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CHARACTERIZATION OF MICROTOPOGRAPHY AND ITS INFLUENCE ON VEGETATION PATTERNS IN CREATED WETLANDS

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Abstract: Created wetlands are increasingly used to mitigate wetland loss. Thus, identifying wetland creation methods that enhance ecosystem development might increase the likelihood of mitigation success. Noting that the microtopographic variation found in natural wetland settings may not commonly be found in created wetlands, this study explores relationships between induced microtopography, hydrology, and plant species richness/diversity in non-tidal freshwater wetlands, comparing results from two created wetland complexes with those from a mature reference wetland complex in northern Virginia. Elevation, steel rod oxidation depth, and species cover were measured along replicate multiscale (0.5 m-, 1 m-, 2 m-, and 4 m-diameter) tangentially conjoined circular transects in each wetland. Microtopography was surveyed using a total station and results used to derive three roughness indices: tortuosity, limiting slope, and limiting elevation difference. Steel rod oxidation depth was used to estimate water table depth, with data collected four times during the growing season for each study site. Plant species cover was estimated visually in 0.2 m^2 plots surveyed at peak growth and used to assess species richness, diversity, and wetland prevalence index. Differences in each attribute were examined among disked and non-disked created wetlands and compared to a natural wetland as a reference. Disked and non-disked created wetlands differed in microtopography, both in terms of limiting elevation difference and tortuosity. However, both were within the range of microtopography encompassed by natural wetlands. Disked wetlands supported higher plant diversity and species richness than either natural or non-disked wetlands, as well as greater within-site species assemblage variability than non-disked wetlands. Irrespective of creation method, plant diversity in created wetlands was correlated with tortuosity and limiting elevation difference, similar to correlations observed for natural wetlands. Vegetation was more hydrophytic at disked sites than at non-disked sites, and of equivalent wetland indicator status to natural sites, even though all sites appeared comparable in terms of hydrology. Results suggest that disking may enhance vegetation community development, thus better supporting the goals of wetland mitigation.

Key Words: biodiversity, disking, species richness, surface roughness, wetland creation, wetland mitigation

INTRODUCTION

Microtopography, loosely defined as topographic variability on the scale of individual plants (Huenneke and Sharitz 1986, Titus 1990, Bledsoe and Shear 2000), describes soil surface variation within an elevation range from roughly one centimeter to as much as one meter, encompassing both vertical relief and surface roughness. Microtopography is included in the broader notion of topographic heterogeneity, which includes patterns of elevation at many spatial scales formed by geologic, hydrologic, physical, and biological processes (Larkin et al. 2006). Microtopography can influence wetland hydrology, physicochemistry, and habitat variability, and it is thus important in determining vegetation patterns and, ultimately, ecosystem function. Consequently, the manipulation of microtopography to promote plant community and ecosystem development has implications for wetland creation and restoration.

Created wetlands often show little evidence of ecosystem development comparable to that of their natural counterparts, and many wetlands created to mitigate wetland losses fail to meet basic success criteria within the time frame legally mandated for monitoring (National Research Council 2001, Spieles 2005). Although the legal framework may be insufficient to ensure that mitigation wetlands perform equivalent function to the wetlands they replace, identifying wetland creation methods that enhance ecosystem development might increase the probability of mitigation success, both legal and functional, thus increasing the likelihood that lost wetland ecosystem services will, in fact, be replaced. In the construction of mitigation wetlands, grading is ordinarily performed to assure surface variation within a centimeter or two of the site plan elevation, so the microtopographic variability more typical of natural settings is reduced (Stolt et al. 2000). Although not legally mandated, microtopography is sometimes adopted as a performance/monitoring criterion in compensatory mitigation since it is understood to promote floral and faunal diversity (Norfolk District Army Corps of Engineers and Virginia Department of Environmental Quality 2004). Thus, microtopography is sometimes intentionally induced after wetland creation or restoration by a variety of techniques, including bucket-mounding, hand-mounding, tire-rutting, and disking (or disk-harrowing).

Microtopographic relief affects the proximate hydrologic conditions experienced by an individual seed or plant (Pollock et al. 1998, Bledsoe and Shear 2000), but it may also affect wetland hydrology more broadly. Under conditions of standing water, microtopographic features may cause increased flow resistance (Harvey et al. 2003). The implication that increased microtopography enhances water retention in a wetland is supported by field experiments in which disked wetland restoration plots had higher water retention and higher water table levels than non-disked plots, whether for above or belowground water table conditions (Tweedy et al. 2001). Thus, roughing the surface (as by disking) may help in restoring wetland hydrology to agricultural lands, and it has been proposed as a way to reduce the amount of seeding needed (Bledsoe and Shear 2000).

Topographic heterogeneity on the scale of a few centimeters in relief has been shown to promote species richness and abundance in experimental wetland mesocosms (Vivian-Smith 1997). Surface variation on a similar scale also promoted differential germination of species in prepared-bed and pot experiments (Harper et al. 1965). Studies of woody seedling distributions support the importance of microtopography in determining wetland plant species distribution, with preferential establishment of species and of growth forms (tree, shrub, vine) dependent on microtopographic setting (Collins et al. 1982, Huenneke and Sharitz 1986, Titus 1990). Furthermore, sedimentation has been linked to reductions in plant species richness through the loss of microtopographic features associated with *Carex* tussocks (Werner and Zedler 2002). Generally stated, processes explaining the effects of microtopography on wetland plant community structure may include: 1) water retention, 2) microsite variations in extent and frequency of inundation due to elevation, 3) propagule dispersal, 4) microsite variations in habitat (e.g., soil physicochemical properties, temperature, light penetration), 5) protection from erosion/deposition, and 6) increased surface area and exposure of soil to the atmosphere.

Because ecological phenomena may only be apparent at certain scales, it is important to recognize the significance of experimental scale; the notion of "micro"-topography itself demands that scale be considered. A proper investigation takes into account the *extent* (overall area of study) and *grain* of the study (i.e., *resolution*, the unit size of individual study plots), attempting to ensure that experimental results are not skewed by these scale-determining factors (Wiens 1989, Reed et al. 1993, Stohlgren et al. 1997). Only a few examples of multiscale microtopography studies have been published (Pollock et al. 1998, Morzaria-Luna et al. 2004), and these suggest that while there is greater variability at smaller scales, microtopographic effects are evident and consistent across scales from 0.1–1000 m^2.

Most ecological studies have categorized microtopography qualitatively with descriptors such as mound/pit or hummock/hollow/flat (Huenneke and Sharitz 1986, Paratley and Fahey 1986, Titus 1990, Bruland and Richardson 2005). Microtopography is difficult to measure and quantify, however, as it encompasses and combines elements of surface relief and surface roughness. Relief is the vertical extent of a topographic profile, whereas roughness is the extent of topographic variability (as opposed to smoothness), although the term roughness is also commonly used to refer to the combination of relief and roughness (Figure 1). Although relief can be measured and its variance quantified (Allmaras et al. 1966), it is an incomplete descriptor. Agricultural tillage studies have approached the quantification of topography formally, often in the context of erosion or depression storage, and typically at the clod or crumb scale (Romkens and Wang 1986, 1987, Potter and Zobeck 1990, Potter et al. 1990, Saleh 1993, Hansen et al. 1999, Kamphorst et al. 2000).

This study examined the effects of artificially induced microtopography on hydrologic conditions and vegetation patterns in non-tidal freshwater mitigation wetlands, with the goal of informing wetland creation practices. Several index measures were employed to quantify microtopography and separate out components of roughness and relief. A

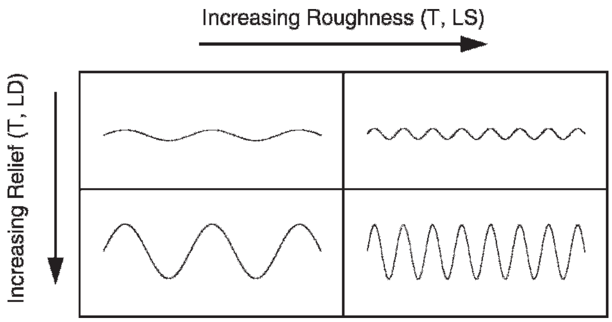

Figure 1. Basic illustration of the distinction between roughness and relief, represented as hypothetical surface cross-sectional profiles. As roughness increases, so do the index measures tortuosity (T) and limiting slope (LS). As relief increases so do tortuosity and limiting elevation difference (LD).

natural wetland was examined as a comparison to address how microtopography differs between created and natural wetlands. Our research hypotheses were: 1) that created and natural wetlands differ quantitatively in terms of microtopography, and that disked wetlands have greater microtopography than non-disked; 2) that increased microtopography is associated with a higher water table, and consequently with more hydrophytic vegetation; and 3) that increased microtopography is associated with greater species richness, diversity, and cover of vegetation, in both created and natural wetlands. Since disking is a method which can be used to rapidly and widely induce microtopography, the comparison of disked to non-disked created wetlands was of particular interest. Due to increased microtopography, disked wetlands were expected to have greater species richness, diversity, and plant cover, and a higher water table, than non-disked wetlands.

METHODS

Site Details

Field research was carried out in summer 2005 at created and natural wetlands in Virginia, USA (mean annual precipitation 1,085 mm, mean annual temperature min 7.0°C / max 19.3°C). Created wetlands were North Fork and Cedar Run mitigation banks in Prince William County; natural wetlands were at Huntley Meadows Park in Fairfax County (Figure 2). 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 north of the marker.

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 are in the Coastal Plain province, comparatively flat and underlain by unconsolidated sediment. North Fork Mitigation Wetland is a 125-acre wetland complex created on land formerly used as cattle pasture, graded in 1999–2000, and hydroseeded in fall 2000 and spring 2001. Study sites were located in the "Main Pod," surrounding an open water area fed by the North Fork of Broad Run, with vegetation in its fifth growing season (sites A, B, C, and D). Cedar Run Mitigation Bank is a 610-acre multiple-wetland complex developed on land formerly used for agriculture. Study sites E and F were located in Cedar Run 1, a 67-acre wetland created/graded in 2004, while sites G and H were in a portion of a smaller adjacent mitigation wetland which was graded in 2004; sites E, F, G, and H were hydroseeded in fall 2004, and were thus in their first growing season. While the mitigation projects at North Fork and Cedar Run sites E and F were disked prior to seeding to provide a more heterogeneous soil surface, the mitigation project at Cedar Run sites G and H was not. Owing to incomplete availability of data, direct comparison of the seed mixes actually used in the created wetlands was not possible. However, these wetlands were seeded with commercially available wetland plant seed mixes appropriate for the region and the intended hydrology (e.g., wetland meadow as opposed to obligate wetland). From the information available, these seed mixes would have included ~20 plant species, mostly within the genera *Carex* (Cyperaceae), *Juncus* (Juncaceae), and *Scirpus* (Cyperaceae). The 1,425-acre Huntley Meadows Park prominently features beaver-engineered wetlands, some of which were in existence before the park was established in 1975. Here, study sites J and L were in mature (> 30 years old) wetland, while sites I and K were in wetland adjacent to a more recently established (~10 years old) beaver pond.

Field data were collected throughout the growing season, between May and December. Each site was examined using a set of tangentially conjoined circular transects (hereafter referred to collectively as a *multiscale transect*), with field measurements and samples taken at regular intervals along the circular paths (Figure 3). The circular transect approach designed for this study was intended to be directionally unbiased; any confounding directional effects such as disking orientation, wind, direction of hydrologic flows, and orientation of incident sunlight were minimized. This approach covers a more limited spatial extent than do linear transects, and so reflect more localized conditions.

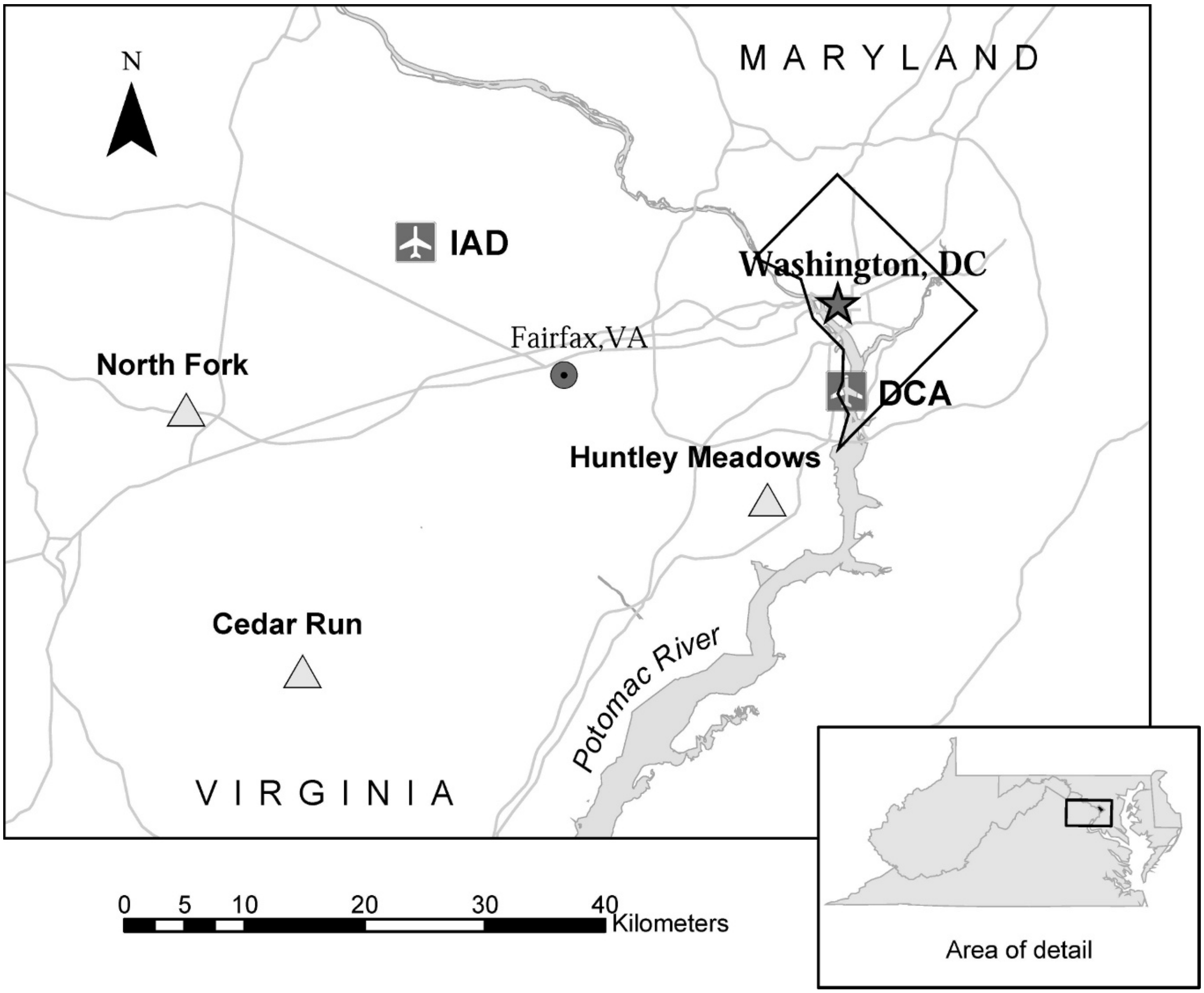

Figure 2. Study location map. Airport weather stations from which precipitation data were collected are also indicated: Reagan Washington National (DCA) and Dulles International (IAD).

Multiple scales were adopted to aid in identifying any scale-dependent effects; transects were laid out as 0.5 m-, 1 m-, 2 m-, and 4 m-diameter circles using crosslinked polyethylene tube hoops.

Microtopography

Field measurement of microtopography consisted of elevation measurements taken using conventional surveying equipment (Sokkia SET4110 total station). At the beginning of the study (between June 23 and July 15), and prior to other measurements, elevations were measured at 10 cm intervals along the 0.5 m-, 1 m-, and 2 m-diameter transects (a total of 108 measurements) at each site and at 20 cm intervals along the 4 m-diameter transect (62 measurements per site) at half the sites in each wetland. Conditions for surveying were generally dry (with soil yielding minimally underfoot), although care was taken not to alter the existing microtopography during elevation measurement; likewise, throughout the study, field work was conducted as much as possible to minimize disturbance of microtopography in the vicinity of the multiscale transects. Coordinate data were recorded to the nearest millimeter, although at the distances used, the total station has nominal sub-millimeter precision for elevation (Sokkia Co. 1997). Measurement intervals were chosen as appropriate to the overall scale of interest (plant-scale), the equipment used (survey rod base diameter of ~6 cm), and the transect sizes.

Microtopography was quantified using three index measures. For a two-dimensional path, such as a cross-sectional elevation profile, the ratio of the

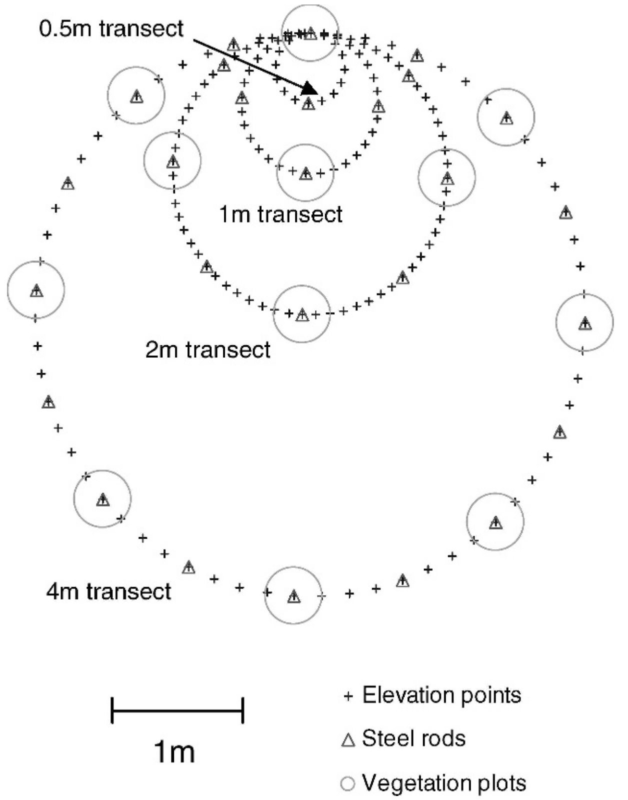

Figure 3. Multiscale circular transects. Elevation data points are at 10 cm intervals (20 cm intervals for the 4 m diameter transects). Steel rod rust depth measurements are at 80 cm intervals. Vegetation plots (0.2 m^2) are at 160 cm intervals.

over-surface distance to the corresponding straight-line path is referred to as "tortuosity" (Kamphorst et al. 2000), and it can either be calculated from elevation data (Werner and Zedler 2002) or measured directly (Saleh 1993, Merrill 1998). This unitless measure is a simple indicator of microtopography, sensitive to changes in both roughness and relief, but incapable of distinguishing a low-relief high-roughness surface (upper-right in Figure 1) from a high-relief low-roughness one (lower left in Figure 1). Although it appears to perform well for measuring the change in soil surface roughness due to rainfall (Bertuzzi et al. 1990), tortuosity is not regarded as a good predictor for depression storage of runoff (Kamphorst et al. 2000). Tortuosity (T) was calculated using elevation data and the known transect lengths. Point-to-point distances were summed for each transect, then divided by the corresponding planar transect distance (Kamphorst et al. 2000). The method used was analogous to that of Werner and Zedler (2002), although the measurement intervals were finer (10–20 cm versus ~1 m) and transects were shorter and circular.

A geostatistical approach using a combination of limiting slope (LS) and limiting elevation difference (LD) was proposed by Linden and Van Doren (1986) to physically characterize soil surfaces. LS and LD are indices derived from the variogram of change in elevation versus the horizontal interval of measurement (lag distance). The LD index (in elevation units, cm in this study) represents the limit of elevation change approached for large intervals, thus expressing relief. It is somewhat comparable to the random roughness index of Allmaras et al. (1966) and can be used to estimate maximum depression storage (Bertuzzi et al. 1990, Kamphorst et al. 2000). The LS index (a unitless metric) represents the rate of change in elevation as the interval between measurements approaches zero, pertaining to microrelief at small sampling intervals (i.e., roughness); in tillage studies it has been correlated with tortuosity and fractal indices (Bertuzzi et al. 1990). LS and LD were adopted to distinguish roughness from relief. LS and LD were determined by mean absolute-elevation-difference analysis of the first-order variogram after correcting for slope (Linden and Van Doren 1986), treating change in elevation as a function of the distance between two points. Slope correction for elevation data was achieved by nonlinear (wave form) regression, with appropriate periodicity (i.e., 2π times the transect radius). The mean absolute elevation difference (ΔZ_h) is defined as

$$\Delta Z_h = \sum_{i=1}^{n} |Z_i - Z_{i+h}| \Big/ n$$

where:

Z_i is the slope-corrected elevation of a given point;
Z_{i+h} is the slope-corrected elevation of a point h intervals from Z_i; and
n is the number of pairs of points used in the calculation.

Linear regression was used to relate ΔZ_h to the lag distance X_h, the horizontal distance between a pair of points h intervals apart, fitting the equation

$$\Delta Z_h = 1/[(b(1/X_h)) + a]$$

and treating $1/\Delta Z_h$ as a function of $1/X_h$. LS and LD were calculated from the fitted-line parameters a and b (LS = $1/b$ and LD = $1/a$). This approach is equivalent to using Lineweaver-Burk (or double-reciprocal) plots to solve for Michaelis-Menten enzyme kinetics constants.

T, LS, and LD indices were calculated for each circular transect. For the LS and LD indices, lag intervals were considered for every point on the circular transect, with intervals continuing past the starting point on the transect as the last points on the transect were reached. Because the lag distances were chord distances, approaching as a limit the transect diameter, those used for regression differed for each scale: for the 0.5 m-diameter transects, three lag distances (10 cm, 20 cm, 30 cm as measured along the transect circle) were used for analysis; for 1 m-diameter transects, five lag distances (10–50 cm) were analyzed; for 2 m-diameter transects, ten lag distances (10–100 cm) were analyzed; and for 4 m-diameter transects, ten lag distances (20–200 cm) were analyzed. Since microtopography might vary within a circular transect, "proximal" values for T, LS, and LD indices were also calculated for each transect point based on near-neighbor points and used to express localized microtopography. These indices were proximal tortuosity (pT), proximal limiting slope (pLS), and proximal limiting elevation difference (pLD); they differ from their full-transect counterparts (T, LS, and LD) in that they are based on a small subset of points, with smaller lag intervals represented by more observations, whereas the full- transect indices were based on a larger set of elevation points with equal counts of elevation differences for each lag interval. Near-neighbor points were treated as those within 0.5 m of the point of interest, except for the case of 4 m transects, where, due to the 20 cm spacing between points, near-neighbor points were treated as within 0.6 m. In determining proximal indices, two guiding principles were applied: first, the points included should not account for more than half the data points in a circular transect; second, lag distances used should not exceed those used for transect-level indices. Consequently, the following lag distances were used: 0.5 m transects: 10–30 cm (measured along the transect circle); 1 m transects: 10–50 cm; 2 m transects: 10–60 cm; and 4 m transects: 20–60 cm. Index calculations were carried out using the mathematics application Maple version 10 (Maplesoft Inc. 2005).

Hydrology

Because installing wells/piezometers would have disrupted the surrounding microtopography, water table depth was estimated using 2.4 mm-gauge (3/32″) steel welding rods (Bridgham et al. 1991). Rods were driven either to refusal or to a depth of approximately 80 cm and spaced at 80 cm intervals (total 28 measurements per multiscale transect; Figure 3). Rods were left in place for a minimum of 4 weeks, then removed and exchanged for new ones. A total of four deployments were performed beginning in June, with the final collections taking place in December. However, because sampling dates were staggered among study wetlands, there were a total of 12 sampling dates. Upon removal, the below-surface depth beyond which no oxidation was apparent was recorded and interpreted as water table depth.

Vegetation

Macrophyte species composition and cover were sampled using 0.2 m^2 circular plots located at 160 cm intervals along each circular transect (Figure 3). Vegetation data were collected from August 23–26, 2005. Species were field-identified (Newcomb 1977, Brown 1979, Tiner et al. 1988) and percent cover visually estimated, with a minimum cover percentage of 1 percent. Visual estimates of less than 15% cover were reported in increments of 1%, while those of 15% or more were reported in 5% increments. Cover was also estimated for non-plant surface features, such as large rocks or logs. Due to multiple herbaceous canopy layers, the sum of species cover estimates could exceed 100%, even when visual estimate of total cover was less than 100%. Species were assigned a wetland indicator category (Reed et al. 1988, Pepin 2000).

Taxon counts for each vegetation plot, including unidentified taxa, were used to determine species richness (S) per plot, and, for multiscale transects, species richness per m^2. For the latter, taxon-sampling curves were used to derive S for $n = 5$ survey plots using EstimateS (Colwell 2005), based on the mean for 50 randomized runs without replacement. To characterize plant diversity, we used the Shannon diversity index (H′), which takes into account both the number of species and their relative abundances, without making assumptions about underlying distributions (Hayek and Buzas 1997, Jørgensen et al. 2005). For this study, H′ was determined based on percent cover, rather than by count of individuals, similar to a method used to evaluate plant community diversity (Mitsch et al. 2005). Natural log Shannon diversity values were calculated for each sample plot and for each multiscale transect using EstimateS (Colwell 2005).

Vegetation plots were assigned a wetland prevalence index (P.I.) value according to the weighted average of indicator ranks, excluding unidentified and non-listed species (Wentworth et al. 1988). Under this classification, each wetland indicator category was assigned a rank value as follows: OBL (obligate wetland) = 1, FACW (facultative wetland) = 2, FAC (facultative) = 3, FACU (facultative upland) = 4, UPL (upland) = 5, with no adjustment for +/− designations. Rank values were weighted according to the associated percent cover, and the weighted ranks were averaged to reach an indicator rank for the sample area, with lower index values corresponding to prevalence of more hydrophytic vegetation. The prevalence index was calculated as:

$$\text{P.I.} = \frac{\Sigma A_i W_i}{\Sigma A_i}$$

where:

A_i = abundance of species i;
W_i = wetland indicator category for species i; and
i = individual species.

Statistical Analysis

Two separate parametric analyses were conducted to compare sites based on creation method (disked, non-disked, natural). First, to address how microtopography differed and to examine issues of scale, full-transect indices (LS, LD, T) were examined. Second, to address how disking relates to vegetation patterns and hydrology, proximal indices (pLS, pLD, pT) were considered in connection with vegetation parameters and steel rod oxidation measurements, using a nested design to partition out variance attributable to site. Two-way multivariate analysis of variance (MANOVA) was used to examine LS, LD, and T for differences attributable to creation method and transect scale (0.5 m, 1 m, 2 m, 4 m) for the combined dependent variable, followed by post-hoc Dunnett's T3 pairwise comparisons. A nested-design two-factor MANOVA (site nested within creation method) was used on the vegetation survey plot data to examine differences among creation methods as to the combined dependent variable of pLS, pLD, pT, H′, S, P.I., percent cover, and steel rod oxidation depth, followed by post-hoc Dunnett's T3 pairwise comparisons. MANOVA analyses were conducted using Type IV sum-of-squares and an alpha level of 0.05 (due to unequal sample sizes, Pillai's Trace was adopted as a more robust alternative to Wilks' Λ), and performed using SPSS (SPSS Inc. 2004). A nested (site nested within creation method) two-factor nonparametric analysis of similarity (ANOSIM) was carried out for species assemblage data ($\alpha = 0.05$). Decomposition of the Bray-Curtis similarity used for ANOSIM was used to characterize within-site similarity and between-site dissimilarity, as well as to express the contributions of individual species to similarity/dissimilarity. ANOSIM and related routines were performed using PRIMER (PRIMER-E Ltd. 2006).

To better conform to the assumptions of MANOVA, appropriate transformations (Osborne 2002) were applied for tortuosity (T and pT, base 10 log), limiting elevation difference (LD and pLD, natural log), and wetland prevalence index (natural log). Multivariate outliers were identified by Mahalanobis distance, using the Chi-square critical value ($p < 0.001$, with df = number of dependent variables) as the criterion for exclusion of outliers from analysis. For ANOSIM of vegetation abundance data, square-root transformation was applied to the data matrix prior to Bray-Curtis ordination in order to downweight the influence of highly abundant species (Clarke and Warwick 2001, Clarke and Gorley 2006). For transformed variables, mean values reported in figures and tables are reported in original untransformed units. Since the relationship between microtopographic indices and vegetation/hydrologic variables was conjectured to be monotonic (but not necessarily linear), and because the study design was observational, correlations were examined using non-parametric Spearman rank correlation coefficients ($\alpha = 0.05$) using untransformed variables, without excluding outliers.

RESULTS

Microtopography

Visual inspection of transect elevation profiles suggested empirically that disked, non-disked, and natural sites were microtopographically distinct (Figure 4), with more pronounced vertical relief evident in disked and natural wetlands than in non-disked wetlands. Circular transect microtopographic index values ranged from 0.06–1.7 for LS (excluding two negative values likely causing the two Mahalanobis outliers), from 0.4–12.4 cm for LD, and from 1.001–1.043 for T (Table 1). The combined dependent variable of LS, LD, and T indices differed among creation methods (Pillai's Trace = 0.460, $F_{6,54} = 2.69$, $p = 0.024$), while there were no significant differences for scale (Pillai's Trace = 0.254, $F_{9,84} = 0.86$, $p = 0.56$). Differences existed for LD ($F_{2,28} = 7.62$, $p = 0.002$) and T ($F_{2,28} = 3.47$, $p = 0.045$) indices, but not for LS ($F_{2,28} = 0.83$, $p = 0.45$). LD was significantly higher for disked ($p = 0.002$) and natural ($p = 0.026$) wetlands than for non-disked wetlands (disked [$\bar{x} = 3.4$] ≈ natural [$\bar{x} = 2.5$] > non-disked [$\bar{x} = 1.2$]). T was also higher for disked than for non-disked wetlands ($p < 0.001$), although neither differed significantly from natural wetlands (disked [$\bar{x} = 1.014$] > non-disked [$\bar{x}$ =

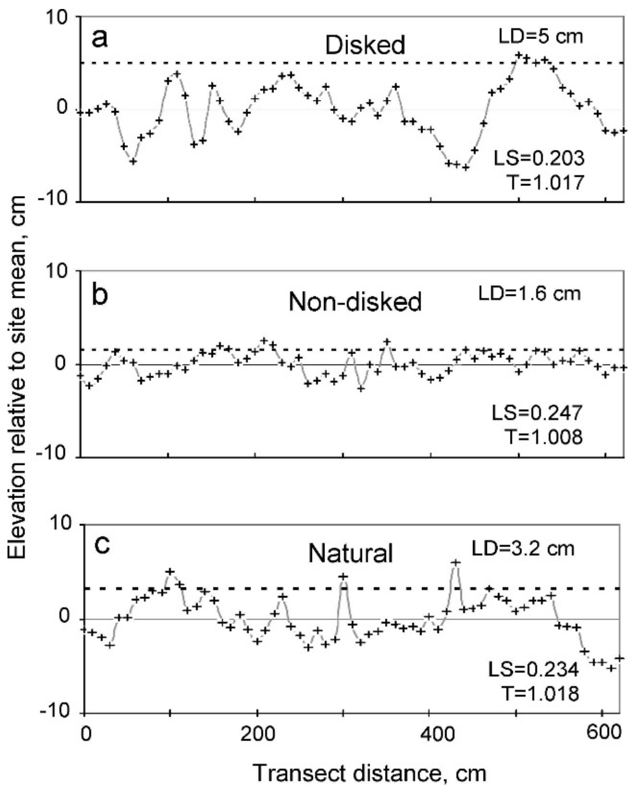

Figure 4. Representative transect elevation profiles for a) disked site F, Cedar Run; b) non-disked site G, Cedar Run; and c) natural site I, Huntley Meadows. Limiting elevation difference (LD) indicated by dashed line. Data and index values for LS, LD, and T are from 2 m-diameter circular transects of overall length 6.2 m.

1.002]; natural [$\bar{x}$ = 1.012]). Excluding the one Mahalanobis outlier (n = 97), the plot-level combined dependent variable also differed among creation methods (Pillai's Trace = 0.924, $F_{16,158}$ = 8.48, $p < 0.001$), but only pLD differed significantly ($F_{2,85}$ = 3.88, p = 0.024). Mean pLD was higher for disked than for either non-disked (p = 0.018) or natural wetlands (p = 0.012), while the latter two did not differ (disked [$\bar{x}$ = 3.5] > non-disked [$\bar{x}$ = 2.1] ≈ natural [$\bar{x}$ = 1.8]).

Hydrology

The record of water table depths during the study period indicated that all the study sites met the legal assessment criteria for wetland hydrology (Federal Interagency Committee for Wetland Delineation 1989). Notwithstanding the drought period, the overall pattern of water table depth readings supported the notion that the study sites were hydrologically comparable, even though the created wetlands were perched, whereas the natural sites were groundwater-connected. Growing-season water table depths ranged from zero to > 69 cm, with a notable drop in depth coinciding with a period without precipitation in September (Figure 5a and b). Over the entire study period, site mean water table depths ranged from 3.4–29.2 cm below the surface (Table 1). However, the first two weeks of September were abnormally dry (drought severity D0), followed by three weeks of moderate drought (drought severity D1), which ended with heavy rains on October 7 (National Drought Mitigation Center 2005). Because the steel rod method is less reliable when the water table drops significantly (Bridgham et al. 1991), and since the steel rod data collection dates differed for each wetland, the steel rod oxidation depths used for analysis encompassed only those measurements taken between August 19 and September 8, reflecting the water table for the pre-drought period (and peak growth). During this time, the mean daily precipitation for the antecedent 30 day period was comparable among study wetlands, averaging ~0.2 cm per day (Figure 5a). Steel rod oxidation depth differed by creation method ($F_{2,85}$ = 6.32, p = 0.003), but the difference was significant only between disked and natural wetlands (p = 0.047, disked [$\bar{x}$ = 15.6] < natural [$\bar{x}$ = 20.4]; non-disked [$\bar{x}$ = 25.4]). For steel rod observations across all sites (n = 248), no correlation was evident between rod oxidation depth and pLS (r_{Sp} = −0.032, p = 0.61), pLD (r_{Sp} = 0.014, p = 0.83), or pT (r_{Sp} = 0.019, p = 0.76). Nonetheless, the steel rod oxidation depth did correlate weakly, but positively with elevation (relative to the corresponding multiscale transect mean, r_{Sp} = 0.16, p = 0.014), validating the expectation that microtopographic high points lie higher in relation to the water table, and are thus drier.

Vegetation

Field identification of macrophytes resulted in a total count of 72 taxa, with five identified to genus and 60 identified to species. Accounting for a small proportion of cover were seven taxa that could not be field-identified, either because they were seedlings or because they lacked distinguishing morphologic characteristics. Twenty-seven species had average abundances exceeding 2 percent cover for at least one study location (Table 2). Although the disked sites appeared to have greater vegetation cover than non-disked sites, and although total percent cover differed by creation method ($F_{2,85}$ = 9.74, $p <$ 0.001), the difference between disked and non-disked sites was not significant (p = 0.051), although disked and natural sites differed (p = 0.016, disked [$\bar{x}$ = 125] > natural [$\bar{x}$ = 103]; non-disked [$\bar{x}$ = 84]).

Table 1. Tortuosity (T), limiting slope (LS), and limiting elevation difference (LD, cm) for each transect scale; mean water table depth (WTD ± SE, cm), mean percent cover (%Cover ± SE), mean wetland prevalence index (P.I. ± SE) and corresponding category, species richness (S_{obs}) as estimated from taxon-sampling curves for n = 5 samples (1 m^2), 50 randomized runs; mean Shannon diversity index (H′ ± SE); percent within-site similarity (%Similarity) as determined from decomposition of average within-group Bray-Curtis similarity. For LS index, "neg" indicates negative/uninterpretable values.

		North Fork (disked)				Cedar Run (disked)		Cedar Run (non-disked)		Huntley Meadows (natural)			
	Scale	A	B	C	D	E	F	G	H	I	J	K	L
T	0.5 m	1.011	1.016	1.005	1.001	1.023	1.012	1.002	1.001	1.043	1.003	1.001	1.035
	1 m	1.020	1.026	1.010	1.002	1.013	1.021	1.004	1.002	1.005	1.006	1.001	1.012
	2 m	1.013	1.030	1.005	1.004	1.020	1.017	1.008	1.002	1.018	1.006	1.004	1.015
	4 m	1.015	1.012	-	-	1.011	-	1.004	-	1.023	1.004	-	-
LS	0.5 m	0.259	0.351	0.086	0.168	0.180	1.707	0.928	0.083	neg	0.086	neg	0.321
	1 m	0.227	0.249	0.328	0.062	0.152	0.260	0.156	0.117	0.104	0.209	0.084	0.254
	2 m	0.209	0.524	0.088	0.070	0.248	0.203	0.247	0.074	0.234	0.109	0.132	0.188
	4 m	0.471	0.725	-	-	0.220	-	0.173	-	0.352	0.145	-	-
LD	0.5 m	2.0	2.2	4.7	0.5	12.4	1.5	0.6	0.5	1.8	2.1	0.4	4.3
	1 m	4.6	5.4	1.7	1.9	6.0	4.9	1.2	0.8	3.2	1.5	0.9	2.0
	2 m	2.8	3.4	3.7	4.2	4.0	5.0	1.6	1.6	3.2	2.4	1.3	3.3
	4 m	3.6	3.2	-	-	5.1	-	2.1	-	4.4	2.1	-	-
WTD		19.2 ± 1.1	18.9 ± 1.1	3.4 ± 0.5	12.9 ± 1.3	18.9 ± 1.2	21.6 ± 2.0	20.0 ± 1.7	27.5 ± 4.3	16.8 ± 1.4	29.2 ± 2.5	11.4 ± 2.0	18.1 ± 1.9
%Cover		129 ± 9	90 ± 14	114 ± 11	166 ± 12	132 ± 8	128 ±12	109 ± 4	44 ± 8	120 ± 4	87 ± 6	107 ± 4	101 ± 8
P.I.		1.4 ± 0.1	1.7 ± 0.1	1.3 ± 0.2	1.3 ± 0.1	1.7 ± 0.1	1.4 ± 0.1	2.0 ± 0.1	3.6 ± 0.2	2.0 ± 0.1	1.1 ± 0.1	1.4 ± 0.2	1.6 ± 0.1
		OBL	FACW	OBL	OBL	FACW	OBL	FACW	FACU	FACW	OBL	OBL	FACW
S_{obs}		11.2	19.5	18	19.2	22.2	16	14.4	10	9.3	13.3	8	14
H′		1.01 ± 0.08	1.54 ± 0.10	1.48 ± 0.21	1.52 ± 0.11	1.68 ± 0.10	1.21 ± 0.08	0.59 ± 0.10	1.06 ± 0.14	0.90 ± 0.08	1.11 ± 0.12	0.65 ± 0.15	1.03 ± 0.17
%Similarity		53	35	41	50	39	52	68	60	58	47	63	35

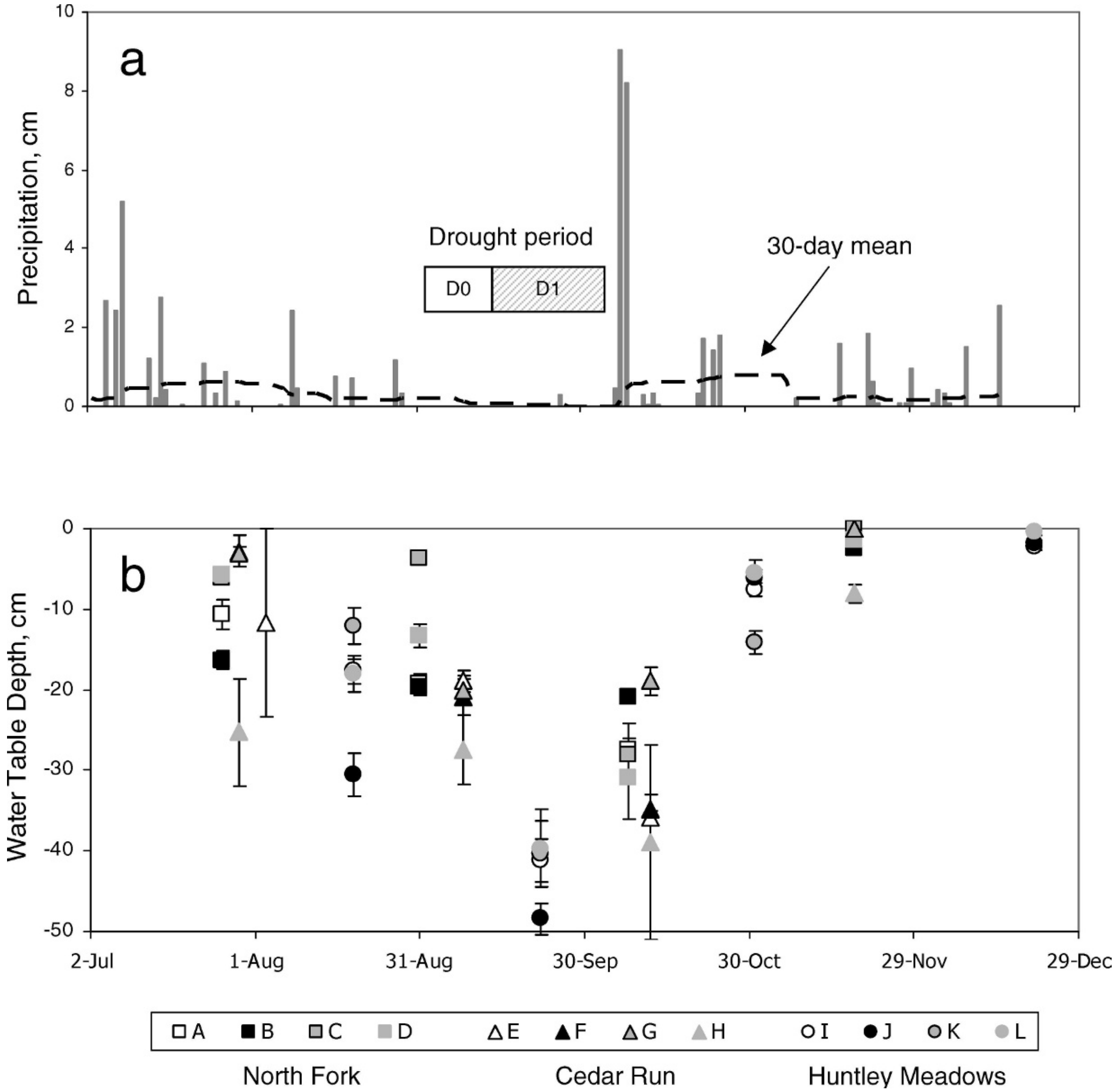

Figure 5. a) Daily precipitation, averaged from airport weather station data, Reagan Washington National and Dulles International airports, July to December 2005. Mean daily precipitation for the preceding 30 days is indicated by dashed line. Period of drought shown, with drought severity index: D0 = abnormally dry, D1 = moderate drought. b) Water table depth (± 1 SE) as measured by steel rod rust depth by date of collection, 2005. Readings reflect the previous month's approximate water table depth. North Fork, sites A–D; Cedar Run, sites E–H; Huntley Meadows, sites I–L.

Geographically, species richness (S) was highest for Cedar Run (42 species total, 30 for disked and 19 for non-disked sites), followed by North Fork (31 species) and Huntley Meadows (26 species). S ranged from 8 to 22.2 species among multiscale transects (Table 1). Considering survey plots across all sites (n = 106), S correlated with both pT (r_{Sp} = 0.208, p = 0.032) and pLD (r_{Sp} = 0.235, p = 0.015). Within Cedar Run (n = 34), the correlations were stronger, although again the correlation for pLD (r_{Sp} = 0.533, p = 0.001) was stronger than that for pT (r_{Sp} = 0.424, p = 0.013). Plot-level species richness differed by creation method ($F_{2,85}$ = 23.89, $p < 0.001$) and was higher for disked plots than for non-disked (p = 0.009) and natural ($p < 0.001$) plots (disked [$\bar{x}$ = 7.9] > natural [$\bar{x}$ = 5.0] ≈ non-disked [$\bar{x}$ = 4.8]).

Plot-level Shannon diversity index (H′) values ranged from 0–2.13, while transect-level values ranged from 0–2.56. Because the Shannon index increases with sampling effort (Hayek and Buzas 1997), transect-level values could not be compared across different scales. At the sample plot level, H′ differed by creation method ($F_{2,85}$ = 19.01, p <

Table 2. Percent cover and wetland indicator category (Reed 1988) for common species (> 2% average cover at any location). Percent cover totals may exceed 100% due to multiple layers of cover. Mean ± one SE.

Species	Indicator[1]	North Fork (disked)	Cedar Run (disked)	Cedar Run (non-disked)	Huntley Meadows (natural)
Alisma plantago-aquatica L.	OBL	1 ± 1	5 ± 3	0	0
Ambrosia artemisiifolia L.	FACU	0	0	4 ± 2	0
Bidens cernua L.	OBL	7 ± 3	1 ± 1	0	0
Carex frankii Kunth	OBL	10 ± 4	0	0	0
Carex lurida Wahlenb.	OBL	1 ± 1	0	0	4 ± 1.7
Carex vulpinoidea Michx.	OBL	6 ± 3	0	0	0
Carex sp.	–	0	3 ± 1	1 ± 0	0.1 ± 0.04
Cyperus strigosus L.	FACW	0	11 ± 3	0	0
Diodia virginiana L.	FACW	0	4 ± 1	0.1 ± 0.1	0
Echinochloa crus-galli (L.) Beauv.	FACW−[2]	22 ± 4	19 ± 7	61 ± 10	3 ± 1.9
Eleocharis obtusa (Willd.) Schult.	OBL	28 ± 5	29 ± 7	6 ± 3	1 ± 0.8
Juncus effusus L.	FACW+	3 ± 1	2 ± 1	0	6 ± 2.8
Juncus tenuis Willd.	FAC−	9 ± 3	10 ± 3	0	0
Leersia oryzoides (L.) Sw.	OBL	1 ± 0	17 ± 6	0	30 ± 5.0
Lindernia dubia (L.) Pennell	OBL	0	3 ± 1	0.3 ± 0.1	0.1 ± 0.1
Ludwigia alternifolia L.	FACW+	6 ± 3	2 ± 1	0	0
Ludwigia palustris (L.) Ell.	OBL	18 ± 4	12 ± 6	1 ± 0	1 ± 0.5
Microstegium vimineum (Trin.) A. Camus	FAC	0	0	0	24 ± 5.5
Panicum virgatum L.	FAC	0.3 ± 0.3	4 ± 2	6 ± 4	0
Polygonum hydropiper L.	OBL	4 ± 2	3 ± 2	0.1 ± 0.1	0
Polygonum punctatum Ell.	OBL	0.2 ± 0.1	1 ± 1	0	5 ± 2.3
Polygonum sagittatum L.	OBL	0.1 ± 0.1	0	0	4 ± 1.8
Saururus cernuus L.	OBL	0	0	0	12 ± 4.0
Scirpus atrovirens Willd.	OBL	2 ± 2	0	0	0
Scirpus cyperinus (L.) Kunth	FACW+	0	0	0	4 ± 2.9
Setaria glauca (L.) Beauv.	FAC	0	5 ± 2	0	0
Setaria viridis (L.) Beauv.	NL	0	0	6 ± 4	0

[1] OBL = obligate wetland; FACW = facultative wetland; FAC = facultative; FACU = facultative upland; NL = not listed. +/− indicates more/less frequently found in wetlands for a given indicator category.
[2] Indicator category reflects corrected status (Pepin 2000) for *E. crus-galli*.

0.001), with significant differences among all methods (disked [$\bar{x}$ = 1.38] > natural [$\bar{x}$ = 0.96] > non-disked [$\bar{x}$ = 0.72]). Across all survey plots (n = 106), H′ was significantly correlated with both pLD (r_{Sp} = 0.32, p = 0.001) and pT (r_{Sp} = 0.31, p = 0.001), although not with pLS (r_{Sp} = −0.064, p = 0.51). These general correlations were not observed consistently. While they were evident for Cedar Run for both pLD (r_{Sp} = 0.57, p < 0.001) and pT (r_{Sp} = 0.45, p = 0.007), they were not for North Fork (pLD r_{Sp} = −0.15, p = 0.38; pT r_{Sp} = 0.10, p = 0.55). Considering disked and non-disked created wetland survey plots as a pooled group (n = 70), H′ was positively correlated with both pLD (r_{Sp} = 0.27, p = 0.022) and pT (r_{Sp} = 0.30, p = 0.013). At the natural wetland survey plots (n = 36), H′ correlated with pT (r_{Sp} = 0.33, p = 0.047), but not pLD (r_{Sp} = 0.28, p = 0.098).

Although water table depth could affect S and H′, particularly where conditions are relatively constant (e.g., inundation), and although it should largely determine the wetland prevalence index (P.I.), the steel rod oxidation depth was not correlated with S (p = 0.68), H′ (p = 0.87), or P.I. (p = 0.23). The wetland prevalence index ranged from 1.0–4.0 (Table 1), although most were below 2.5, thus within the wetland vegetation range. An exception was site H at Cedar Run, where the vegetation was markedly different from that observed at other sites, with prevalence of non-hydrophytic vegetation (P.I. = 3.6, or FACU) and low percent cover ($\bar{x}$ = 44%). Prevalence indices differed by creation method ($F_{2,85}$ = 24.92, p < 0.001), where disked and natural wetland plots had significantly lower P.I. values (i.e., prevalence of more hydrophytic vegetation) than non-disked wetland plots (disked [$\bar{x}$ = 1.4] ≈ natural

Table 3. Percent contribution to within-site similarity (from ANOSIM) for the four major contributors to similarity: barnyardgrass (*E. crus-galli*), blunt spikerush (*E. obtusa*), rice cutgrass (*L. oryzoides*), and marsh seedbox (*L. palustris*). Also given are overall mean percent and percentages for created and natural wetlands.

		E. crus-galli	*E. obtusa*	*L. oryzoides*	*L. palustris*
Created wetlands	A	42	36	< 1	15
	B	16	2	2	22
	C	7	26	2	30
	D	12	29	< 1	14
	E	2	8	7	11
	F	18	51	11	5
	G	75	13	0	2
	H	0	0	0	0
Natural wetlands	I	0	0	33	0
	J	1	1	20	13
	K	0	0	75	0
	L	19	0	8	2
Overall mean %		16.0	13.8	13.1	9.4
Created mean %		21.5	20.6	2.7	12.4
Natural mean %		4.9	0.4	34.0	3.6

[$\bar{x}$ = 1.4] < non-disked [$\bar{x}$ = 2.6]). Even though hydrology should largely determine the prevalence of hydrophytes, the steel rod oxidation depth difference between disked and non-disked plots (p = 0.099, mean difference of 9.8 cm) appeared insufficient to explain the large difference in P.I. (a full indicator category, OBL versus FACW/FAC). The equivalence of P.I. between disked and natural wetlands suggested that their differing steel rod oxidation depths (p = 0.047, mean difference of 3.8 cm) did not affect the prevalence of hydrophytes.

Creation methods differed in community composition (Global R = 0.715, p = 0.002), while significant assemblage differences were also attributable to site (Global R = 0.634, p = 0.001). Pairwise comparisons showed that disked and natural wetlands differed (R = 0.921, p = 0.005), but that disked and non-disked wetlands did not (R = 0.396, p = 0.11). Although the test for difference between non-disked and natural wetlands was not significant (R = 0.786, p = 0.067), it likely reflects the small number of non-disked replicates. Clarke and Gorley (2006) emphasize that the R statistic is more important for interpretation than is the p-value when the number of replicates is small; the large R statistic here suggests significant differences between non-disked and natural sites.

Decomposition of Bray-Curtis similarity showed that the within-site similarity between samples was generally higher (i.e., greater homogeneity) for sites with less microtopography (Table 1). There were marked contrasts in within-site similarity between disked sites (E and F) and non-disked sites (G and H) at Cedar Run, and between beaver pond sites (I and K) and mature wetland sites (J and L) at Huntley Meadows. Decomposition of similarity percentages by species suggested that four common species were important contributors to within-site similarity (Table 3), as well as to difference between sites: barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.), blunt spikerush (*Eleocharis obtusa* (Willd.) Schult.), rice cutgrass (*Leersia oryzoides* (L.) Sw.), and marsh seedbox (*Ludwigia palustris* (L.) Ell.). *Echinochloa crus-galli*, an annual graminoid often found in association with *E. obtusa* and *L. palustris* (Pepin 2000), was abundant at Cedar Run, and was the overwhelming component of cover observed in the non-disked wetland (and at site G).

DISCUSSION

Microtopography in Created and Natural Wetlands

The range of values obtained for T (Table 1) fell within a range overlapping that obtained by Werner and Zedler (2002) for *Phalaris*- and *Typha*-dominated wetlands (1.00–1.02), but considerably lower than those for *Carex*-dominated wetlands (1.06–1.16) (although the methods used in this study differed, particularly in terms of the interval of measurement). For created wetlands, the microtopography of disked sites differed from that of non-disked sites in terms of both tortuosity and relief, confirming our hypothesis that disked microtopography is greater than non-disked. The distinction was particularly apparent for relief; whereas disked sites had LD greater than 3 cm, non-disked sites had LD of 2 cm or less. Disked LD exceeded the relief of heterogeneous experimental treatments (Vivian-Smith 1997), while non-disked LD approached the condition of homogeneous treatments in that study. Disked relief is also sufficient to affect the frequency and spatial variation of flooding (Pollock et al. 1998, Bledsoe and Shear 2000).

Although disked and non-disked microtopography clearly differed, created and natural microtopography did not, in contrast to our hypothesis that created and natural wetlands would differ quantitatively. While natural LD was similar to disked LD and larger than non-disked LD, natural pLD was similar to non-disked pLD and less than disked pLD, suggesting that natural microtopographic relief encompasses the range of relief found in both disked and non-disked created wetlands. Although this finding contrasts with that of Stolt et al. (2000), at the comparatively small scale of this investigation, the distinction between created and natural microtopography may be subtle. At our study's scale, disked relief was comparable to the high end of the relief found in natural wetlands, while non-disked relief fell at the low end.

Wetland microtopography has typically been examined at resolutions (or grain sizes) on the order of meters or square meters and/or spatial extents greater than 10 m or 100 m^2 (Pollock et al. 1998, Bledsoe and Shear 2000, Stolt et al. 2000, Werner and Zedler 2002, Bruland and Richardson 2005). The present study examines wetland microtopography at grain sizes of 10–20 cm (or 0.2 m^2 for vegetation plots) and spatial extent 4 m or less ($\sim$12.5 m^2), extents comparable to those of Morzaria-Luna et al. (2004), with the smaller transects comparable in extent to the experiment of Vivian-Smith (1997). At our study's resolution, wetland microtopography differed minimally from extents of 0.5–4 m, a result echoing that of Morzaria-Luna et al. (2004). This finding validates the use of the proximal indices pT and pLD, since these indices were calculated based on near-neighbor elevations. It also suggests that mesocosm-scale experiments in microtopography might be extrapolated at least as far as the 4 m transect spatial extent. At finer grain sizes (e.g., seed-scale as opposed to plant-scale), this may not necessarily be the case. Moreover, at larger spatial extents, broader-scale patterns in microtopography (such as hummock/hollow) may be more important.

Measures of Microtopography

Although LD and LS were adopted to quantify relief and roughness separately, LD proved more useful than LS. The LS and pLS indices failed to distinguish the study sites (Table 1, Figure 6c). Some of the regressions had negative slopes, resulting in negative (uninterpretable) LS values, implying a non-zero mean absolute elevation difference (ΔZ) as the lag distance approaches zero. In Lineweaver-Burk linear regression, however, such a result can occur when the smallest-interval ΔZ value exceeds those of larger intervals. While this provides qualitative information (i.e., microtopographic roughness more apparent at small intervals than at larger ones), it suggests caution in interpreting LS as a physical parameter, supporting the contention that LS only describes variogram slope, not surface slope (Kamphorst et al. 2000). Several differences in method may explain why LS and pLS results appeared less robust than those of Linden and Van Doren (1986). First, elevation data were collected along circular transects, rather than in oriented grids; second, the smallest interval used was 10 cm, as opposed to 5 cm. For the larger transects, the largest lag intervals exceeded those used in the original method. Moreover, the proximal indices were derived from a small number of elevation measurements. Whereas the original study reported that most regressions had close fits to the Lineweaver-Burk plots ($R^2 > 0.90$), in our study only half the regressions used to calculate LS and LD had comparable fit, and about a third had rather poor fit ($R^2 < 0.50$).

LD appeared to perform reasonably well as a measure of relief, with values appropriate to the respective elevation profiles (Figure 4); pLD values were clustered about their respective transect-level LD index values and produced few univariate outliers. LD and pLD were thus useful in characterizing microtopography, although they were computationally intensive. A simpler measure of relief, such as random roughness (Allmaras et al. 1966) might be more appropriate for future studies. Quantification of relief is essential, however; consideration of tortuosity alone would suggest that disked sites C and D were similar to non-disked sites G and H (Figure 6a), whereas these sites differed in relief, measured as pLD (Figure 6b).

Hydrology

The correlation between relative elevation and steel rod oxidation depth suggests that relief should affect proximate hydrologic conditions, but the weakness of the correlation may reflect steel rod oxidation depth variability. Indeed, steel rod depth standard deviations more than doubled those of elevation. However, the inferred variability in water

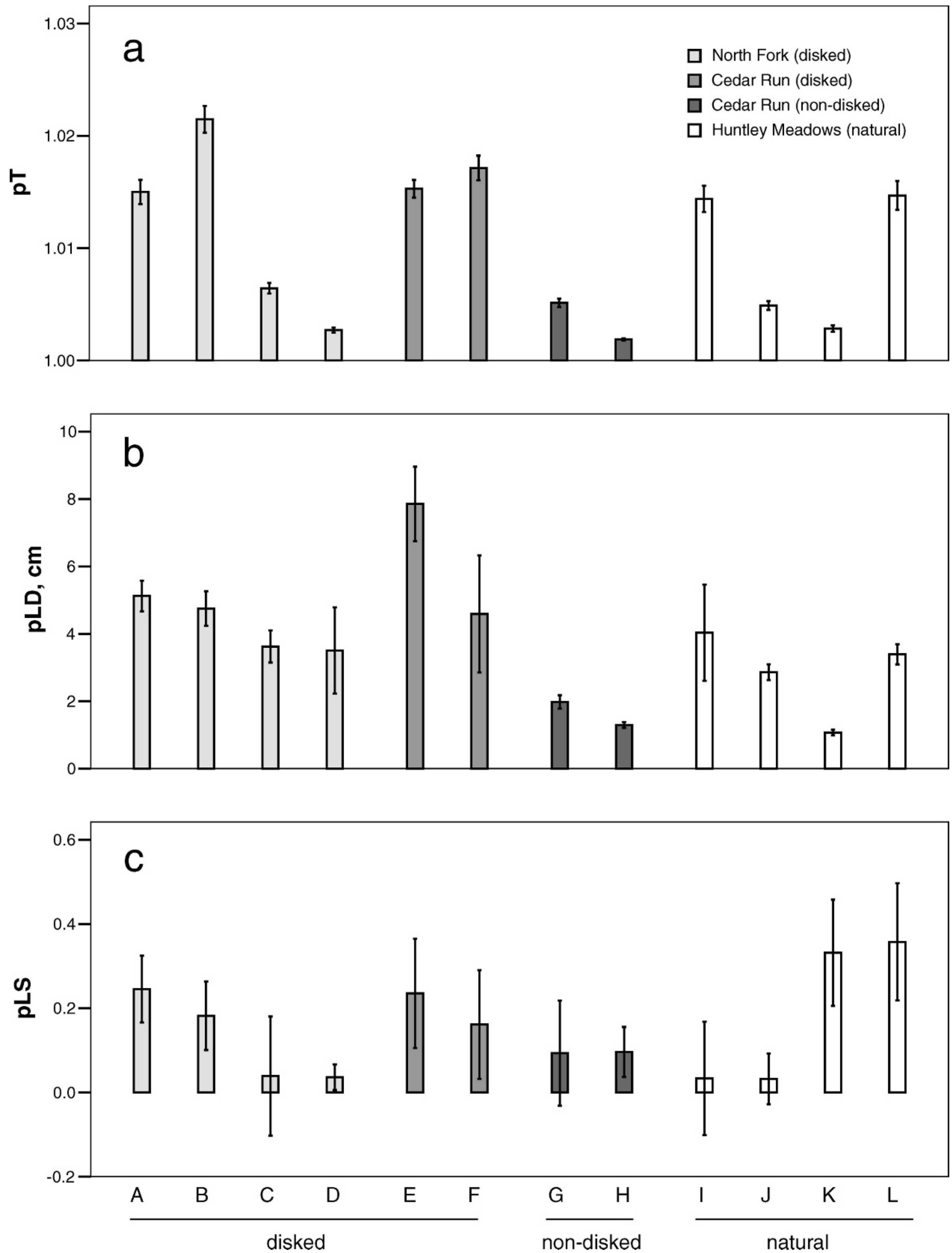

Figure 6. Proximal microtopographic index values, as determined for each transect point, by site, excluding 36 Mahalanobis outliers (n = 1674). a) Proximal tortuosity (pT); b) proximal limiting elevation difference (pLD); c) proximal limiting slope (pLS). Mean ± one SE.

table depth may reflect redoximorphic conditions independent of water table depth (e.g., soil texture, compaction, or organic/microbial content). As used in this study, the steel rod oxidation method had drawbacks, particularly for fine-scale measurement and comparison.

The lack of correlation between steel rod oxidation depth and any of the index measures of microtopography contrasts to the findings of Tweedy et al. (2001) relating higher water table to microtopography, as well as with our corresponding hypothesis. During the growing season, increased water retention may have been offset by increased evapotranspiration, thus masking microtopographic effects. Alternatively, steel rod oxidation may have been too coarse an approach to establish a meaningful correlation with water table depth, which might only vary on the order of 10 cm due to microtopography (Tweedy et al. 2001). Indeed, while the steel rod oxidation depth differed significantly among creation methods, the mean depths were within a 10 cm range. Moreover, since the steel rod analysis only covers a relatively brief period in late summer, it can not reflect seasonal aspects of the hydrology.

Microrelief appeared to increase water retention by storing water in small depressions. Rarely was standing water observed in the low-relief non-disked sites; when present, it was of less than 2 cm depth (Moser, personal observation). In contrast, standing water of several centimeters depth was frequently observed at disked and natural sites, suggesting that microrelief can affect hydroperiod, increasing inundation stress on plants and germinating seeds. The prevalence of hydrophytic vegetation may thus depend more on ephemeral inundation by perched pools than on water table depth.

Vegetation

The observed association between microtopography and both species richness and Shannon diversity in created wetlands confirms the notion that inducing microtopographic heterogeneity in created wetlands promotes diversity (Vivian-Smith 1997, Bruland and Richardson 2005, Larkin et al. 2006). Furthermore, this association mirrored the patterns observed in natural wetlands in our study and in others, (Huenneke and Sharitz 1986, Titus 1990, Werner and Zedler 2002), supporting our hypothesis that increased microtopography is associated with greater species richness and diversity.

Physiogeographic setting, as well as seed source, may explain some of the differences between created and natural wetland assemblages. The higher-elevation clay loams of the Piedmont likely support a vegetation community different from that supported by the lower, sandier soils of the Coastal Plain. Moreover, the even and abundant supply of seed provided for wetland creation contrasts with the spatially variable, population-dependent seed source and distribution in natural wetlands, possibly explaining the richness and diversity in the created wetlands. Spatial variability was more evident at Huntley Meadows, where numerous additional species were observed in the vicinity, whereas the created wetlands lacked such broader-scale diversity. Furthermore, since the created wetlands were in comparatively early successional stages, their plant communities may include species that will not persist in the long term.

A species-area relationship has been suggested as potentially explaining increased species richness with increased microtopography in tussock sedge meadows (Werner and Zedler 2002, Peach and Zedler 2006). In our study, vegetation effects (e.g., tussock effects) were not confounded with microtopographic effects (the Cedar Run sites had no pre-existing biogenic microtopography). Since tortuosity is the 2-dimensional analogue of surface area, the correlation between species richness and pT may support a species-area relationship. However, surface area may only reflect habitat heterogeneity, rather than being an influence itself (Brose 2001). As a measure of relief, the pLD index should more closely reflect habitat heterogeneity than does pT, whether considered in terms of hydrology (Pollock et al. 1998, Bledsoe and Shear 2000) or other factors, such as light penetration (Peach and Zedler 2006). At Cedar Run, the strength of correlation with pLD better supports the hypothesis that species richness is promoted by habitat heterogeneity than by a richness-area relationship.

The four species accounting for most of the assemblage similarities are generalists common in wetland plant communities in Virginia and highly tolerant of disturbance (Virginia FQAI Advisory Committee 2004). The distribution and abundance of these generalists within a site's plant community was important in distinguishing among assemblages. These assemblages varied less where microtopography was limited. It thus appears that increased microtopography reduces the importance of generalists and fosters the establishment of non-generalists, as would be expected through niche differentiation. It should also increase the evenness of species distribution, suggested in part by the correlations between H' and both pT and pLD. The higher within-site assemblage similarity for non-disked sites further supports the notion that decreased microtopography is associated with species dominance (Werner and Zedler 2002, Larkin et al. 2006).

CONCLUSIONS

As a practical consequence of engineering practices, created wetland ecosystems are relatively uniform at the outset, in contrast to natural wetland conditions. An area of concern for mitigation is the extent to which this uniformity may lead to the predominance of few species, diminishing ecosystem functions. Our study showed that disking clearly enhanced microtopography in created wetlands and the increased microtopography was associated with greater species richness, diversity, and percent cover, as well as with the prevalence of hydrophytic vegetation. However, it may represent topographic uniformity when considered at the full extent of a created wetland. Disked microtopography was thus qualitatively different from that induced by excavation (hummock/hollow or mound/pit), which provides greater magnitude of relief but is typically applied over a proportionally smaller area. Disking affects vegetation throughout a wetland, whereas hummocks/hollow creation yields localized benefits (e.g., pools of standing water, patches of vegetation) which may be more relevant to wetland fauna.

Disking appears to prevent the dominance of generalist species, some of which may be undesirable species in mitigation wetlands. Where generalist species are associated with the loss of microtopographic features and biodiversity, even the short-term plant community effects of disking, apparent in this study for Cedar Run, might help guarantee longer-term plant species richness and diversity. In terms of mitigation performance criteria (i.e. legal success), the disked sites clearly had the better prospects. The non-disked site H failed the basic performance criterion of prevalence of hydrophytic vegetation. Disking is therefore recommended as a relatively low-cost method of inducing microtopographic variation that could assist ecosystem development in created mitigation wetlands.

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