

SPATIAL HETEROGENEITY AND DEPENDENCE OF SOILS AND HERBACEOUS PLANT COMMUNITIES IN ADJACENT SEASONAL WETLAND AND PASTURE SITES

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Abstract: Soil processes often exhibit spatial heterogeneity that may influence plant community structure. This study was conducted to determine fine-scale spatial patterns and degrees of variability of soil nutrients and plant communities within different vegetation types in a stream floodplain in southwestern West Virginia. One 5 m × 5 m site was established in each of two vegetation/drainage types: pasture (PA) and seasonal wetland (SW). Sites were located ~25 m apart on flat bottomland. A 10 m × 1 m transect was also established perpendicular to the visible boundary between PA and SW drainage types, but separate from the PA and SW sites. Each site was divided into 1-m² plots (n = 25) and the transect was divided into 0.25-m² plots (n = 40). Mineral soil was taken to a 5 cm depth. Soil organic matter was measured as loss-on-ignition. Extractable NH₄⁺ and NO₃⁻ were determined before and after laboratory incubation (28 days at 27°C) to determine net N mineralization and nitrification. Cations were analyzed using inductively coupled plasma emission spectrometry. Vegetation was assessed using estimated percent cover (sites) and aboveground harvested biomass (transect). Mean organic matter was significantly higher (P < 0.05) in SW than in PA (10.6% and 8.3%, respectively). Nitrification was nearly 100% of mineralization in all soils, and was significantly lower (P < 0.05) in PA than in SW (0.7 and 1.8 µg NO₃⁻-N/g soil/d, respectively). Aluminum was significantly higher (P < 0.05) in SW than in PA (202.1 and 0.5 µg Al/g soil, respectively). Calcium and pH were significantly higher (P < 0.05) in PA than in SW (768.5 µg/g soil and 4.4, respectively). Magnesium was significantly higher (P < 0.05) in SW than in PA (174.2 and 121.9 µg/g soil, respectively). Transect results were similar to PA and SW sites and an abrupt transition was found between PA and SW site types. Vegetation analysis revealed two distinct communities with SW dominated by wetland species and PA dominated by a mixture with slightly more upland species. Transect vegetation also consisted of largely wetland species within wetland and a mixture in pasture, however *Arthraxon hispidus* (Thunb.) Makino dominated for ~1 m at the boundary. Spatial variability of organic matter was much lower than spatial variability of nitrification. Thus, availability of organic substrates to N-processing microbes is less variable than N processing itself, underlining the complexity of biotic factors responsible for regulating soil N processes.

Key Words: nitrification, nitrogen mineralization, nitrogen saturation, soil cations

INTRODUCTION

Heterogeneity – defined by Li and Reynolds (1995) as “the complexity and/or variability of a system property in space and/or time” – can be an important component controlling plant community structure and composition. Spatial heterogeneity in soil resources is considered to play an important role in maintaining biodiversity (Vivian-Smith 1997, Bell et al. 2000, Gallardo et al. 2005) and has been linked with structural attributes of

plant communities (Robertson et al. 1988, Cross and Schlesinger 1999, Hutchings et al. 2003, Gilliam 2006). A clearer understanding of processes associated with spatial heterogeneity should result in improved statistical estimates through choice of sampling schemes and central tendency measures, and even improved management practices through integration of predictive variables from regional, landscape, plot, and micro scales (Parkin 1993).

Soil nutrient dynamics typically exhibit a high degree of spatial heterogeneity (Gilliam et al. 2005,

Smithwick et al. 2005), being controlled by processes that are themselves quite spatially heterogeneous. For example, several studies (Stevenson 1986, Morris and Boerner 1998, 1999, Devito et al. 1999, Ohrui et al. 1999) have reported soil moisture-related controls for soil nitrogen (N) cycling. Other authors (Stevenson 1986, Van der Krift and Berendse 2001) found temperature as an important influence on N dynamics. Vegetation has also been linked with N dynamics (Schlesinger et al. 1996, Cross and Schlesinger 1999, Van der Krift and Berendse 2001). Spatial variability of calcium (Ca) and magnesium (Mg) ions was found by Schlesinger et al. (1996) and Cross and Schlesinger (1999) to be controlled by parent materials. Aluminum (Al) mobility, along with that of Ca and Mg, is often correlated with pH (Postek et al. 1995, Barbour et al. 1999). Feedback can occur in which two processes affect each other. For example, N availability can select for plant communities which, in turn, may further alter N availability (Wedin and Tilman 1990). Indeed, soils beneath macrophytic patches are commonly shown to be enriched in organic matter and N (Schlesinger et al. 1996, Thompson et al. 2006).

The process of wetland creation, e.g., for mitigation purposes, potentially alters spatial heterogeneity of both vegetation and several ecologically important processes that influence vegetation (Stolt et al. 2001). Consequently, an understanding of the effects of inundation on spatial heterogeneity is important in assessing the efficacy of the creation effort. Previous work in western West Virginia showed that effects of mitigation wetland creation varied greatly among soil nutrients, with rapid changes observed for N and much slower changes for base cations (Gilliam et al. 1999). This work, however, lacked an appropriate design to assess fine-scale spatial heterogeneity.

Accordingly, the purpose of this study was to examine fine-scale spatial variability of both soil nutrients and vegetation in a seasonal wetland imbedded in a pasture matrix. Our approach followed that of Mancera et al. (2005), who assessed fine-scale variation in marshland vegetation relative to environmental variables in a coastal riverine wetland landscape. Our specific objectives were to 1) characterize and compare soil N dynamics, pH, organic matter, and extractable soil nutrients within seasonal wetland and adjacent pasture using square grids with cells at 1 m intervals, 2) characterize and compare vegetation in these same sites, and 3) repeat these same comparisons using finer-scale sampling (0.5 m intervals) along a transect spanning the two sites.

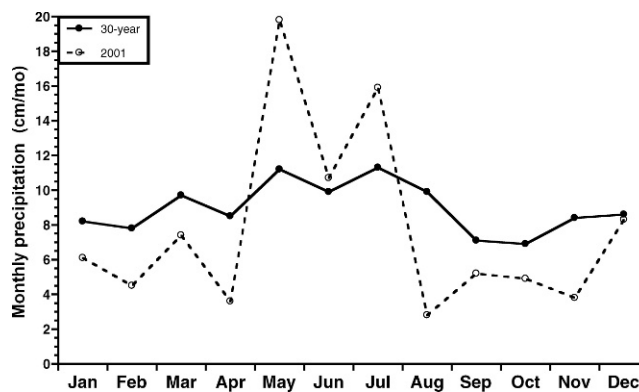


Figure 1. Monthly precipitation for the research site. Shown are 30-yr means taken from the U.S. Weather Service (<http://cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl>) and for the year of study (2001).

MATERIALS AND METHODS

Site Description

This study was carried out at the Mill Creek mitigation area, an abandoned pasture located in a 3rd-order stream floodplain in Wayne County, West Virginia, near the town of Saltpetre. The pasture covered an approximately 1 ha area flanked east and west with hills dominated by mixed deciduous forest. Within the pasture matrix is a seasonal wetland of approximately 250 m². Although the history of how this wetland developed is unclear, it likely is the result of a slight but notable depression (5–10 cm, Dick 2003) in the otherwise level landscape in which water accumulates to fill this depression during times of high precipitation. This typically occurs in the growing season, and was especially the case during the year of this study (Figure 1). Although less precipitation fell during 2001 (93.1 cm) than the 30-yr mean (107.5 cm/yr), more fell during May through July, 2001, than was expected from the long-term mean. This site will become a constructed wetland to offset wetland losses incurred during road construction. Elevation within the floodplain is ~195–200 m.

Soils of the study site were of the Kanawha series. Kanawha soils are fine-loamy, mixed, active, mesic Typic Hapludalfs, and are very deep (100–180 cm), well-drained, moderately permeable, and formed in alluvium derived from interbedded shale, siltstone, and sandstone. Kanawha soils are found on high bottoms and low stream terraces with slope ranges from 0%–15%; our slopes were essentially 0%. For more complete description of Kanawha series soils, see the following web site: <http://ortho.ftw.nrcs.usda.gov/osd/dat/K/KANAWHA.html>.

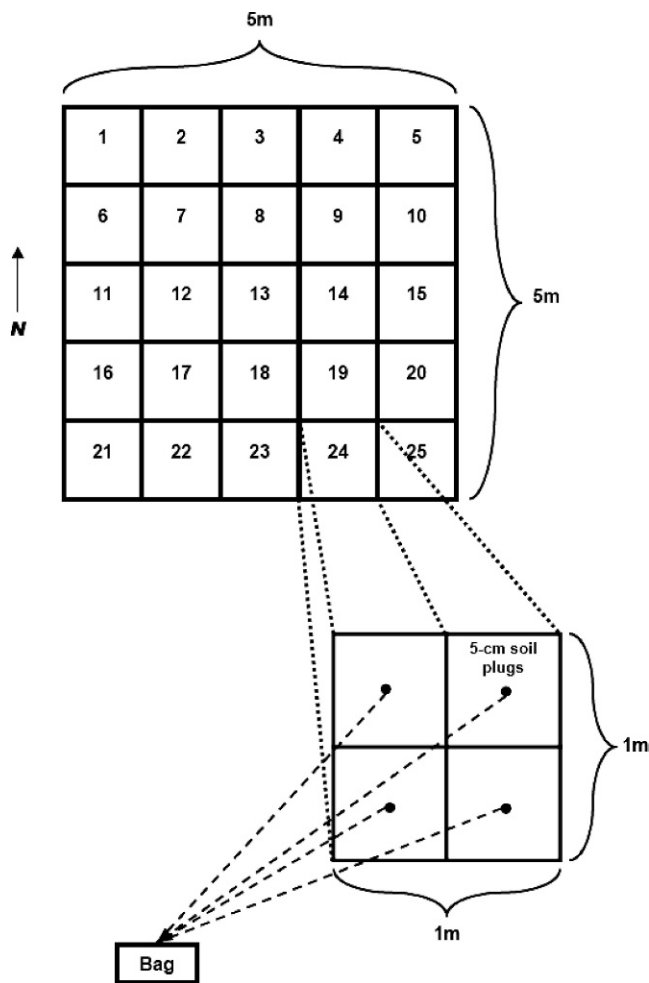


Figure 2. Schematic diagram of sampling design within each of two sites.

Field Sampling

Two 5 m \times 5 m sites were established on the floodplain: one inside the seasonal wetland (SW) and one approximately 25 m away in the pasture (PA). Each 5 m \times 5 m site was divided into 25 1-m² plots and each plot was quartered using a 1-m² PVC frame with center cross. One mineral soil sample was taken from near the center of each 0.25-m² quadrant of 1-m² plots to a depth of 5 cm using a 2 cm diameter soil corer. Four samples (one per quadrant) were placed together in a single sterile polyethylene Whirl Pak bag to create a composite sample for each 1-m² plot for a total of 25 mineral soil samples per site (Figure 2). Soil samples were kept in bags as intact cores and were immediately placed on ice for transport to laboratory. Samples were collected in August 2001.

A 10 m transect was established perpendicular to the seasonal wetland boundary and centered with 5 m extending into both seasonal wetland (SW_I) and

pasture (PA_I) areas, but separate from PA and SW sites. Using this transect as a centerline, a quartered 1-m² PVC frame was used to define 0.25-m² plots ($n = 40$) along the transect (paired plots at 0.5 m intervals). Mineral soil was collected in September 2001 using a hand trowel to a depth of 5 cm as described for the site sampling. Soil samples were immediately placed on ice for transport to the laboratory.

Vegetation cover was estimated within 1-m² plots at PA and SW sites using percent cover estimation in October 2002. Aboveground vegetation was harvested within each 0.25-m² transect plot in October 2001 using garden shears to cut stems at ground level. Vegetation from each transect plot was placed in large, labeled plastic bags for transport back to the laboratory for sorting, drying, and weighing. Botanical nomenclature follows Strasbaugh and Core (1977) and species will be referred to using four-letter codes (Table 1). Wetland indicator status was determined for each species using the PLANTS database (USDA, NRCS 2004).

Laboratory Analyses

After being brought back to the laboratory at Marshall University, samples were homogenized by hand in original collection bags before analysis. Organic matter was determined from oven dried soil samples using a loss-on-ignition method (mass lost over 7 hr at 500°C). Soil samples were extracted (see below) for pre-incubation analysis of KCl-extractable NO₃, NH₄, Al, Ca, Mg, and pH. Remaining soil samples were then incubated in their original polyethylene bags at 27°C for 28 days in a Fisher Scientific Low Temperature Incubator (Model 146E). Previous work on similar soils (e.g., Gilliam et al. 2005) showed 27°C to be the temperature optimum for N mineralization and nitrification. Thus, results reflect N mineralization and nitrification potentials, rather than field (i.e., *in situ*) rates. Soil moisture determined for pre-incubation analyses revealed that moisture generally ranged from 30%–35%, neither varying between sites nor changing over the course of incubation; no water was added at any time before or during the incubation.

Post-incubation extraction and analysis of nutrients were performed following methods described in Gilliam et al. (2005). Briefly, moist soils were extracted with 1N KCl at an extract:soil ratio of 10:1 (v:w). Extracts were analyzed colorimetrically for NH₄ and NO₃ with a Bran+Luebbe TrAAcs 2000 automatic analysis system. Extractable Al, Ca, and Mg were analyzed via inductively coupled plasma emission spectrometry (ICP) with a Varian

Table 1. List of all plant species encountered at Mill Creek study site, Wayne County, West Virginia. Codes will be used to refer to species throughout the text. Wetland indicator status (WIS) for each species taken from USDA, NRCS (2002), Region 1.

Code	Scientific Name	Common Name	WIS*
ACRH	<i>Acalypha rhomboidea</i> Raf.	Common three-seeded mercury	FACU-
AGSP	<i>Agrostis</i> sp.	-	-
ARHI	<i>Arthraxon hispidus</i> (Thunb.) Makino	Jointheaded arthraxon	NI
ASLA	<i>Aster lateriflorus</i> (L.) Britton	Calico aster	FACW-
ASPI	<i>Aster pilosus</i> Willd.	White heath aster	UPL
CAFR	<i>Carex frankii</i> Kunth	Sedge	OBL
CATR	<i>Carex tribuloides</i> Wahl.	Sedge	FACW+
CAVU	<i>Carex vulpinoidea</i> Michx.	Foxtail sedge	OBL
CIAR	<i>Cinna arundinacea</i> L.	Wood reed-grass	FACW+
COCO	<i>Commelina communis</i> L.	Asiatic day-flower	FAC-
CYST	<i>Cyperus strigosus</i> L.	Strawcolored flatsedge	FACW
DISA	<i>Digitaria sanguinalis</i> (L.) Scop.	Crabgrass	FACU-
DIVI	<i>Diodia virginiana</i> L.	Larger buttonweed	FACW
ECCR	<i>Echinochloa crusgalli</i> (L.) Beauv.	Barnyard grass	FACU
ELCA	<i>Elephantopus carolinianus</i> Willd.	Elephant's-foot	FACU
FEEL	<i>Festuca elatior</i> L.	Meadow fescue	FACU-
GLHE	<i>Glechoma hederacea</i> L.	Ground-ivy	FACU
JUEF	<i>Juncus effusus</i> L.	Common rush	OBL
JUTE	<i>Juncus tenuis</i> Willd.	Path rush, wiregrass	FAC-
LYNU	<i>Lysimachia nummularia</i> L.	Moneywort	OBL
OXCO	<i>Oxalis corniculata</i> L.	Creeping lady's sorrel	FACU
OXST	<i>Oxalis stricta</i> L.	Upright yellow wood sorrel	UPL
PAAN	<i>Panicum anceps</i> Michx.	Flat-stemmed panic grass	FAC
PHPO	<i>Phaseolus polystachios</i> (L.) BSP.	Wild kidney bean	NI
POHY	<i>Polygonum hydropiperoides</i> Michx.	Mild water pepper	OBL
POPE	<i>Polygonum pensylvanicum</i> L.	Pennsylvania smartweed	FACW
POSP	<i>Poa</i> sp.	Bluegrass	-
SEGL	<i>Setaria glauca</i> (L.) Beauv.	Yellow foxtail	FAC
SOCA	<i>Solanum carolinense</i> L.	Horse-nettle	UPL
TAOF	<i>Taraxacum officinale</i> Weber.	Common dandelion	FACU-
VEAL	<i>Vernonia altissima</i> Nutt.	Tall ironweed	NI
XAPE	<i>Xanthium pensylvanicum</i> Wallr.	Smooth-body cocklebur	NI

*WIS abbreviations are as follows: OBL (obligate wetland), FACW (facultative wetland), FACW+ (facultative wetland+), FACU- (facultative upland-), FAC (facultative), FAC- (facultative-), UPL (obligate upland), FACU (facultative upland), and NI (no indicator).

Liberty 110 ICP Emission Spectrometer. Extractable N pools were determined as the pre-incubation levels of NH_4 and NO_3 . Net N mineralization was calculated as post-incubation N (NH_4 plus NO_3) minus pre-incubation N pools (NH_4 plus NO_3); net nitrification was calculated as post-incubation NO_3 minus pre-incubation NO_3 .

Data Analysis

Prior to statistical analysis, the cumulative data sets (site and transect studies) were each tested for normality using Shapiro-Wilk test in Statistix 7.0 (Analytical Software 2000). All site study variables conformed to a normal distribution and were therefore used as untransformed data. All transect variables except Mg conformed to normality.

Magnesium data departed only slightly for normality ($W = 0.95$; $P < 0.10$) and any attempts to transform them resulted in further departure. Therefore, transect Mg data were used untransformed.

Means were compared between site types using t-tests (Analytical Software 2000). Because spatial heterogeneity within a given site is reflected in the variance associated with the mean, differences in degree of spatial variability between sites were determined with F tests, which test for homogeneity of variances of two means (Zar 1999). Relationships among variables, sites, and vegetation were assessed with canonical correspondence analysis (CCA) using CANOCO version 4.5.

Species diversity was calculated using the Shannon-Wiener Index (H'). This was based on cover for site data and on above-ground biomass for transect

Table 2. Soil and vegetation variables (mean \pm standard deviation) in 1-m² plots (n = 25) within pasture (PA) and seasonal wetland (SW) sites. Significant differences between variances determined by the F test and between means by the t-test (Zar 1999). Significant differences between sites at P < 0.05, P < 0.01, and P < 0.001 indicated by *, **, and ***, respectively.

	PA	SW	F	t
Net N mineralization rate ($\mu\text{g N/g soil/d}$)	0.5 \pm 0.8	1.6 \pm 1.0	1.6	4.2***
Net nitrification rate ($\mu\text{g NO}_3\text{-N/g soil/d}$)	0.7 \pm 0.9	1.9 \pm 1.3	1.9	3.7***
NH ₄ ⁺ pool ($\mu\text{g NH}_4\text{-N/g soil}$)	5.7 \pm 6.5	9.0 \pm 10.0	2.5*	1.4
NO ₃ ⁻ pool ($\mu\text{g NO}_3\text{-N/g soil}$)	9.8 \pm 3.3	5.9 \pm 2.5	1.8	4.8***
Organic matter (%)	8.3 \pm 0.6	10.6 \pm 1.3	4.2***	7.9***
pH	4.4 \pm 0.25	3.9 \pm 0.04	31.8***	9.9***
Ca ($\mu\text{g/g soil}$)	769 \pm 645	302 \pm 106	37.1***	3.6**
Mg ($\mu\text{g/g soil}$)	122 \pm 120	174 \pm 33	13.4***	2.1*
Al ($\mu\text{g/g soil}$)	0.5 \pm 1.4	202 \pm 41	854.2***	24.4***
Species diversity (H')	1.38 \pm 0.15	1.83 \pm 0.12	1.7	11.5***
Species evenness (J)	0.78 \pm 0.06	0.87 \pm 0.04	2.0*	5.6***
Species richness (S) (species/1 m ²)	5.9 \pm 1.1	8.3 \pm 1.0	1.3	8.4***

data, using \ln_e -transformed p_i values. Species evenness (J) was calculated using the Pielou Index (Barbour et al. 1999). Species richness (i.e., species density) was determined as number of species per cell (1 m² for grid data, 0.25 m² for transect data).

Transect samples were designated as SW_t or PA_t (inside or outside of seasonal wetland, respectively) based on their position along the transect (n = 20 per site type). Variability of soil nutrients for SW_t and PA_t was assessed with F tests, whereas means were compared with t-tests. Relationships between variables, distance along transect, and vegetation were assessed with CCA using CANOCO version 4.5.

Geostatistics were used to determine spatial pattern and degrees of spatial dependence of soil and vegetation variables and to compare these patterns between sites and along the transect, following approaches described in Schlesinger et al. (1996) and Iqbal et al. (2005). A semi-variogram was constructed for each variable using a spherical model with the computer program VESPER, version 1.62 (Minasny et al. 2005). We recognized three patterns resulting from our geostatistical analyses. The first pattern is *spatial dependence*, wherein four values are relevant in interpreting spatial pattern: 1) the nugget effect, which describes variability at 0 distance (hence, microvariability or error), 2) the structural component, which describes spatially-correlated variability, 3) the sill, which is total variability, or sample variance, and 4) the lag distance, which is the distance within which the variable is spatially dependent and beyond which is spatially independent. The second pattern is *randomness*, resulting when the nugget effect is high enough to approximate the sill (i.e., nugget:sill ratio \approx 1). The third pattern is *linearity*, which results

when spatial dependence occurs, but does so at scales far greater than that found in the sample space and thus is linear within the sampled distance.

RESULTS

Sites

Soil. Mean net N mineralization and net nitrification rates were three times higher (P < 0.001) in SW than in PA; however, spatial heterogeneity of these processes did not vary significantly between sites (Table 2, Figures 3 and 4). By contrast, levels of extractable NH₄ (i.e., NH₄ pools) were similar between sites, yet differed significantly in degree of spatial variability; NO₃⁻ pools were significantly higher for PA, but more variable in SW (Table 2). Relative nitrification rates (i.e., the percent of mineralized N that becomes nitrified) were high at both sites (Figure 5).

Means for all other measured soil variables were significantly different between sites. Furthermore, their degree of spatial heterogeneity also varied significantly between sites (Table 2). Organic matter and extractable Mg and Al were significantly higher in SW, whereas pH and Ca were higher in PA (Table 2).

Vegetation. Vegetation of PA was predominantly upland species, although a few wetland species (OBL and FACW), such as CIAR and JUEF, were found at low cover and frequency (Table 3). Vegetation in SW was dominated by species typically found in wetlands including JUEF, LYNU, POPE, POHY, CATR, and ASLA (Table 3).

Total species richness (i.e., for entire site) was higher in PA than SW (19 vs. 15 species/25 m²,

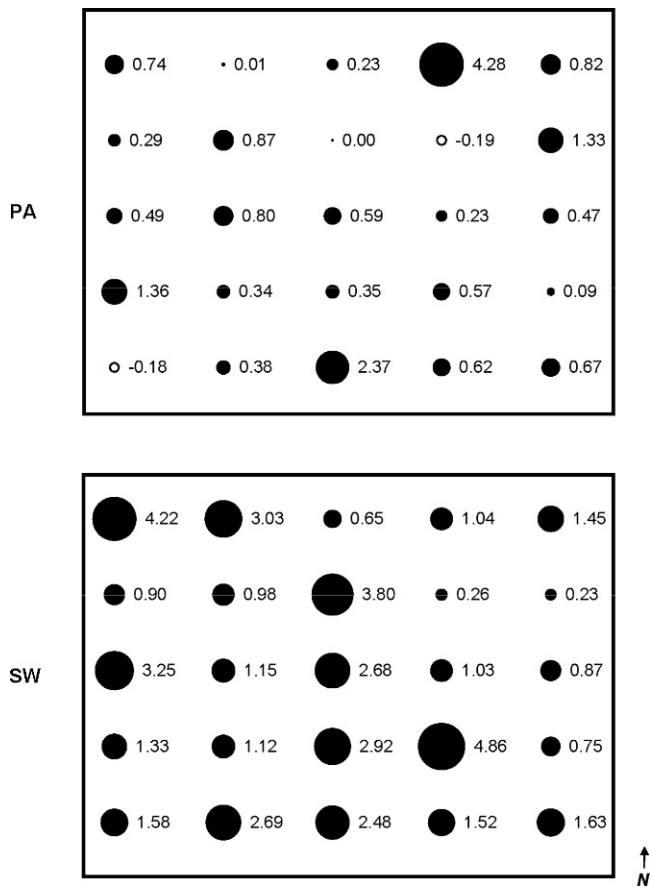
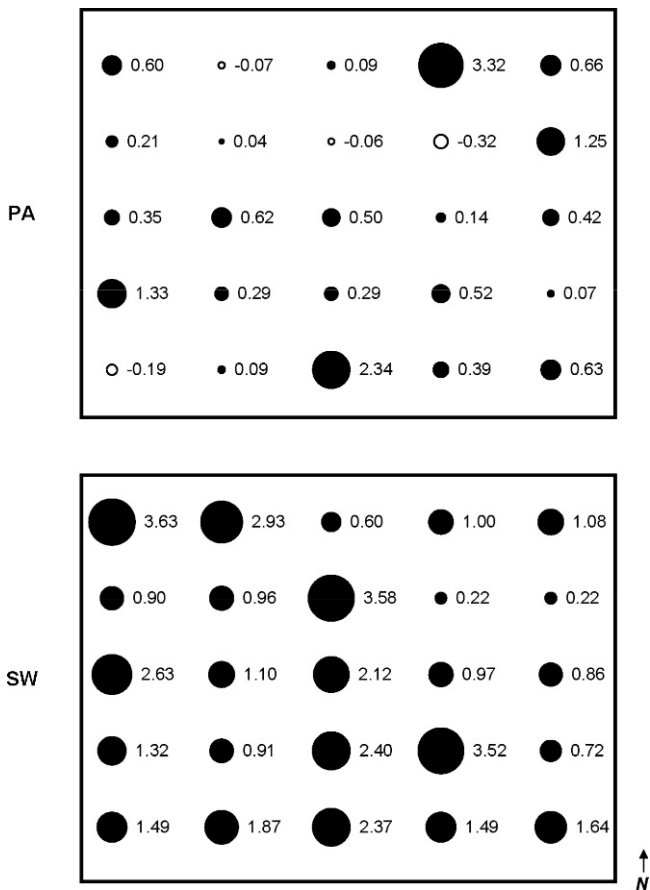


Figure 3. Bubble map of net N mineralization rate for individual plots of pasture (PA), and seasonal wetland (SW) sites. Bubbles represent plots numbered 1–25 starting in the upper left corner across then down. Bubble area is proportional to recorded values, which are presented next to each bubble ($\mu\text{g N/g soil/d}$).

Figure 4. Bubble map of net nitrification rate for individual plots of pasture (PA), and seasonal wetland (SW) sites. Bubbles represent plots numbered 1–25 starting in the upper left corner across then down. Bubble area is proportional to recorded values, which are presented next to each bubble ($\mu\text{g NO}_3^- \text{-N/g soil/d}$).

respectively). Mean species richness (S) at the 1-m² plot scale was significantly higher in PA versus SW, as were Shannon-Weiner diversity (H') and evenness (J) (Table 2). Plot-scale variability in species richness, diversity, and evenness generally did not differ between sites (Table 2).

Multivariate analysis (CCA) displayed a clear separation of PA and SW plots (Figure 6). Axes 1 and 2 described 40.0% and 2.6% of variance in the data, respectively. Based on vector length, extractable Al was the overriding environmental factor separating PA and SW plots. Magnesium, Ca, NO₃, and pH were of lesser importance in discriminating between sites. Plant species associated with SW plots in ordination space were either obligate wetland species (e.g., LYNU and POHY) or facultative wetland species (e.g., ASLA, JUEF, and POPE). Plant species associated with PA were either upland (e.g., ASPI) or facultative upland species (e.g., FEEL).

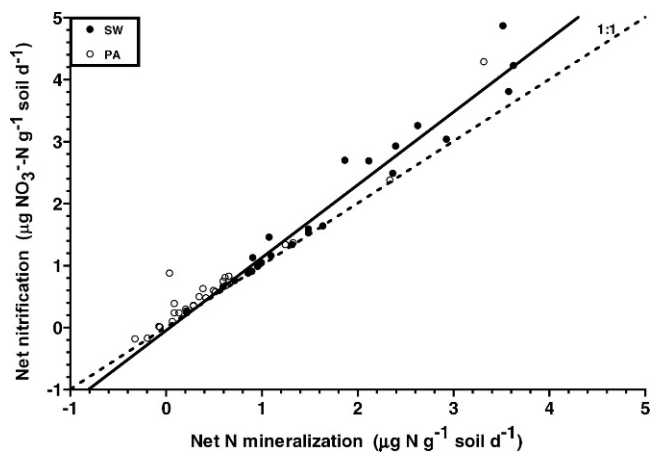


Figure 5. Net nitrification versus net N mineralization in pasture (PA) and seasonal wetland (SW) soils. Separate linear regression were not significantly different between sites; solid line represents linear regression for both site combined: $y = 0.04 + 1.15x$, $r^2 = 0.96$. Dashed line is shown to indicate 100% relative nitrification.

Table 3. Mean percent cover (n = 25 1-m² plots/site) of species encountered within 5-m × 5-m sites located within seasonal wetland (SW) and pasture (PA) sites. An asterisk (*) between values indicates significant difference (P < 0.05), based on a t-test. See Table 1 for species abbreviations.

Species	SW		PA		Wetland Indicator Status
	%		%		
JUEF	60.8	*	1.8		OBL
LYNU	54.6	*	-		OBL
POPE	27.0	*	-		FACW
ASPI	26.4	*	58.4		UPL
POHY	25.8	*	-		OBL
ECCR	18.6	*	-		FACU
CATR	14.2	*	-		FACW+
ASLA	13.0	*	-		FACW-
COCO	9.0	*	-		FAC-
SOCA	7.0		7.2		UPL
SEGL	1.6		3.2		FAC
CAVU	1.2		1.2		OBL
XAPE	0.6	*	-		NI
FEEL	0.4	*	71.0		FACU-
ACRH	0.4	*	-		FACU-
POSP	-	*	23.0		-
CIAR	-	*	7.0		FACW+
VEAL	-	*	5.8		NI
DISA	-	*	2.8		FACU-
ARHI	-	*	2.6		NI
ELCA	-	*	1.8		FACU
PHPO	-	*	1.2		NI
JUTE	-	*	1.2		FAC-
GLHE	-	*	0.6		FACU
PAAN	-	*	0.6		FAC
OXST	-	*	0.6		UPL
TAOF	-	*	0.2		FACU-
CYST	-	*	0.2		FACW

Transect

In presenting the results for soil and vegetation analyses along the transect between site types, we distinguish between the plots on the basis of their location on either side of the boundary. Thus, plots on the PA side of the boundary are designated PA_t, whereas those on the SW side are designated SW_t. It merits repeating that the transect was established to examine spatial variation in both soil and vegetation at even finer scales (i.e., 0.25-m² scale) than was used for site comparisons. We also carried this out to investigate the nature of variation in soil and plant species along the transition (i.e., ecotone) between site conditions.

Soil. Although mean net N mineralization and net nitrification rates were not different (P < 0.05) on either side of the transect boundary, spatial heterogeneity of N mineralization was significantly higher in SW_t than in PA_t (Table 4). Spatial heterogeneity in extractable N (both NH₄ and NO₃ pools) varied significantly between SW_t and PA_t; mean extractable NO₃ was significantly higher in PA_t (Table 4). Except for OM, which had neither means nor spatial heterogeneity that differed significantly between SW_t and PA_t, all other measured soil parameters had means that were significantly different and exhibited significantly different spatial heterogeneity between sites, with pH, Ca, and Mg higher and more variable in PA_t than SW_t, and Al higher and less variable in SW_t than in PA_t (Table 4).

Vegetation. Plant communities contrasted sharply on either side of the site boundary at the center of

Table 4. Soil and vegetation variables (mean ± standard deviation) in 0.25-m² plots (n = 40) along a 10-m transect in an abandoned pasture. Transect was centered (5 m outside and 5 m inside) and perpendicular to the visible boundary between the seasonal wetland and pasture sites. Samples were assigned as SW_t or PA_t based on position relative to the boundary; n = 20 for each of SW_t (inside) and PA_t (outside). Significant differences between variances determined by the F test; significant differences between means determined by the t-test (Zar 1999).

	PA _t	SW _t	F	t
Net N mineralization rate (µg N/g soil/d)	1.2 ± 0.8	1.3 ± 1.3	2.5*	0.2
Net nitrification rate (µg NO ₃ -N/g soil/d)	1.2 ± 0.7	1.1 ± 0.7	1.2	0.4
NH ₄ pool (µg NH ₄ -N/g soil)	2.4 ± 1.4	2.0 ± 0.6	5.4***	1.2
NO ₃ pool (µg NO ₃ -N/g soil)	4.4 ± 2.1	2.3 ± 1.2	2.8*	4.0***
Organic matter (%)	8.5 ± 0.6	8.5 ± 0.9	1.8	0.1
pH	4.2 ± 0.14	4.0 ± 0.03	27.6***	8.0***
Ca (µg/g soil)	1464 ± 213	991 ± 105	4.1**	8.9***
Mg (µg/g soil)	169 ± 28	110 ± 16	3.1**	8.1***
Al (µg/g soil)	1.1 ± 4.4	59 ± 14	10.7***	17.4***
Species diversity (H')	0.87 ± 0.27	0.78 ± 0.36	1.9	0.9
Species evenness (J)	0.62 ± 0.18	0.48 ± 0.18	1.1	2.5*
Species richness (S) (species/0.25 m ²)	4.4 ± 1.3	5.1 ± 1.3	1.3	8.4***

Table 5. Mean biomass of vascular plant species encountered along a 10-m transect in Wayne County, WV. Order based on mean dry weight of aboveground biomass for 0.25-m² plots (n = 40). Transect was centered (5 m outside and 5 m inside) and perpendicular to visible boundary of seasonal wetland. Plots assigned as seasonal wetland (SW_t) or pasture (PA_t) based on position along transect relative to boundary (n = 20 outside; n = 20 inside). An asterisk (*) between values indicates significant difference (P < 0.05), based on a t-test. Species codes are defined in Table 1. Graminoids contains POSP and another unidentifiable grass-like species, which could not be accurately separated and identified.

Species	Wetland Indicator Status		
	SW _t g/0.25 m ²	PA _t g/0.25 m ²	
ASPI	54.3	* 0.9	UPL
CAFR	13.2	* –	OBL
ARHI	7.4	8.0	NI
CATR	5.8	* –	FACW+
JUEF	3.7	* –	FACW+
LYNU	3.6	* –	OBL
Graminoids	1.1	* 9.1	–
AGSP	0.8	* –	–
DISA	0.2	* 21.9	FACU–
SOCA	0.2	* 2.1	UPL
DIVI	0.1	* 0.0	FACW
POPE	< 0.1	< 0.1	FACW
VEAL	–	* 0.5	NI
XAPE	–	* 0.5	NI
OXCO	–	* 0.1	FACU
SEGL	–	* < 0.1	FAC

the transect. Whereas PA_t was dominated by DISA and graminoids, SW_t was dominated by ASPI, CAFR, and CATR (Table 5). The only species of equal importance to both site types was ARHI, which was dominant in plots immediately on either side of the boundary (Table 5).

Spatial heterogeneity did not vary significantly between PA_t and SW_t for any of the diversity parameters (H', J, S), nor did mean species diversity vary significantly (Table 4). By contrast, mean evenness was significantly higher for PA_t, whereas mean richness was higher for SW_t (Table 4).

CCA displayed a clear separation of PA_t and SW_t (Figure 8). Axes 1 and 2 described 39.6% and 21.5% of variance in the data, respectively. Primary environmental gradients, based on vector length, were related to soil reaction, with increasing Al associated with plots toward SW_t and increasing pH and base cations (Ca and Mg) associated with plots toward PA_t. Important plant species associated with SW_t plots in ordination space included an upland species (ASPI), an obligate wetland species (CAFR),

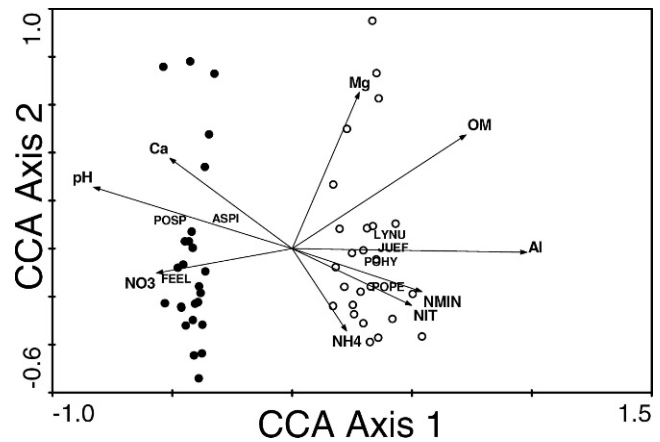


Figure 6. CCA ordination plot for PA (solid circles) and SW (open circles) sites. Lines radiating from origin represent environmental gradients. The top seven species (based on cover) are included; species codes follow Table 1.

and a facultative wet species (CATR). Plant species associated with PA_t included several grasses (GRAM) and facultative upland species (DISA).

Geostatistics

All spatial patterns (spatially dependent, linear, and random) were found among soil and vegetation variables at the PA site. Net N mineralization, NO₃, pH, Mg, species diversity, richness, and plant cover displayed spatial dependence, whereas net nitrification, NH₄, soil organic matter, and Al were linear, and Ca was random at the PA site (Table 6). All vegetation variables and soil variables were spatially dependent at the SW site, except for Ca, which exhibited a linear pattern of variation with distance (Table 6).

As with the PA site, all three spatial patterns were found along the transect. Net N mineralization, net nitrification, NO₃, soil organic matter, and Ca were spatially dependent. Soil pH, Mg, and Al were linear, and NH₄ was random (Table 7).

DISCUSSION

The intermittent inundation of the seasonal wetland, which is expected to be associated with changes in O₂ availability and soil oxidation-reduction (redox) status, appears to influence several soil processes (e.g., N mineralization), extractable soil nutrients, and characteristics of vegetation. In addition, and more central to the primary impetus behind this study, it also appears to alter spatial heterogeneity of these variables. Furthermore, var-

Table 6. Summary of geostatistical analyses of soil and vegetation variables for pasture and seasonal wetland sites. “Sill” is calculated as the sum of “nugget” variance and structural variance (“C1”). “N:S” is the ratio of nugget to sill values. “A1” denotes the lag distance within which a given variable is spatially dependent and beyond which is spatially independent (also sometimes referred to as the range). These statistics are not shown for variables for which the relationship between semi-variance and lag distance was either random or linear. All geostatistical variables are unit-less, except for A1, which is in meters.

Variable	Model	Pasture					Seasonal Wetland					
		Nugget	C1	Sill	N:S	A1	Model	Nugget	C1	Sill	N:S	A1
N mineralization	spherical	0.57	0.04	0.61	0.93	3.49	spherical	0.62	0.41	1.03	0.60	0.84
Nitrification	linear						spherical	0.84	0.73	1.57	0.54	0.47
NH ₄	linear						spherical	32.39	57.40	89.79	0.36	0.00
NO ₃	spherical	0.00	7.68	7.68	0.00	0.39	spherical	0.31	4.55	4.87	0.06	0.37
Organic matter	linear						spherical	0.00	1.57	1.57	0.00	1.59
pH	spherical	0.03	0.05	0.08	0.34	4.45	spherical	0.00	0.00	0.00	0.00	2.02
Ca	random						linear					
Mg	spherical	0.00	18147	18147	0.00	3.69	spherical	171.00	991.40	1162.40	0.15	3.29
Al	linear						spherical	0.00	1609.30	1609.30	0.00	1.47
Species diversity (H')	spherical	0.01	0.01	0.02	0.32	1.31	spherical	0.01	0.01	0.01	0.42	0.86
Species richness	spherical	0.18	0.97	1.15	0.16	2.31	spherical	0.56	0.41	0.97	0.58	4.14
Cover	spherical	120.00	580.20	700.20	0.17	1.41	spherical	281.60	968.30	1249.90	0.23	0.69

iation in spatial pattern and heterogeneity between site types differed among soil and plant variables, i.e., whereas some (e.g., nitrification rate and NO₃ pools) did not vary between sites, others (e.g., NH₄ pools and organic matter) exhibited greater heterogeneity in the SW site, and still others (e.g., pH) exhibited greater heterogeneity in the PA site.

This has important implications for assessing wetland conditions and endpoints during the creation of mitigation wetlands. We discuss our results for the two sampling approaches separately, beginning with comparisons between the SW and PA site types, followed by examination of variation in soil and vegetation parameters along the transect. Finally, we make inter-site comparisons for spatial pattern and dependence of soil and vegetation variables by interpreting the results of geostatistical analyses of site and transect data.

Sites

There were some unexpected results in our study regarding soil N, including rates of N processing and the relative size of extractable N pools. First, net N mineralization was essentially 100% net nitrification, indicating that essentially all N mineralized by microbes is eventually converted to NO₃⁻ by nitrifying bacteria, independent of site type (Figure 5). Such high relative nitrification rates are symptomatic of a phenomenon called nitrogen saturation, which arises when N supply exceeds biotic N demand and is usually associated with high rates of atmospheric deposition of N (Fenn et al. 1998). Though this has been described for forested regions of the north-central part of West Virginia (Gilliam et al. 2005), it has not been described for herb-dominated communities in the western parts of

Table 7. Summary of geostatistical analyses of soil and vegetation variables for the sample transect between pasture and seasonal wetland sites. See Table 6 for explanation of geostatistical variables. All geostatistical variables are unit-less, except for A1, which is in meters.

Variable	Model	Nugget	C1	Sill	N:S	A1
N mineralization	spherical	0.21	0.65	0.85	0.24	0.00001
Nitrification	spherical	0.33	0.14	0.47	0.70	0.48
NH ₄	random					
NO ₃	spherical	1.21	3.75	4.96	0.24	3.88
Organic matter	spherical	0.15	0.44	0.59	0.26	1.14
pH	linear					
Ca	spherical	28129	50000	78129	0.36	5.29
Mg	linear					
Al	linear					

the state. It should be noted, however, that results for our study represent net N mineralization and nitrification potentials, rather than rates that represent true field conditions.

Second, we had expected net N mineralization (and especially net nitrification) to be higher in PA soils because of the potential limitation of low O₂ availability to nitrifiers at the SW site. Indeed, our results for soil N dynamics contrast with those of some other studies. Zak and Grigal (1991) found that net N mineralization and nitrification in upland forest soils in Minnesota were > 5 times those of wetland forest soils, despite being separated by very short distances (~2–5 m, similar to separation of sites in our study). Working in Ontario watersheds, Devito et al. (1999) also found 5- to 6-fold higher net N mineralization rates in upland forest soils versus adjacent peatland soils. Again, however, it is unclear how much of our unexpected results arose from the controlled conditions of the incubation (i.e., more O₂ availability during sub-sampling from bags and constant temperature at 27°C).

On the other hand, our findings are consistent with the seasonal character of the SW site, wherein drawdown of water during dry periods repeatedly reconverts the site to non-wetland status, i.e., from reducing to oxidizing conditions. Although soil redox was not measured in this study, it is clear the redox of SW soils must be sufficiently high for long enough periods to support active populations of nitrifying bacteria. Such a dynamic system for the SW with regards to soil N is consistent with findings of Gilliam and Fisher (1995) and Gilliam et al. (1999) that demonstrated a sensitive response of soil N to rapid changes in redox conditions following mitigation wetland creation at another West Virginia site close to our study. Bossio et al. (2006) demonstrated that soil microbes responded sensitively to gradients in soil aeration in restored wetlands of California. Pett-Ridge et al. (2006) showed that in soils that experience frequent depletion and re-supply of O₂, microbial response (i.e., tolerance and resilience) can control spatial and temporal patterns of soil N cycling.

We suggest that higher organic matter in SW versus PA soils arises from the lower O₂ availability during extended periods of inundation that would limit rates of decomposition (Axt and Walbridge 1999). Bruland and Richardson (2006) found similar contrasts in comparing paired created versus native wetlands, with 11.8% versus 29.0% soil organic matter, respectively. Site-related differences in both amounts and spatial heterogeneity are likely related to dominant vegetation. Disappearance of soil organic matter is affected by quantity and quality

of plant substrates (Aerts 2006, Bossio et al. 2006). In addition, the dominant species for SW was *Juncus effusus*, which has a decidedly caespitose growth form, thus creating discrete patches of detritus, both aboveground as litter and belowground as fine roots.

Contrasts between sites for pH and cations, including spatial heterogeneity, are likely related to differences in redox, wherein PA soils are consistently oxidizing and SW soils fluctuate between reducing during inundation and oxidizing during seasonal drawdown (Gilliam et al. 1999). Soil acidity is typically higher under reducing conditions, creating uniform conditions in SW soils of lower pH and resulting higher solubility of Al and lower solubility of Ca (Darke and Walbridge 2000). Pellerin et al. (2002) found similar patterns of contrast in Ca and Al in seasonally saturated versus upland soils in Maine, i.e., higher Al/lower Ca versus lower Al/higher Ca, respectively.

Differences between sites in species composition are what were expected of wetland versus upland plant communities (Table 3, Figure 6), suggesting that the SW site, though distinctly seasonal in periods of inundation, is truly of a wetland status. The two predominant plant species for SW, *J. effusus* and *Lysimachia nummularia*, are classified in the PLANTS Database (USDA, NRCS 2004) as FACW+ and OBL wetland species, respectively. By contrast, PA was dominated by *Festuca elatior* and *Aster pilosus*, classified as FACU- and UPL, respectively. Canonical correspondence analysis demonstrated an essential lack of overlap of overall community composition between sites (Figure 6) and confirmed differences in soil conditions (Table 2). Soil Al had the longest vector length (Figure 6), suggesting that it may be particularly important in determining spatial patterns of species composition between sites or is responding to some factor that also varies between sites.

The diversity index used in our study, the Shannon-Wiener Index (H'), reflects both numbers of species (richness, also called species density—S) and the equitability with which importance (measured here as percent cover) is distributed among those species (evenness—J). Thus, the significantly higher H' found for SW compared to PA resulted both from greater numbers of species per plot (higher S) and from greater equitability (higher J) at SW (Table 2).

Transect

Despite sampling what we anticipated to be a gradient between the two site types, soil conditions

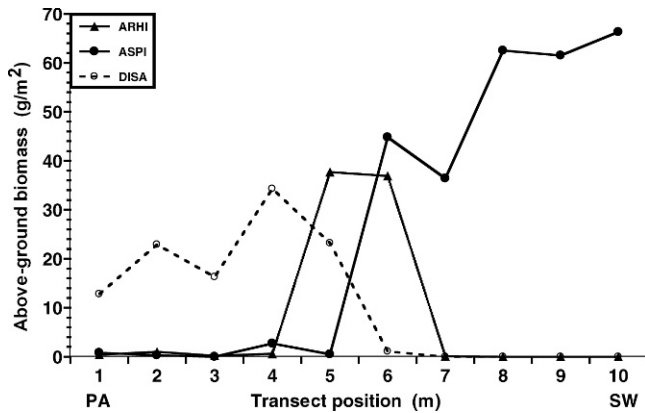


Figure 7. Changes in above-ground biomass of the top three abundant species along the transect between site types: ARHI (*Arthraxon hispidus*), ASPI (*Aster pilosus*), DISA (*Digitaria sanguinalis*). Distance class indicates distance along the transect from PA (1 m) to SW (10 m).

along the transect appeared to reflect the more discrete differences displayed for the inter-site comparisons (Tables 2, 4). Notable exceptions to this, however, were 1) general lack of significant differences in net N mineralization/nitrification between PA_t (plots on the PA side of the transect) versus SW_t (plots on the SW side of the transect), 2) significant differences between PA_t and SW_t in spatial heterogeneity of soil N, and 3) lack of differences in soil organic matter, including both means values and spatial heterogeneity, between PA_t and SW_t. Soil pH and extractable cations displayed identical patterns of contrast between PA_t and SW_t as was found between site types. Pellerin et al. (2002) found spatial patterns of extractable Ca and Al along a moisture gradient (i.e., transect) that were similar to our results. That is, Al increased, and Ca decreased, with increasing soil moisture along the gradient.

Although sampling vegetation within transects along ecotones has proven useful in characterizing species' response to environmental gradients (Roovers et al. 2004), species composition within our transect displayed a more narrow ecotone between site types than expected. The sharp separation found in the CCA for site comparisons between PA and SW using 1-m² plots (Figure 6) was largely found in the CCA for transect data based on 0.25-m² plots (Figure 8). Further, t-test comparisons of individual species for PA versus SW (Table 3) were similar to those for PA_t versus SW_t (Table 5).

One exception to this was in the importance of *Arthraxon hispidus* in the middle of the transect (i.e., at the boundary between site types), as evidenced in empirical values of plant biomass versus distance on the transect (Figure 7) and in the location of ARHI

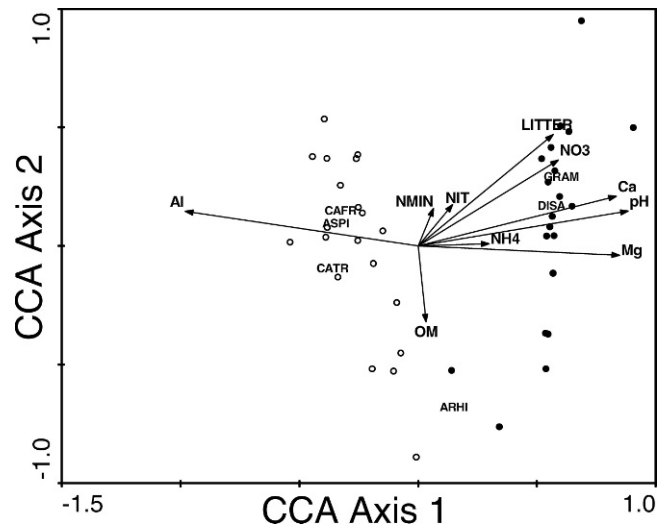


Figure 8. CCA ordination plot for transect along a pasture/seasonal wetland boundary gradient. Lines radiating from origin represent environmental gradients. The top six species/species groups (based on biomass) are included; species codes follow Table 1, except that "GRAM" represents unidentified graminoid species. Open symbols are SW_t; closed symbols are PA_t.

in ordination space (Figure 8). We suggest that this pattern for ARHI arises for two reasons. First, because it is not a wetland species (USDA, NRCS 2004), it is limited by increasingly saturated soils towards SW. Second, because it is a ruderal (i.e., "weedy") species, it does not compete well with dominant PA species, particularly the dominant species, *F. elatior*. Thus, it is confined to the narrow (~1 m) ecotone between SW and PA sites.

Geostatistics

There were sharp contrasts between sites in spatial pattern and spatial dependence for most soil and vegetation variables. Only three soil variables, NO₃, pH, and Mg, were spatially dependent in the PA site, whereas virtually all soil variables exhibited spatial dependence in the SW site (Table 6). We suggest that these differences are driven primarily by differences in spatial patterns of vegetation, particularly plant cover, that arise from the periodic inundation at the SW site. Inundated conditions have selected for the dominance of wetland species at the SW site (Table 3), especially the creeping, mat-producing growth of *L. nummularia* and the cespitose growth form of *J. effusus*. These obligate wetland species (Table 1) were the dominant species of the SW site, combining for > 40% of the total vegetation cover of that site (Table 3). Dense patches created by the growth habit of these species

establish “islands of fertility,” enhancing soil organic matter (through litter and fine root production) and, thus, soil nutrients, especially N. Although they worked in a sharply contrasting ecosystem (i.e., desert), Schlesinger et al. (1996) found similar results, with desert shrubs creating patches of high fertility in the soil beneath them. Spatial patterns found for the transect generally exhibited gradients of change from the SW to the PA site.

Synthesis and Conclusions

This study has demonstrated pronounced differences in soil characteristics and plant species composition between an area that experiences periodic inundation (the SW site) and the pasture the surrounds it (the PA site). Most of these (e.g., high Al mobility in more acidic soils of SW, higher H⁺ in SW) were expected, whereas others (e.g., higher net nitrification rates in SW) were not. More relevant to the main impetus of the study, however, were the differences between site types in spatial heterogeneity of soil properties and vegetation. Indeed, we have suggested that inundation has selected for a patterned vegetation that, in turn, has created spatial dependence in most soil variables.

These results have practical applications in three areas involving the wetland creation/restoration. 1) Sampling designs used to assess the effects of inundation on soil and vegetation. Because spatial heterogeneity itself is potentially altered by the process of inundation, numbers of plots used may need to vary between pre- and post-inundation periods. 2) Vegetation may be more important than soil properties to delineate wetland status of seasonally-inundated sites (Meganigal et al. 1993, Mitch and Gosselink 2000). Data from this study confirm conclusions of earlier studies at nearby sites (e.g., Gilliam and Fisher 1995, Gilliam et al. 1999) that soil N is particularly unsuitable to assess efficacy of wetland creation or restoration because soil N dynamics change rapidly and sensitively to changes in redox conditions. On the other hand, data specifically from our study suggest that extractable soil cations such as Al may also be useful in wetland delineation. 3) Sites such as ours that display high rates of net nitrification create challenges in wetland creation/restoration not to increase production of N₂O through the anaerobic, bacterially-mediated process of denitrification. Bedard-Haughn et al. (2006) demonstrated that 75% of N₂O emissions from ephemeral (seasonal) wetlands in Saskatchewan, Canada, arose from denitrification of soil NO₃ that accumulated through the seasonal period of inundation.

Although it is beyond the scope of this study, our results lead us to speculate that nitrification might remain high at the PA and SW sites until after wetland creation. If this were to occur, NO₃ should accumulate in the soil, increasing the size of the NO₃ pool. In the absence of uptake of NO₃ by plants (which will be largely submerged), this excess NO₃ may be lost to the atmosphere via denitrification as N₂O, a greenhouse gas that has been shown to contribute to global warming.

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