Despite numerous correlations (r_{sp}), moisture was a significant covariate only within created wetlands for total C, total N, and extractable Ca and among all sites for total P and ortho-P (Table 3). For C, N, and Ca, the Huntley Meadows (natural) sites were excluded from ANCOVA to satisfy the assumption of homogeneity of regression slopes, enabling ANCOVA adjustment for means comparison among created wetlands. Moisture was not a significant covariate for K, Fe, or Mn, whereas the assumption of homogeneity of regression slopes could not be met for Mg, Al, and $\text{NH}_4\text{-N}$ (for $\text{NH}_4\text{-N}$, the homogeneity assumption could be met within created wetlands, but moisture was nonetheless not a significant covariate). Thus, group means were selectively ANCOVA adjusted (Table 3).

As measured, soil total C and N were lower for created (C range 0.3–4.0%, mean 1.2%; N range 0.01–0.26%, mean 0.11%) than for natural wetlands (C range 0.7–7.7%, mean 2.5%; N range 0.06–0.39%, mean 0.19%). Adjusted for the covariate moisture, however, no significant mean difference was evident either for total C ($F_{[2,8,7]} = 1.96$, $p = 0.20$; Fig. 2) or for total N ($F_{[2,6,9]} = 2.64$, $p = 0.14$; Fig. 2). $\text{NO}_3\text{-N}$ concentrations ranged from 0 to 11.7 $\mu\text{g N/g}$ ($\bar{x} = 2.2$ $\mu\text{g N/g}$), whereas $\text{NH}_4\text{-N}$ concentrations ranged from 0.1 to 35 $\mu\text{g N/g}$ ($\bar{x} = 8.4$ $\mu\text{g N/g}$). Average $\text{NO}_3\text{-N}$ concentrations differed among the study wetlands ($F_{[3,9,0]} = 6.22$, $p = 0.014$; Fig. 2); concentrations were higher for North Fork than for Huntley Meadows. $\text{NO}_3\text{-N}$ concentrations were lowest at Cedar Run, and there was no apparent difference between the disked and the nondisked sites. Average $\text{NH}_4\text{-N}$ concentrations also differed ($F_{[3,9,1]} = 12.75$, $p = 0.001$; Fig. 2), with higher concentrations for disked Cedar Run and Huntley Meadows than for North Fork and nondisked Cedar Run (the lowest).

Mehlich-3 extractable total P and orthophosphate-P had similar ranges (0–46 $\mu\text{g/g}$) and were highly correlated (Table 2), with linear regression slope approximating equality ($[\text{orthophosphate-P}] = 0.998 \times [\text{total P}] - 0.810$; $R^2 = 0.917$); any extraction of organic P (nonmolybdate-reactive P) was apparently minimal, and the two methods are thus essentially equivalent as used here. However, because ICP-OES resolution was limited at low P concentrations, the orthophosphate-P determinations are presumed

Table 2. Spearman rank correlations among measured soil/microtopographic parameters.

	<i>pT</i>	<i>pLD</i>	Elevation	% Moisture	C	N	NO ₃	NH ₄	P	<i>oP</i>	K	Ca	Mg	Fe	Mn
<i>pLD</i>	0.616														
Elevation	-0.018	-0.058													
% Moisture	0.083	0.221	-0.012												
% C	-0.027	0.100	0.040	0.836											
% N	-0.042	0.076	0.047	0.841											
NO ₃ -N	-0.058	-0.015	-0.008	0.411	0.974	0.524									
NH ₄ -N	0.048	0.102	-0.128	0.444	0.474	0.426	-0.027								
P	-0.109	0.041	-0.067	0.365	0.385	0.314	-0.176	0.711							
<i>oP</i>	-0.082	0.027	-0.091	0.355	0.398	0.336	-0.220	0.757	0.901						
K	- 0.214	-0.122	- 0.214	0.041	0.174	0.160	0.207	0.252	0.370	0.324					
Ca	0.150	0.044	0.023	- 0.286	- 0.244	-0.181	0.354	-0.514	- 0.606	- 0.615	0.078				
Mg	0.045	0.007	0.027	-0.035	-0.030	0.054	0.489	- 0.545	- 0.595	- 0.632	0.075	0.877			
Fe	-0.003	0.115	-0.086	0.448	0.513	0.429	-0.085	0.692	0.759	0.763	0.389	- 0.429	- 0.418		
Min	0.224	0.141	0.057	- 0.284	- 0.262	-0.215	0.165	- 0.312	- 0.477	- 0.436	-0.034	0.838	0.658	- 0.329	
Al	- 0.214	-0.073	-0.025	0.204	0.333	0.306	0.129	0.259	0.542	0.429	0.636	-0.033	0.076	0.552	-0.040

Values in boldface indicate that correlation is significant at the 0.01 level and values underlined indicate that correlation is significant at the 0.05 level.

more reliable; these alone were used for PCA. Mean extractable orthophosphate-P differed among the study wetlands ($F_{[3,9,4]} = 8.59, p = 0.005$; Fig. 2). Similarly, mean extractable total P differed among the study wetlands ($F_{[3,9,4]} = 8.14, p = 0.006$, Huntley Meadows [$\bar{x} = 15.1 \mu\text{g P/g}$] > disked Cedar Run [$\bar{x} = 8.6$] \approx nondisked Cedar Run [$\bar{x} = 6.1$] \approx North Fork [$\bar{x} = 2.1$], with disked Cedar Run > North Fork).

Based on the Mehlich-3 [P/(Al + Fe)] molar ratios determined for this study, all sites fell within the “below optimum” category for P availability (Beegle et al. 1998; Sims et al. 2002). Ratios at North Fork and nondisked Cedar Run were especially low ($\bar{x} = 0.004$ and $\bar{x} = 0.005$, respectively), whereas those at disked Cedar Run ($\bar{x} = 0.023$) were comparable to those for Huntley Meadows ($\bar{x} = 0.024$). The iN:iP means suggested N limitation for disked Cedar Run and Huntley Meadows ($\bar{x} = 2.5$ and $\bar{x} = 1.2$, respectively) and P limitation for North Fork and nondisked Cedar Run ($\bar{x} = 21.1$ and $\bar{x} = 26.7$, respectively); the distributions were severely skewed, however, and iN:iP medians were below 2, except for North Fork (median = 11.4), where 34% of the iN:iP values (15/44) were higher than 16, evenly distributed among sites.

The ranges of Mehlich-3 extractable macronutrient concentrations were 29–3,800 $\mu\text{g Ca/g}$, 10–427 $\mu\text{g Mg/g}$, and 0.1–32 $\mu\text{g K/g}$. Mean concentrations differed among wetland types for Ca ($F_{[2,6,4]} = 14.02, p = 0.005$; Fig. 2) and Mg ($F_{[3,8,1]} = 11.44, p = 0.003$; Fig. 2) but not for K ($F_{[3,8,4]} = 0.577, p = 0.65$; Fig. 2). Concentrations of Mg were significantly lower in the disked compared to nondisked Cedar Run sites (Fig. 2). Micronutrient concentrations ranged from 26 to 487 $\mu\text{g Fe/g}$ and from 8 to 247 $\mu\text{g Mn/g}$. Mean Fe concentrations were higher for natural than for created wetlands and also higher for disked than nondisked created wetlands ($F_{[3,8,6]} = 7.16, p = 0.010$; Fig. 2); mean Mn concentrations were higher for created than for natural wetlands, but similarly higher for disked than for nondisked created wetlands ($F_{[3,8,7]} = 19.11, p < 0.001$; Fig. 2). No significant mean difference among sites was apparent for Mehlich-3 extractable Al, which ranged from 80 to 770 $\mu\text{g/g}$.

The Levene test indicated inequality of variance for all but three of the measured soil parameters (Table 4); consequently, the *p* values of the ANOVA/ANCOVA comparisons ($\alpha = 0.05$) should be understood as non-conservative (ANOVA/ANCOVA is fairly robust to violations of the homogeneity of variance assumption, however, and *p* values were generally well below α). Neither created (disked/nondisked) nor natural wetlands had consistently higher or lower variance, but nondisked variances were consistently the lowest (Table 4).

Numerous significant intercorrelations were apparent among the soil nutrient parameters (Table 2). Strong correlations existed between C and N, extractable total P and orthophosphate-P, and extractable Fe and P (both total P and orthophosphate-P). Correlations with microtopographic parameters were very weak and only evident for

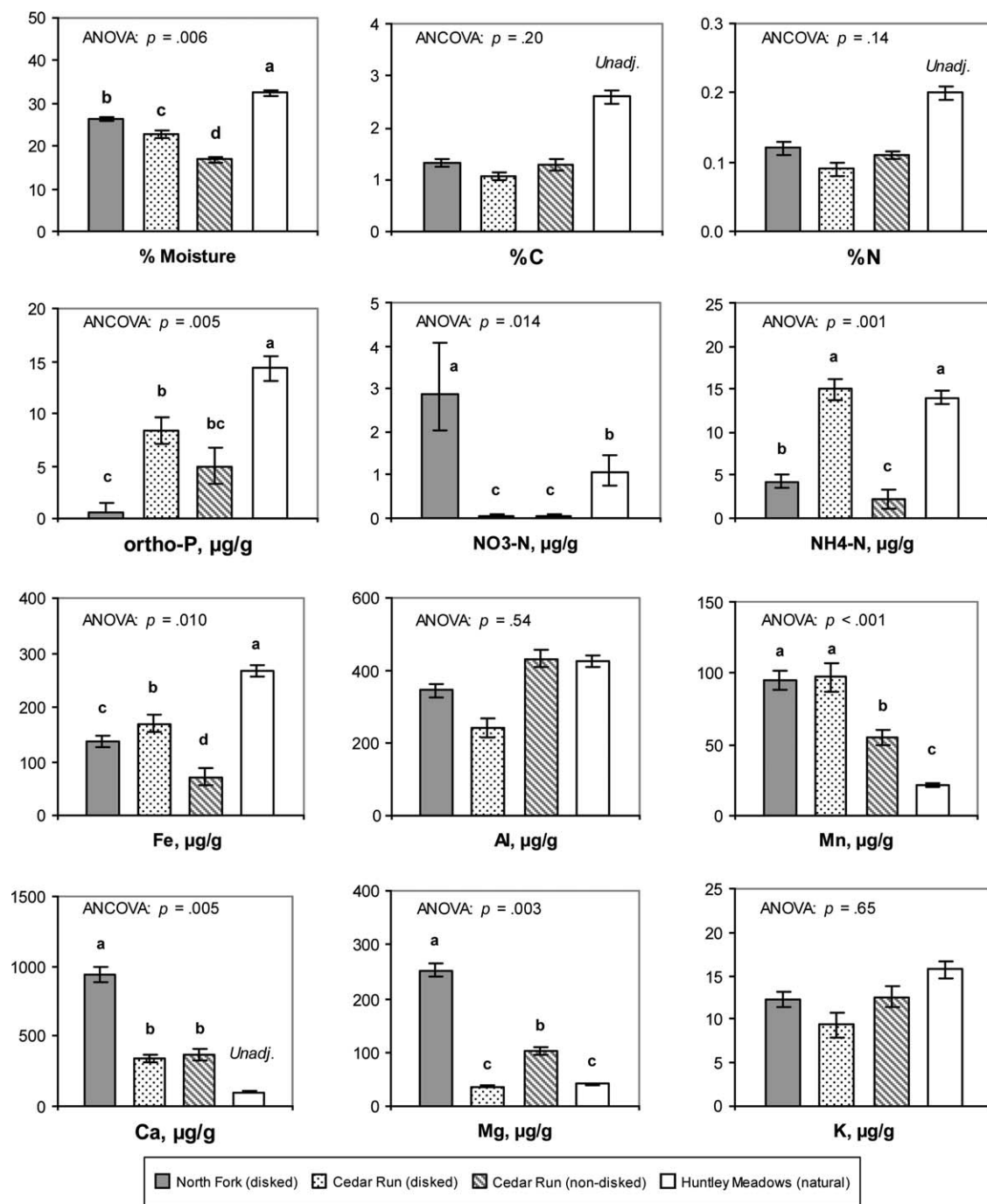


Figure 2. Comparison of group mean values (modified population mean) for nutrient parameters. Log-transformed variables Ca, Mg, Mn, and NO₃-N are reported in original units. Means provided for C%, N%, Ca, P, and ortho-P are moisture adjusted, except where otherwise indicated. Error bars represent ± 1 SE.

K, Mn, Al, and soil moisture. Extractable K and Al were lower and Mn was greater, with increasing pT.

PCA of the nutrient data identified three components with eigenvalues greater than 1 (4.6, 2.3, and 1.5), the first two of which accounted for 63% of the nutrient variability. Explaining 41% of the variability, PCA component 1 had highest factor loadings for orthophosphate-P (0.396),

NH₄-N (0.339), and Fe (0.383) and a high negative loading for Ca (-0.358). Component 2 accounted for 21% of the nutrient variability, with highest component loadings for Mg (0.469) and NO₃-N (0.397) but also a fairly high loading for Ca (0.339). Although the first component axis clearly separates the created from the natural wetlands, with higher component scores for the latter, the second

Table 3. ANCOVA adjustment of means for moisture content.

	<i>North Fork (Disked)</i>		<i>Cedar Run (Disked)</i>		<i>Cedar Run (Nondisked)</i>		<i>Huntley Meadows (Natural)</i>		<i>p</i>
	<i>Unadjusted</i>	<i>Adjusted</i>	<i>Unadjusted</i>	<i>Adjusted</i>	<i>Unadjusted</i>	<i>Adjusted</i>	<i>Unadjusted</i>	<i>Adjusted</i>	
C (%)	1.59	1.31	1.00	1.06	0.67	1.27	2.60	na	<0.001
N (%)	0.14	0.12	0.09	0.09	0.07	0.11	0.20	na	<0.001
P (µg/g)	2.2	2.1	7.5	8.6	3.0	6.1	17.0	15.0	0.009
ortho-P (µg/g)	0.7	0.6	7.2	8.4	1.7	5.0	16.3	14.3	0.011
Ca (µg/g)	846	944	344	337	464	369	101	na	0.004

Values given are unadjusted and adjusted means and *p* value for significance of covariate. na, not adjusted.

component axis mainly distinguishes the two created wetland locations, with higher component scores for North Fork sites than for Cedar Run sites (Fig. 3).

The first PCA factor suggests a gradient from the more mineral soils found in the Piedmont to more organic and comparatively nutrient-rich soil of the Coastal Plain (Fig. 3, note also that the two Huntley Meadows wetland groups have similar spreads, but the older wetland is shifted right). Interpretation of the second component is less clear, especially because the Huntley Meadows sites span the range of component scores, but the created wetlands are clearly separated along the second axis by extractable soil cation concentrations. On either component axis, a broader range is evident for the natural (Huntley Meadows) sites than for any of the created wetlands, and soil total C and N seems to increase along both axes. Though the third component axis accounted for 13% of the nutrient variability, this component axis (not shown) did not strongly differentiate the comparison groups.

Discussion

Created wetlands are commonly located on former agricultural lands and thus tend to have mineral soils that

gradually accumulate organic matter with age; the relatively low ranges of soil total C and N in this study were fairly typical for created wetlands (Stolt et al. 2000; Anderson et al. 2005). Natural wetlands feature comparatively organic soils, suggested in this study by greater soil C and N, and to some extent by greater soil moisture, reflecting lower bulk density and increased pore space. Created wetland soil moisture, C, and N also increased with both disking and age. Higher P and Fe in natural wetlands may reflect the presence of humic-Fe-P complexes, characteristic of more organic soil.

The contrast between the more recently flooded mineral/clay soils of the created wetlands and the comparatively more developed organic sandy soils of the natural wetlands may explain the negative correlations between mineral cation elements (Ca and Mn) and C, N, and P. Chemical properties of the weathering rock substrate may be a source of site differences as well; North Fork, for instance, is geologically associated with extrusive basalt, so higher Ca and Mg should be expected. Greater groundwater connectivity and soil permeability also distinguishes the natural from the created wetland study sites. Thus, soil samples collected during a low-water season at a site with greater groundwater recession might be expected to have

Table 4. Summary of multiple comparison groupings for equality of variance ($\alpha = 0.05$, Bonferroni adjusted).

	<i>Levene's Test for Equality of Variance</i>				<i>North Fork (Disked)</i>	<i>Cedar Run (Disked)</i>	<i>Cedar Run (Nondisked)</i>	<i>Huntley Meadows (Natural)</i>
	<i>df1</i>	<i>df2</i>	<i>F</i>	<i>p</i>				
Moisture	11	150	5.63	<0.001	B	B	C	A
Total C*	7	97	1.91	0.077	—	—	—	*
Total N*	7	97	2.62	0.016	—	—	—	*
NO ₃ -N	11	147	9.70	<0.001	A	C	C	B
NH ₄ -N	11	147	13.87	<0.001	C	A	D	B
Total P (ICP)	11	149	4.09	<0.001	C	A	BC	AB
o-P (colorimetry)	11	149	7.16	<0.001	B	A	B	A
K	11	149	2.61	0.005	A	A	AB	B
Ca*	7	98	1.16	0.33	—	—	—	*
Mg	11	149	2.40	0.009	A	AB	AB	B
Mn	11	149	0.61	0.82	—	—	—	—
Fe	11	149	4.56	<0.001	B	A	C	AB
Al	11	149	2.85	0.002	B	AB	B	A

Groups sharing the same letter within a row are statistically indistinguishable (A, highest variance; D, lowest). Overall test for total N was significant ($\alpha = 0.05$), but multiple comparisons were not. Asterisks indicate exclusion of sites from ANCOVA and associated Levene's test.

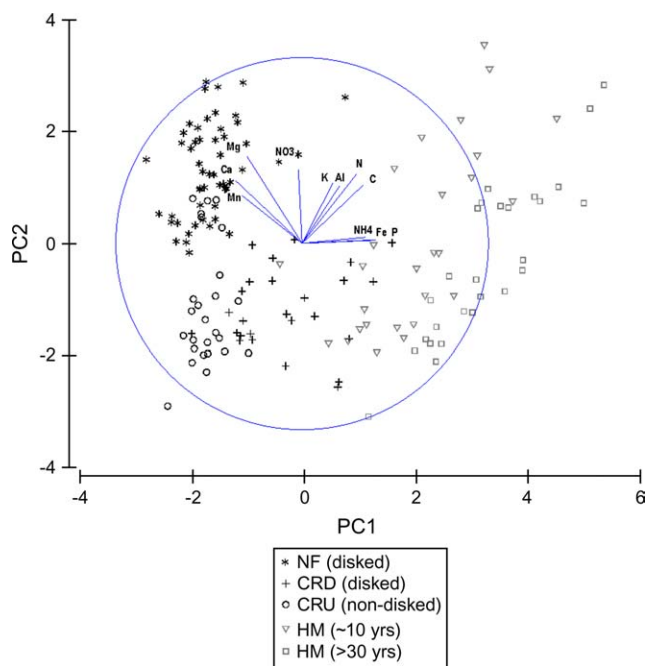


Figure 3. PCA ordination of normalized nutrient data, first two component axes.

diminished quantities of soluble nutrients as was observed for Ca, Mg, and Mn at Huntley Meadows. Current and prior land use may also be a factor; the agricultural/pastoral rural setting of the created wetland sites may promote nutrient depletion, whereas Huntley Meadows' urbanized setting may contribute nutrients to the wetland.

Due to cultivation and chemical soil amendments, agricultural lands tend to lack nutrient heterogeneity. The low microtopographic relief ordinarily imparted by wetland creation practices further imposes uniformity of soil conditions. Such conditions were apparent from low variances in nutrient concentrations and comparatively low microtopographic index values for nondisked sites but not for the (disked) created wetlands generally. The PCA ordination suggests that two of the created wetlands (North Fork, all of which was disked, and nondisked Cedar Run) had less nutrient variability than natural wetlands, evident from the relative spread of points for each study location along the first two component axes. The variability within the disked Cedar Run wetland, however, was more comparable to that of the natural wetland.

Significant inequalities of variance were observed for inorganic N, orthophosphate-P, and K, nutrients that are critical for plant growth. Although it is difficult to make a fair comparison between the created and the natural wetlands based on gravimetric determinations of nutrient concentrations (Wheeler et al. 1992; Bridgman et al. 1998), it is worth noting that the variances of disked wetlands compared favorably with those of the natural wetlands. Nondisked wetlands had comparatively low variance, supporting the contention that nutrients are

spatially homogeneous in microtopographically homogeneous created wetlands (Bruland et al. 2006).

The contrast between disked and nondisked created wetlands at Cedar Run is striking, given their shared setting and conditions. Although of the same age, disked sites had higher moisture content than nondisked, possibly attributable to increased storage in soil voids or to increased depression storage. The microrelief induced by disking also appears to enhance availability of certain nutrients as well as nutrient variability. The disked Cedar Run sites had higher Mehlich-3 extractable Fe and Mn and much (7 \times) higher $\text{NH}_4\text{-N}$ than the nondisked sites, even though total soil N was comparable. The latter may indicate increased prevalence of nitrogen mineralization relative to nitrification, as might be expected when anaerobic conditions predominate due to greater soil moisture, or it might indicate better nutrient retention. However, it could be a consequence of soil inversion and consequent exposure of previously unavailable organic N substrate to microbial activity, particularly because disking was recent, within a year (Silgram & Shepherd 1999; Calderon & Jackson 2002).

The range of Mehlich-3 extractable P was somewhat lower than values reported for other created freshwater wetlands (Anderson et al. 2005). Available P was low or very low for created wetlands and low to medium for natural wetlands (Tisdale 1993; Sims et al. 2002). North Fork, in particular, had very low P concentrations (moisture-adjusted $\bar{x} = 0.6 \mu\text{g}$ ortho-P/g) and iN:iP ratios suggesting P limitation. In this study, the iN:iP and $[\text{P}/(\text{Al} + \text{Fe})]$ ratios reflect soil conditions at peak growth, when a great extent of P cycling within the system might be expected to be in living plant material, as opposed to in the soil. However, low P availability and/or P limitation at this time could affect the growth of late season-developing plants (Boeye et al. 1999).

The intercorrelations among total C and N and P and Fe (and to a lesser extent Al) suggested the importance of humic-metal complexes with adsorbed P, potential sources of P for plant uptake. This result accords with other studies associating extractable Al and Fe with soil organic content (Axt & Walbridge 1999; Darke & Walbridge 2000). Because Fe appears to play a role in P availability, the significant differences in Fe group variances take on greater importance than the somewhat less definitive differences in Al group variances. Although orthophosphate-P did not differ between disked and nondisked created wetlands, mean differences in Fe may be important both because P limitation was implicated and because P availability influences plant community composition (Güsewell & Koerselman 2002).

Differences in $\text{NH}_4\text{-N}$ are also important, as this form of N is readily available to plants, and N is commonly limiting (or co-limiting) in freshwater wetlands (Bedford et al. 1999). At very low nutrient levels, vegetation diversity is likely to decline (Tilman 1997; Güsewell et al. 2005), so to the extent that disking enhances retention and

variability of nutrients, it is likely to promote diversity as well as productivity during early ecosystem development; moreover, nutrient heterogeneity may also reduce competitive exclusion (Tilman 1997). The concomitant plant and functional diversity may enhance ecosystem stability and resilience (Tilman 1996; Loreau 2000).

Explanatory mechanisms were not strongly evident from the study data. The correlation between moisture content and pLD confirmed our expectations based on the utility of limiting elevation difference in predicting depression storage (Kamphorst et al. 2000); it also comports well with the empirical observation that sites with greater microtopographic relief were often associated with the presence and persistence of standing water. If Fe concentrations are attributable to the microtopographic effects of disking, the results are consistent with net upward translocation of Fe and P from reducing to oxidizing soil layers (Fiedler et al. 2004). However, relative elevation correlated with neither Fe nor P, in contradiction. It has been suggested that upward transport of Fe and P is limited to recycling within the top 30 cm of soil (Hunt et al. 1997). As such, the effect of soil inversion by disking would not be expected to increase Fe or P. A possible explanation is that more pronounced flooding in the disked soils leads to development of poorly crystalline hydroxides of iron that are more easily extracted and enhanced release of phosphate to solution (Patrick & Khalid 1974; Gambrell & Patrick 1978); indeed, some evidence suggests that Fe is less crystalline in microlows than in microhighs (Darke & Walbridge 2000). Alternatively, disked microtopography may simply prevent leaching of Fe to soil layers below the root zone and runoff-induced loss.

Conclusions

Though disking clearly provides microtopographic variability not otherwise evident in created wetlands, it does so at a specific scale, with vertical relief on the order of that shown to promote floristic diversity in controlled experiments (Vivian-Smith 1997). Measured as tortuosity or as limiting elevation difference, this effect was apparent at all the spatial extents (i.e., transect scales) in the companion study (Moser et al. 2007). Consequently, though disking promotes microtopographic heterogeneity evident at small spatial extents, it nonetheless represents topographic uniformity when considered at the full spatial extent of a created wetland. Disking-induced microtopography is thus qualitatively different from excavated hummocks/hollows, which provide greater topographic relief in distinct locations. Because disking covers a wide area, its effects apply broadly, whereas hummock/hollow topography yields localized benefits (e.g., pools, patches of vegetation).

A number of soil characteristics associated with disked microtopography are beneficial in wetland mitigation. Increased soil moisture with increasing microrelief suggests that microtopography enhances wetland hydrology, a legal and functional mitigation success criterion, and

resulting anaerobic conditions may increase the prevalence of wetland plants. Increased variability of soil nutrients and hydrologic conditions are expected to promote plant diversity by catering to a wider spectrum of plant capabilities and demands. In terms of functional replacement of lost wetlands, the enhanced soil development and nutrient variability should promote a greater complexity of processes and interactions than might be supported by more typical wetland creation methods. As a relatively low-cost method to establish microtopography in mitigation wetlands, disking is recommended, though it should not preclude other methods of inducing microtopography.

Implications for Practice

- In contrast to natural wetlands that are intended to replace, created mitigation wetlands are often characterized by uniformity of soil conditions, including hydrology, nutrients, and microtopography.
- Created wetlands may be disked to establish microtopographic variability, affecting the distribution of nutrients as well as the frequency and duration of flooding, creating heterogeneous soil conditions comparable to those in natural wetlands.
- Disking also appears to increase retention of soil nutrients and moisture, enhancing accumulation of organic material and promoting the development of organic soils from the mineral soils typically used to create mitigation wetlands.
- Disking-induced microtopography may help ensure that created mitigation wetlands adequately replace lost wetland functions as well as meet criteria for legal mitigation success.

Acknowledgments

The authors gratefully acknowledge the efforts of R. Andrews and S. Coleman in surveying and sample/data collection, as well as the help of J. O'Reilly, M. Doughten, and D. Hogan in lab analyses. For site access, map data, and guidance, thanks to D. Lawlor and G. Roisum of the Fairfax County Park Authority and L. Giese, F. Graziano, and M. Rolband of Wetland Studies and Solutions, Inc. We also thank two anonymous reviewers for suggested improvements to the original manuscript. The study was supported by Wetland Studies and Solutions, Inc., the Cosmos Club Foundation of Washington, D.C., and 2006 NIWR/USGS National Competitive Grant Program (06HQGR0189).

LITERATURE CITED

- Aldous, A., P. McCormick, C. Ferguson, S. Graham, and C. Craft. 2005. Hydrologic regime controls soil phosphorus fluxes in restoration and undisturbed wetlands. *Restoration Ecology* 13:341–347.

- Anderson, C. J., W. J. Mitsch, and R. W. Nairn. 2005. Temporal and spatial development of surface soil conditions at two created riverine marshes. *Journal of Environmental Quality* **34**:2072–2081.
- Axt, J. R., and M. R. Walbridge. 1999. Phosphate removal capacity of palustrine forested wetlands and adjacent uplands in Virginia. *Soil Science Society of America Journal* **63**:1019–1031.
- Baldwin, D. S., and A. M. Mitchell. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. *Regulated Rivers: Research & Management* **16**:457–467.
- Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology* **80**:2151–2169.
- Beegle, D. B., A. N. Sharpley, and D. Graetz. 1998. Interpreting soil test phosphorus for environmental purposes. Pages 22–40 in J. T. Sims, editor. *Soil testing for phosphorus: environmental uses and implications*. Southern Cooperative Series Bulletin No. 389. University of Delaware, Newark.
- Boeye, D., B. Verhagen, V. Van Haesebroeck, and M. El-Kahloun. 1999. Phosphorus fertilization in a phosphorus-limited fen: effects of timing. *Applied Vegetation Science* **2**:71–78.
- Boutin, C., and P. A. Keddy. 1993. A functional classification of wetland plants. *Journal of Vegetation Science* **4**:591–600.
- Bridgham, S. D., K. Updegraff, and J. Pastor. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* **79**:1545–1561.
- Bruland, G. L., and C. J. Richardson. 2005. Hydrologic, edaphic, and vegetative responses to microtopographic reestablishment in a restored wetland. *Restoration Ecology* **13**:515–523.
- Bruland, G. L., C. J. Richardson, and S. C. Whalen. 2006. Spatial variability of denitrification potential and related soil properties in created, restored, and paired natural wetlands. *Wetlands* **26**:1042–1056.
- Calderon, F. J., and L. E. Jackson. 2002. Rototillage, disking, and subsequent irrigation: effects on soil nitrogen dynamics, microbial biomass, and carbon dioxide efflux. *Journal of Environmental Quality* **31**:752–758.
- Crick, J. C., and J. P. Grime. 1987. Morphological plasticity and mineral nutrient capture in 2 herbaceous species of contrasted ecology. *New Phytologist* **107**:403–414.
- Darke, A. K., and M. R. Walbridge. 2000. Al and Fe biogeochemistry in a floodplain forest: implications for P retention. *Biogeochemistry* **51**:1–32.
- Fiedler, S., D. Wagner, L. Kutzbach, and E. M. Pfeiffer. 2004. Element redistribution along hydraulic and redox gradients of low-centered polygons, Lena Delta, northern Siberia. *Soil Science Society of America Journal* **68**:1002–1011.
- Gambrell, R. P., and W. H. Patrick Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. Pages 375–423 in D. D. Hook and R. M. M. Crawford, editors. *Plant life in anaerobic environments*. Ann Arbor Science Publishers, Ann Arbor, Michigan.
- Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**:259–281.
- Güsewell, S., K. M. Bailey, W. J. Roem, and B. L. Bedford. 2005. Nutrient limitation and botanical diversity in wetlands: can fertilisation raise species richness? *Oikos* **109**:71–80.
- Güsewell, S., and M. Koerselman. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspectives in Plant Ecology Evolution and Systematics* **5**:37–61.
- Hinsinger, P. 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* **237**:173–195.
- Hooper, D. U., M. Solan, A. Symstad, S. Diaz, M. O. Gessner, N. Buchmann, et al. 2002. Species diversity, functional diversity, and ecosystem functioning. Pages 195–208 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, United Kingdom.
- Hunt, R. J., D. P. Krabbenhoft, and M. P. Anderson. 1997. Assessing hydrochemical heterogeneity in natural and constructed wetlands. *Biogeochemistry* **39**:271–293.
- Kamphorst, E. C., V. Jetten, J. Guerif, J. Pitkanen, B. V. Iversen, J. T. Douglas, and A. Paz. 2000. Predicting depression storage from soil surface roughness. *Soil Science Society of America Journal* **64**:1749–1758.
- Karlin, E. F., and L. C. Bliss. 1984. Variation in substrate chemistry along microtopographical and water-chemistry gradients in peatlands. *Canadian Journal of Botany* **62**:142–153.
- Kleinman, P. J. A., and A. N. Sharpley. 2002. Estimating soil phosphorus sorption saturation from Mehlich-3 data. *Communications in Soil Science and Plant Analysis* **33**:1825–1839.
- Koerselman, W., and A. F. M. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* **33**:1441–1450.
- Kozłowski, T. T. 1984. Plant responses to flooding of soil. *Bioscience* **34**:162–167.
- Larkin, D., G. Vivian-Smith, and J. B. Zedler. 2006. Topographic heterogeneity theory and ecological restoration. Pages 142–164 in D. A. Falk, M. A. Palmer, and J. B. Zedler, editors. *Foundations of restoration ecology*. Island Press, Washington, D.C.
- Linden, D. R., and D. M. Van Doren. 1986. Parameters for characterizing tillage-induced soil surface-roughness. *Soil Science Society of America Journal* **50**:1560–1565.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**:3–17.
- McJannet, C. L., P. A. Keddy, and F. R. Pick. 1995. Nitrogen and phosphorus tissue concentrations in 41 wetland plants—a comparison across habitats and functional groups. *Functional Ecology* **9**:231–238.
- Mehlich, A. 1984. Mehlich-3 soil test extractant—a modification of Mehlich-2 extractant. *Communications in Soil Science and Plant Analysis* **15**:1409–1416.
- Moser, K. F., C. Ahn, and G. B. Noe. 2007. Characterization of microtopography and its influence on vegetation patterns in created wetlands. *Wetlands* **27**:1081–1097.
- Mulvaney, R. L. 1996. Nitrogen—inorganic forms. Pages 1123–1184 in D. L. Sparks, editor. *Methods of soil analysis. Part 3. Chemical methods*. Soil Science Society of America, American Society of Agronomy, Madison, Wisconsin.
- National Research Council. 2001. *Compensating for wetland losses under the Clean Water Act*. National Academy Press, Washington, D.C.
- Patrick, W. H. Jr, and R. A. Khalid. 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science* **186**:53–55.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* **79**:94–105.
- PRIMER-E Ltd. 2006. PRIMER v6.1. PRIMER-E Ltd., Plymouth, United Kingdom.
- Richardson, C. J. 1985. Mechanisms controlling phosphorus retention capacity in freshwater wetlands. *Science* **228**:1424–1427.
- Silgram, M., and M. A. Shepherd. 1999. The effects of cultivation on soil nitrogen mineralization. Pages 267–311 in *Advances in agronomy, vol. 65*. Academic Press, Inc., San Diego, California.
- Sims, J. T., R. O. Maguire, A. B. Leytem, K. L. Gartley, and M. C. Pautler. 2002. Evaluation of Mehlich 3 as an agri-environmental soil phosphorus test for the Mid-Atlantic United States of America. *Soil Science Society of America Journal* **66**:2016–2032.
- Spieles, D. J. 2005. Vegetation development in created, restored, and enhanced mitigation wetland banks of the United States. *Wetlands* **25**:51–63.
- SPSS, Inc. 2004. SPSS 13.0 for windows graduate student version. SPSS, Inc., Chicago, Illinois.

- Stoeckel, D. M., and M. S. Miller-Goodman. 2001. Seasonal nutrient dynamics of forested floodplain soil influenced by microtopography and depth. *Soil Science Society of America Journal* **65**:922–931.
- Stolt, M. H., M. H. Genthner, W. L. Daniels, V. A. Groover, S. Nagle, and K. C. Haering. 2000. Comparison of soil and other environmental conditions in constructed and adjacent palustrine reference wetlands. *Wetlands* **20**:671–683.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350–363.
- Tilman, D. 1997. Mechanisms of plant competition. Pages 239–261 in M. J. Crawley, editor. *Plant ecology*. 2nd edition. Blackwell Science, Inc., Cambridge, Massachusetts.
- Tisdale, S. L. 1993. *Soil fertility and fertilizers*. 5th edition. Prentice Hall, Upper Saddle River, New Jersey.
- Tweedy, K. L., E. Scherrer, R. O. Evans, and T. H. Shear. 2001. Influence of microtopography on restored hydrology and other wetland functions (Meeting Paper No. 01-2061) in 2001. American Society of Agricultural Engineers Annual International Meeting. ASAE, St. Joseph, Michigan.
- Vivian-Smith, G. 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *Journal of Ecology* **85**:71–82.
- Wassen, M. J., H. G. M. Olde Venterink, and E. O. A. M. de Swart. 1995. Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *Journal of Vegetation Science* **6**:5–16.
- Wheeler, B. D., S. C. Shaw, and R. E. D. Cook. 1992. Phytometric assessment of the fertility of undrained rich-fen soils. *Journal of Applied Ecology* **29**:466–475.