WETLANDS, Vol. 25, No. 3, September 2005, pp. 685–696

RELATIONSHIPS AMONG ENVIRONMENTAL FACTORS, VEGETATION ZONES, AND SPECIES RICHNESS IN A NORTH AMERICAN CALCAREOUS PRAIRIE FEN

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Abstract: Pattern and zonation of peatland vegetation are regulated by environmental gradients, as well as by effects of biomass and competitive exclusion on distribution of species richness. The interplay of these factors has not been closely examined in calcareous prairie fens, which are isolated, species rich, calcareous peatlands in the Prairie Peninsula region of North America. We used multivariate analyses to classify vegetation and to quantify species richness in relation to substrate conditions and vegetation structure in a 23-ha calcareous prairie fen in northeast Illinois, USA. Plant assemblages formed a floristic continuum across sedge meadow, graminoid fen, calcareous seep, marl flat, and spring run vegetation, with complete dissimilarity between spring run and sedge meadow. These vegetation zones corresponded to gradients of decreasing organic content and cation exchange capacity, and increasing pH, Na, Mg, and total Ca concentrations, which reach extremes in spring run and marl flats. Species richness was unimodal across the fen gradient, fitting an expected model of low richness in vegetation either with large biomass (as shown by low light penetration in tall sedge meadow) or with environmentally harsh conditions and low biomass (shown by high light penetration in short marl flat and spring run vegetation). These biotic and abiotic factors, as well as hydrology, mediate vegetation pattern across the fen.

Key Words: calcareous fen, prairie fen, gradient analysis, environmental gradient, floristic gradient, vegetation zones, unimodal (hump-back) species distribution

INTRODUCTION

Gradients in pH, conductivity, mineral and nutrient concentrations, as well as hydrology, are well-known factors contributing to vegetation patterns or zones in fens (Bridgham et al. 1996), both in North America (Vitt et al. 1975, Slack et al. 1980, Bernard et al. 1983, Glaser 1983, Seischab 1983, Vitt and Chee 1990, Motzkin 1994) and in Europe (Koerselman et al. 1990, Boeye and Verheyen 1994, Wheeler and Proctor 2000). The interaction of substrate chemical and nutrient gradients with biomass and with species pools in regulating distribution of plant species richness has also been confirmed in European fens (Olde Venterink et al. 2001) and in some North American wetlands (Gough et al. 1994, Grace and Pugesek 1997, Grace et al. 2000). However, few studies (e.g. van der Valk 1976) have examined these relationships in Midwest fens. In this paper, we analyze the distribution of vegetation and species richness in relation to environmental gradients in a species rich calcareous prairie fen, a vegetation type for which little specific information is available on how biotic and abiotic factors affect vegetation pattern and structure (Amon et al. 2002). In particular, we are interested in whether vegetation pattern and distribution of species richness in this fen conform to models developed for other wetlands based on substrate and biomass gradients.

Calcareous fens in the glaciated Midwest are isolated peatlands that form a vegetation continuum with surrounding tallgrass prairie and graminoid wetlands. They also support a species-rich and often distinctive calciphytic plant community (Curtis 1959, Moran 1981, Amon et al. 2002). These fens are saturated by ground-water discharge carrying calcium, magnesium, bicarbonate, and sulfate from sand or gravel lenses along glacial moraines, stream valley bluffs, or from porous bedrock, and may have low availability of nitrogen and phosphorous (Carpenter 1995, Bedford and Godwin 2003, Miner and Ketterling 2003). They have been described from Iowa (Anderson 1943, Nekola and Lammers 1989, Pearson and Leoschke 1992, Nekola 1994), southern Wisconsin (Curtis 1959, Zimmerman 1983), southern Michigan (Kohring 1982, Sytsma and Pippen 1982), northern Illinois (Moran 1981, Bowles et al. 1996), northern Indiana (Stewart et al. 1993), and western Ohio (Stuckey and Denny 1981, Schneider 1992).

Calcareous fens often have two distinctive vegetation zones corresponding to either sapric peat substrate with high organic content or more fibric peat and marl substrate with lower organic content (Zimmerman 1983, Carpenter 1995, Amon et al. 2002). Fens on sapric peat in the Midwest Prairie Peninsula (Transeau 1935) have been characterized as prairie fens because of their co-dominance by prairie grasses and sedges, as well as the presence of prairie forbs (Moran 1981). Fens on fibric peat and marl may occur within areas of sapric peat and differ by having more rapid ground-water discharge, greater precipitation of calcium carbonate, and comparatively low cation exchange capacity (Bernard et al. 1983, Seischab 1983). Marl flats develop as initial deposits, as well as on erosional surfaces, and are characterized by copious ground-water discharge and accumulation of $CaCO_3$ as both fine-grained marl and granular or nodular tufa (Miner and Ketterling 2003).

The co-occurrence within sites of peat and marl substrates has potential for development of a strong vegetation-environmental gradient that has not been fully explored in Midwest calcareous fens. Such conditions may allow more competitive species to displace stress-tolerant species (*sensu* Grime 1979) from fertile habitats into environments with low nutrient concentrations and relatively high amounts of carbonates and dissolved salts (van der Valk 1976, Zimmerman 1983, Cooper 1996). If few species are available to occupy this habitat, it would result in vegetation with low species richness. However, where low P availability reduces biomass and competition, greater species richness may result (Boyer and Wheeler 1989, Boeye et al. 1997). The interactions of fertility and biomass in regulating distribution of vegetation and species richness in environmentally heterogeneous fens are thus potentially complex, and biomass (and its covariate, light penetration) may serve as a weak predictor of competition and exclusion where environmental conditions regulate the species pool. The model that appears most applicable to this interaction is a unimodal (hump-backed) distribution of species richness with a peak at mid-level biomass (Grime 1979), which has been applied to North American wetlands (Gough et al. 1994, Grace and Pugesek 1997, Gough and Grace 1999, Grace 1999).

In this study, we address the following questions using data from a Midwest calcareous prairie fen. First, how does the distribution pattern of fen vegetation correspond to gradients of substrate chemistry and mineral and nutrient concentrations across the juncture of peat and marl substrate? Second, how are biomass, as measured by vegetation height, and light penetration distributed across the fen environmental gradient? Third, as predicted, is there a unimodal distribution of species richness in relation to the fen environmental gradient and occurrence of biomass, with lower richness in habitats with tall vegetation and in environmentally stressed habitats with short vegetation?

MATERIALS AND METHODS

Study Area

The 23-ha Bluff Spring Fen (hereafter Bluff Fen) is located about 50 km west of Lake Michigan and Chicago, in Cook Co., Illinois, USA at approximately 42° N and 88°15′ W. This is one of 12 calcareous prairie fens in Illinois that were found to contain vegetation undisturbed by historic over-grazing or drainage alteration (Moran 1981). Bluff Fen occupies a sand and gravel basin in late Wisconsinan (Woodfordian-age) glacial outwash of the West Chicago Moraine (Willman and Lineback 1970, Willman 1971), in which elevation above sea level ranges from 220 m along spring runs in the fen basin to 232 m atop adjacent gravel hills (Stoynoff and Hess 1986). The fen is in the watershed of the Fox River, a tributary of the Illinois River.

The Bluff Fen vegetation is graminoid-dominated and has been classified *a priori* along a topo-edaphic gradient (Figure 1) (Bowles et al. 1996). Graminoid fen and sedge meadow vegetation occur on saturated peat in the upper fen basin, which has a sub-surface water table, while calcareous seep vegetation occurs on lower terraces where the water table is at or above the land surface, displaying visible ground-water discharge. Marl flat and spring run vegetation occur where stronger seepage has eroded peat and flows over marl substrate (Miner and Ketterling 2003). Ground-water monitoring subsequent to our study period also indicate a topo-edaphic gradient in water-table fluctuation, as measured by the Coefficient of Variation, with up to 2.5 times more variation in graminoid fen than in marl flat (J. Miner, unpublished data). The surface-water flow in marl flat and spring run habitats is thus stronger and more constant than in other fen habitats (Carpenter 1995, Amon et al. 2002). Fire is a natural process that maintains prairie fen vegetation (Curtis 1959, Moran 1981, Zimmerman 1983), and Bluff Fen is managed by dormant season burning and removal of invasive shrubs (Stoynoff and Hess 1986, Bowles et al. 1996).

Vegetation Sampling and Data Analyses

Vegetation data were collected during the 1992 growing season from 0.25 m^2 sample plots positioned

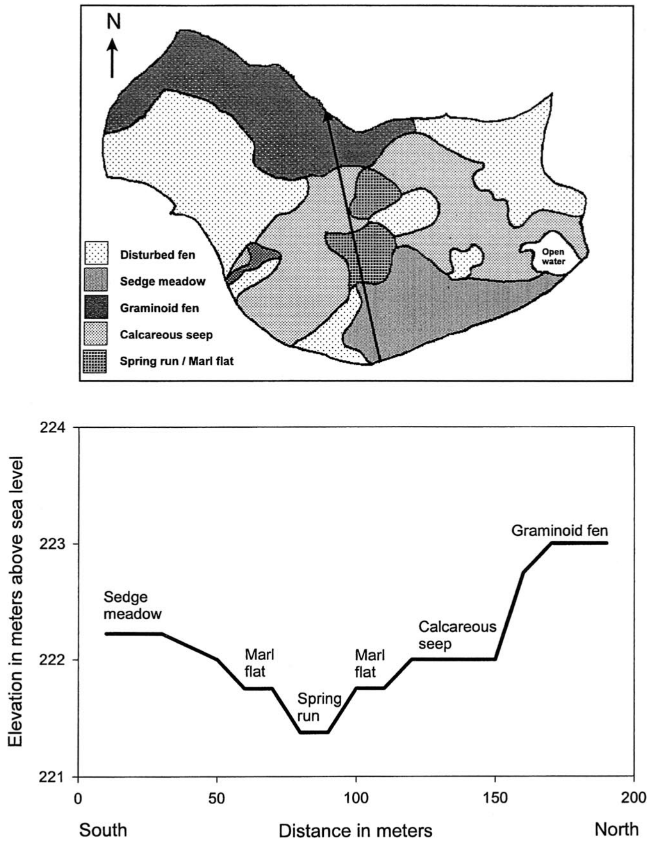

Figure 1. Upper: Bluff Spring Fen plant communities; solid line and arrow represent location and direction of relief cross section. Lower: community locations in relation to relief cross section.

at 5-m intervals along stratified random transects; only plots from relatively undisturbed fen areas were used for this study (see Bowles et al. 1996). Nomenclature follows Swink and Wilhem (1994). Plant species percent cover was estimated from these plots using a square decimeter grid as a template. Community assemblages were classified for subsequent substrate analysis by Two-Way Indicator Species Analysis (TWINSPAN) using default settings on PC-ORD software corrected for data input order stability (Tausch et al. 1995, Oksanen and Minchin 1997, McCune and Mefford 1999). We provided identities for groups produced by TWINSPAN in a two-step process. First, each sample plot was assigned the a priori community name from Bowles et al. (1996) based on its occurrence within mapped vegetation types (Figure 1). Then, each TWINSPAN group was assigned the community name corresponding to highest percent occurrence of each plot name in that group. Sørensen correlation coefficients were calculated to determine percent similarity between the a priori and TWINSPAN groups.

Sample plots were ordinated using two-dimensional global non-metric multidimensional scaling of species percent cover with a Sørensen distance measure on PC-ORD software (McCune and Mefford 1999). The ordination was seeded with data from a DECORANA graphic output file of the same data set. Reduction in stress, the departure from monotonicity between original and ordinated data, was evaluated by a Monte Carlo test (McCune and Mefford 1999). To evaluate the ordination visually, input stands were coded by their TWINSPAN classifications.

For each TWINSPAN vegetation group, we calculated mean species richness per plot and the number of species reaching their greatest frequency in that community. We used a one-way ANOVA to test a null hypothesis of no difference in mean plot species richness among these groups. Because the unequal sample sizes produced by TWINSPAN affect total species richness sampled in each community, we also extrapolated total richness using first- and second-order jackknife estimates (Palmer 1990, 1991). To estimate the effect of biomass, we used surrogate measures of maximum vegetation height and light penetration, which may affect species richness to a greater extent than biomass in herbaceous vegetation (Grace 1999, Grace 2001, Kotowski et al. 2001). These measures were taken at the end of the growing season (when biomass would be at a maximum) from ten random points along transects within each vegetation group, which were also random with respect to vegetation plots. Light in full sun and light penetration at ground level were measured using a Li-Cor LI-190 SA Quantum Sensor, which records instantaneous photosynthetically active radiation (PAR in micro-mol s^{-1} m^{-2}). Percent light penetration at each point was calculated as the percentage of maximum PAR based on its measure in full sun. These percent light penetration and vegetation height data were log-transformed and analyzed with a one-way ANOVA for differences among communities. Light penetration data were also correlated with measures of vegetation height.

Soil Substrate Sampling and Analyses

Substrate samples were collected from 27 randomly selected vegetation plots stratified by the TWINSPAN classification, with n = 5 samples for each class except sedge meadow (n = 7). Each sample comprised approximately 250 g of ground-water-saturated substrate excavated to a depth of 10 cm and was refrigerated in a clean polyethylene bag until analyzed. To approximate the soil solution from which plants obtain nutrients (Larcher 1975), analyses were made directly from these samples using percent base saturation to measure mineral and nutrient concentrations. For pH, the solution was adjusted to a 1:1 soil:water paste. Samples

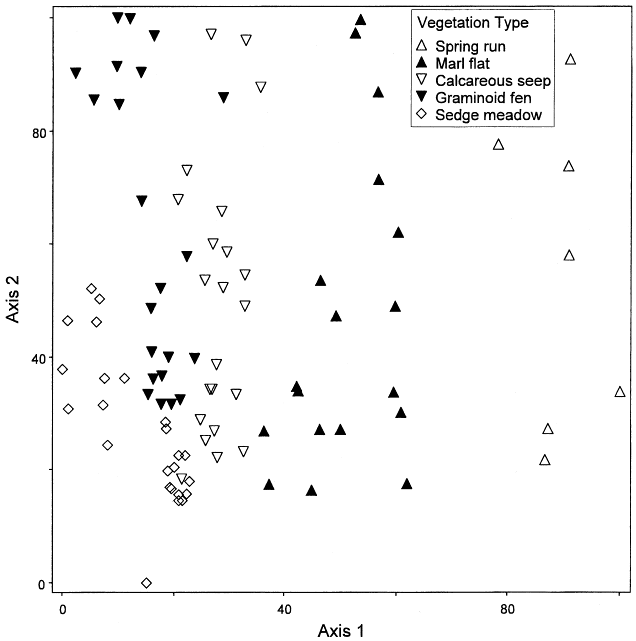

Figure 2. Non-metric Multidimensional Scaling ordination of Bluff Spring Fen plant communities. Vegetation types represent TWINSPAN classification (Table 1).

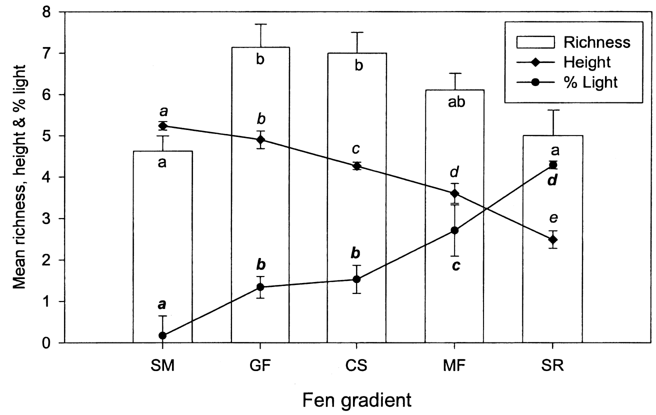

Figure 3. Relationship between plot species richness, vegetation height, and percent light penetration along the Bluff Springs Fen vegetation gradient. Species richness ANOVA: $F_{4,45} = 5.59$, $P < 0.001$; vegetation height ANOVA: $F_{4,45} = 361.95$, $P < 0.0001$; light penetration ANOVA: $F_{4,45} = 150.36$, $P < 0.0001$. Bars represent standard errors for species richness, and standard deviations for vegetation height and % light. Duncan's multiple range test: similar lower case letters are not different at <0.05 (lower case = species richness, lower case italic = vegetation height, lower case bold italic = percent light penetration). Fen gradient represents the TWINSPAN classification (Table 1): SM = Sedge Meadow, GF = Graminoid Fen, CS = Calcareous Seep, MF = Marl Flat, SR = Spring Run.

were analyzed for pH, cation exchange capacity (CEC), percent organic carbon content, Bray 1 phosphorous (P1), and total calcium concentrations and percent base saturation of K, Mg, Ca, and Na. Organic carbon was determined by dichromate reduction using the Walkley-Black procedure (Nelson and Sommers 1982). Because of calcium carbonate saturated ground water, CEC was determined by the NaCl method for acid and alkaline soils (Rhodes 1982). Elements, except for P, were extracted using ammonium acetate, pH 7.0 (Soil Survey Staff 1992) and analyzed by atomic absorption spectrophotometry. Phosphorous concentrations were determined using the Bray and Kwartz (1945) extraction method.

The relationship of vegetation with soil chemistry and mineral and nutrient concentrations was analyzed by Canonical Correspondence Analysis (CCA) in PC-ORD (McCune and Mefford 1999), as well as by direct analysis of soil variation across the first axis. In both cases, replicates were within TWINSPAN groups. For the CCA vegetation matrix, species percent cover values were used for the 27 plots from which soil samples were taken, resulting in a subset of the entire matrix used for NMS and for TWINSPAN. For the CCA soil matrix, all data were log-transformed. CCA options were set to optimize plots using biplot scaling, with linear combinations of soils data used for plot scores in the vegetation matrix; PC-ORD uses an iterative method of CCA following ter Braak (1986). A Monte Carlo test (100 runs) was used to test the null hypothesis of no relationship between the CCA vegetation and soil matrices. One-way ANOVA was used to test whether significant gradients for soil variables occurred across the NMS vegetation gradient, as classified by TWINSPAN. Mean pH was calculated using hydrogen ion concentrations. For these tests, all percentages were arcsine-transformed (Zar 1974), while untransformed means are presented graphically. Comparisons among means were made by Duncan's multiple range test at the 0.05 probability level.

RESULTS

Classification and Ordination

Three TWINSPAN divisions classified vegetation data corresponding to the *a priori* community classification (Table 1). The first division separated two groups, one corresponding to sedge meadow, graminoid fen, and calcareous seep, and the second to marl flat and spring run. The second division separated sedge meadow, spring run, and marl flat, and the third division separated graminoid fen from calcareous seep. The Sorenson correlation coefficient between number of plots shared by the *a priori* and TWINSPAN groups was 53.6% for calcareous seep and 70% or higher for all others. A floristic gradient also occurred across the fen, with 42–71% species similarity between adjacent

TWINSPAN groups. However, there was 0% similarity between spring run and both graminoid fen and sedge meadow and <5% similarity between spring run and calcareous seep. Thus, a 100% replacement of species occurred across the fen, with spring run and sedge meadow forming gradient extremes and calcareous seep and graminoid fen centrally located. Two- and three-dimensional scaling ordination solutions provided significantly more reduction in stress than expected by chance ($p = 0.05$) after 20 Monte Carlo runs. The two-dimensional ordination strongly corresponded to the TWINSPAN classification. Graminoid fen, calcareous seep, marl flat, and spring run vegetation aligned along the first ordination axis, while sedge meadow vegetation tended to separate from graminoid fen along the second axis (Figure 2).

Composition and Structure

Seventy plant species were sampled among the five TWINSPAN classes (Table 1). Total species richness was highly correlated with sample size ($r^2 = 0.76$), ranging from 11 species in spring run (n = 7 plots) to 42 species in calcareous seep (n = 28 plots), and jackknife estimates of species richness did not alter this pattern. There were no significant differences in either the number of species restricted to any community ($X^2 = 1.405$, $P = 0.843$) or in the number of species reaching their greatest frequency in any community ($X^2 = 5.364$, $P = 0.254$). However, mean species richness per plot had a unimodal relationship with the vegetation gradient identified by the scaling ordination and by TWINSPAN, with lower values in sedge meadow and in spring run (Figure 3). Vegetation height was negatively correlated with PAR ($r^2 = 0.75$, $P < 0.00001$). Mean percent light penetration and mean vegetation height differed significantly across the fen gradient, with lower light penetration and taller vegetation in sedge meadow and higher light penetration and shorter vegetation in spring run and marl flat (Figure 3).

Spring run and marl flat vegetation shared 50% of their species. Spring run was dominated by the grass *Deschampsia caespitosa* and the alga *Chara* spp., while the sedges *Eleocharis rostellata* and *Rhynchospora capillacea*, and the goldenrod *Solidago uliginosa* had ≥50% plot frequencies. Only two spring run species, *D. caespitosa* and a horsetail (*Equisetum* sp.), did not occur in adjacent marl flats, which were dominated by the shrub *Potentilla fruticosa*, the goldenrod *Solidago ohioensis*, and the sedge *Carex sterilis*. No other marl flat species had ≥50% frequency, although the sedge *Cladium mariscoides* and the prairie forb *Silphium terebinthinaceum* were most abundant in this vegetation.

Calcareous seep and graminoid fen had the greatest similarity between community groups, sharing 70.9% of their species. Calcareous seep was dominated by the sedge *Carex stricta* and the goldenrod *Solidago ohioensis*. No other species had ≥50% frequency, although the forbs *Rudbeckia hirta* and *Smilacina stellata* and the prairie grass *Andropogon scoparius* were abundant. Graminoid fen was dominated by *Solidago altissima* and *Aster umbellatus*, with ≥50% frequency for the forb *Smilacina stellata*, the shrub *Cornus racemosa*, and *Carex stricta*. The prairie grasses *Andropogon gerardii* and *Muhlenbergia mexicana*, prairie forbs *Silphium integrifolium* and *Solidago gigantea*, and wetland grass *Calamagrostis canadensis* were also abundant in graminoid fen.

Sedge meadow vegetation had 51.6% species similarity with graminoid fen and 47.8% similarity with calcareous seep. It was dominated by the sedge *Carex stricta*; the cattail *Typha latifolia* was the only other species with ≥50% frequency and was absent from other communities. *Calamagrostis canadensis* was the third most abundant sedge meadow species, followed by the prairie forb *Pycnanthemum virginianum* and *Solidago gigantea*.

Vegetation-Soil Relationship

The CCA vegetation ordination corresponded to the TWINSPAN classification and the scaling ordination (Figure 4). On the first CCA axis, spring run samples had the highest positive scores, followed by marl flat samples. They were both strongly separated from calcareous seep and graminiod fen, which had low first axis scores, while sedge meadow tended to separate from graminoid fen by having lower second axis scores. The first CCA axis also explained most of the variation and its eigenvalue was significantly greater than expected by chance (Table 2). The second and third axes explained less variation and were not significant ($P > 0.05$). Percent base saturation of Mg had a strong positive correlation with the first axis, while percent base saturation of Na and pH had weaker positive correlations (Table 2). Organic content, CEC, and % base saturation of Ca all had high negative correlations with the first axis. On the second axis, pH, P, and total Ca had strong positive correlations. The first axis gradient probably results from exchange site replacement of K by Na and Ca by Mg as a result of mass flow and precipitation of $CaC0_3$. The secondary axis gradient corresponds primarily to increasing pH in relation to increased levels of total Ca not yet converted to $CaC0_3$.

With the exception of P, all soil substrate variables differed significantly across the fen community gradient (Figure 5). All significance tests are provided in

Table 1. TWINSPAN classification of plant species sampled at Bluff Spring Fen Nature Preserve. Data are species frequencies within each community class. Superscripts: 1 = typical mesic or wet-mesic prairie species (Moran 1981, Swink and Wilhelm 1994), 2 = prevalent Illinois fen species (Moran 1981). Jackknife estimates of species richness are based on Palmer (1990, 1991).

	Sedge Meadow	Graminoid Fen	Calcareous Seep	Marl Flat	Spring Run
Valeriana ciliata T&G[2]			18.18	5.56	
Liatris pycnostachya Michx.[1]		4.54	13.64		
Lithospermum canescens (Michx.) Lehm.[1]			4.54		
Rudbeckia hirta L.[1,2]		4.54	45.45		
Andropogon scoparius Michx.[1,2]			27.27		
Scleria verticillata Willd.			9.09		
Ulmus rubra Muhl.			4.54		
Helianthus giganteus L.			18.18		
Spartina pectinata Link.		9.09	18.18		
Scirpus validus Vahl		4.54	4.54		
Andropogon gerardii Vitman[1,2]		18.18	9.09		
Galium boreale L.[2]		18.18	18.18		
Rubus occidentalis L.		4.54	4.54		
Smilacina stellata (L.) Desf.[1]	4.17	50.00	31.82		
Allium cernuum Roth	4.17	18.18			
Aster umbellatus Mill.	8.33	77.27	9.09		
Cornus racemosa Lam.	4.17	54.54	18.18	5.56	
Eupatorium altissimum L.		4.54			
Fragaria virginiana Duchesne		9.09			
Gentiana procera Holm[2]		4.54	9.09		
Muhlenbergia mexicana (L.) Trin.[1]		31.82	13.64		
Rosa blanda Aiton		18.18	4.54		
Silphium integrifolium Michx.[1]		18.18	4.54		
Silphium perfoliatum L.		45.45	4.54		
Stachys palustris L.[1]		9.09			
Thalictrum dasycarpum Fish. & Ave-Lall.[2]		18.18			
Viburnum lentago L.		9.09			
Galium aparine L.		9.09			
Vernonia fasciculata Michx.		4.54			
Monarda fistulosa L.	4.17	13.64	13.64	5.56	
Calamagrostis canadensis (Michx.) P. Beauv[1,2]	41.67	31.82			
Caltha palustris L.	4.17				
Cirsium muticum Michx.[2]	20.83		4.54		
Eupatorium maculatum L.	29.17				
Oxypolis rigidior (L.) Raf.[2]	4.17				
Pedicularis lanceolata Michx.[1]	4.17				
Pycnanthemum virginianum L. T. Durand & B. D. Jacks.[1,2]	33.33	4.54	9.09		
Typha angustifolia L.	4.17				
Typha latifolia L.	50.00				
Aster puniceus var. *firmus* (Nees) T & G	16.67	4.54	4.54		
Aster puniceus L.[2]	8.33	4.54	4.54		
Solidago altissima L.	41.67	63.64	4.54		
Solidago gigantea Aiton[1,2]	20.83	27.27	13.64		
Aster novae-angliae L.[1]	4.17	4.54	9.09		
Helenium autumnale L.[1]	12.50	4.54	27.27		
Lycopus americanus Muhl.[2]	20.83	27.27	27.27		
Carex stricta Lam.[2]	87.50	59.09	86.36	50.00	
Solidago patula Muhl.	12.50		22.73	11.11	
Scirpus acutus Bigelow	16.67	4.54	27.27	16.67	

Table 1. Continued.

	Sedge Meadow	Graminoid Fen	Calcareous Seep	Marl Flat	Spring Run
Senecio aureus L.[1]	4.17		13.64	5.56	
Solidago ohiensis Riddell[2]		9.09	72.73	77.78	
Muhlenbergia glomerata (Willd.) Trin.[2]		9.09	27.27	44.44	
Silphium terebinthinaceum L.[1]			13.64	33.33	
Sorghastrum nutans (L.) Nash[1,2]			4.54	5.56	
Carex sp.				11.11	
Cladium mariscoides (Muhl.) Torr.			4.54	27.78	
Lysimachia quadriflora Sims[2]			4.54	33.33	
Carex sterilis Willd.[2]				66.67	42.86
Eleocharis smallii Britton				5.56	
Juncus brachycephalus Engelm.				22.22	14.29
Lobelia kalmii L.[2]				22.22	28.57
Potentilla fruticosa L.[2]			13.64	72.22	42.86
Eleocharis rostellata Torr.				33.33	57.14
Scirpus pendulus Muhl.				5.56	
Eleocharis tenuis (Willd.) Schult.				5.56	14.29
Rhyncospora capillacea Torr.				11.11	57.14
Solidago uliginosa Nutt.[2]				22.22	57.14
Chara sp.				16.67	71.43
Deschampsia cespitosa (L.) P. Beauv.					100.00
Equisetum sp.					14.29
Total richness	25	37	42	25	11
First-order jackknife estimate	34.9	49.9	55.8	32.9	14.0
Second-order jackknife estimate	42.7	55.8	63.7	37.8	15.9

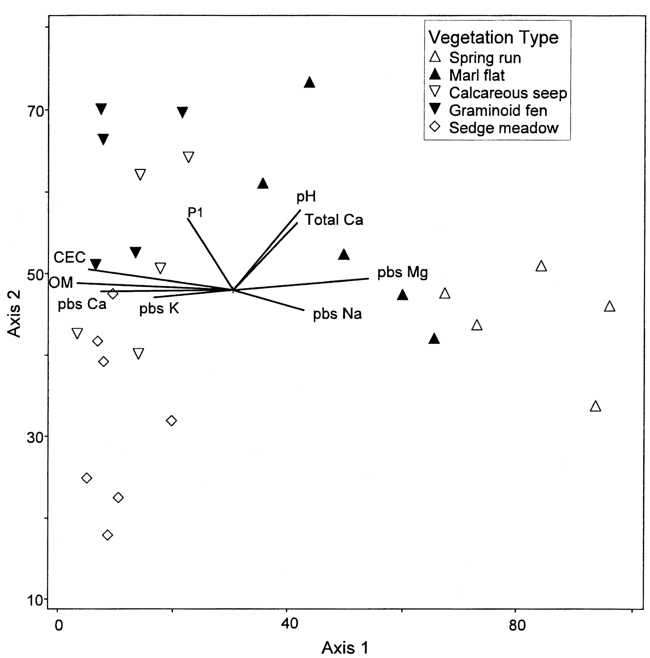

Figure 4. Canonical Correspondence Analysis and bi-plot ordination of Bluff Springs Fen plant communities. Vegetation types represent TWINSPAN classification (Table 1). Line lengths and directions represent correlations of environmental variables with axes (see Table 2).

the Appendix. The fen is alkaline, with mean pH values ranging from 7.12 in sedge meadow to 7.73 in graminoid fen. Total Ca concentrations were most highly correlated ($r = 0.44$) with pH and were below

Table 2. Canonical Correspondence Analysis. Statistics: number of iterations required to stabilize each axis, percent variance explained by each axis, and probabilities that Eigenvalues exceed the range expected by chance. Correlations: intraset correlations (ter Braak 1986) of soil chemistry and mineral and nutrient variables with the first three ordination axes.

	Axis 1	Axis 2	Axis 3
Statistics			
No. iterations	27	55	26
% variance	14.60	8.10	6.40
Eigenvalue	0.0010	0.0681	0.0711
Correlations			
OM	−0.968	+0.060	+0.174
Total Ca	+0.391	+0.562	+0.091
pH	+0.410	+0.674	+0.198
CEC	−0.895	+0.176	−0.109
pbs Mg	+0.833	+0.098	+0.015
pbs Ca	−0.820	−0.013	−0.275
pbs Na	+0.432	−0.173	+0.130
P1	−0.283	+0.602	−0.106
pbs K	−0.487	−0.060	+0.534

20,000 ppm only in sedge meadow. Organic content and CEC were strongly correlated (r = 0.62); both were significantly lower in marl flat and spring run, while OC was also higher in graminoid fen. Percent base saturations of Ca and Mg were highly negatively correlated (r = 0.94), with significantly lower Ca values and higher Mg values in marl flat and spring run. Percent base saturations of Na and Mg were positively correlated (r = 0.48). However, Na had a more narrow range of variation than most other minerals, with the only significant difference for lower mean values in graminoid fen. Percent base saturation of K also had a narrow range of variation, with the only significant difference between graminoid fen and marl flat. Phosphorus values were extremely low, with no significant variation. With exclusion of sedge meadow data, the mean P/total Ca ratio was still not significant (F = 3.02, P = 0.06), with a lower ratio in spring run and a higher ratio in graminoid fen.

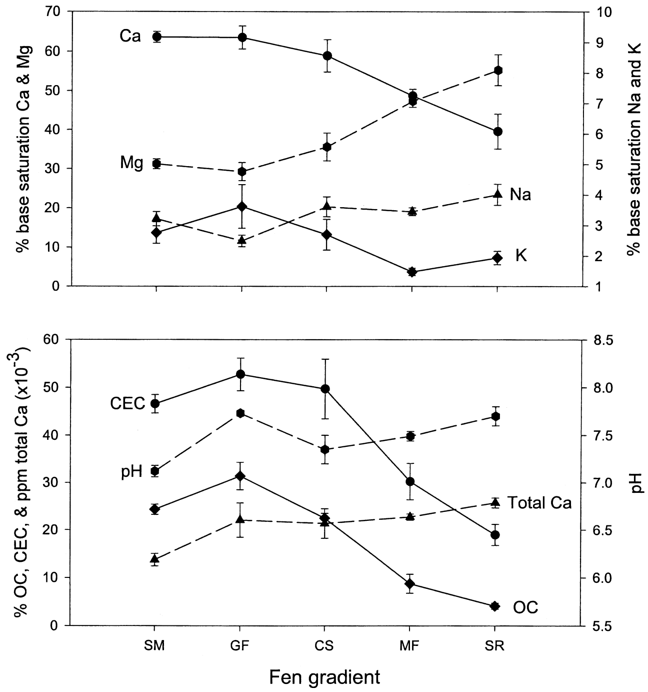

Figure 5. Substrate chemistry and mineral variation in relation to the vegetation gradient at Bluff Spring Fen Nature Preserve. Fen gradient represents the TWINSPAN classification (Table 1): SM = Sedge Meadow, GF = Graminoid Fen, CS = Calcareous Seep, MF = Marl Flat, SR = Spring Run. ANOVA: all probabilities < 0.05. Total Ca, $F_{4,22} = 4.87$, P = 0.006. See Appendix I for F statistics, exact probabilities, and for multiple range tests. Bars represent standard errors.

DISCUSSION

Vegetation Zones and the Environmental Gradient

Our results indicate that vegetation zones at Bluff Fen correspond primarily to substrate gradients of increasing or decreasing base concentrations, as pH values were >7.0 across the entire fen environmental gradient and appear to be regulated by total Ca concentrations. Only sedge meadow vegetation corresponded to combined lower pH and total Ca, and it had the higher organic content and CEC of graminoid fen and calcareous seep vegetation. Because of its base-rich conditions, Bluff Fen qualifies as an alkaline or rich fen (Sjörs 1950, DuRietz 1954, Malmer 1986). The vegetation substrate pattern also appears to correspond to the spring-flush-fen gradient of European mires (Wheeler and Proctor 2000). As found in comparisons among fens by Carpenter (1995), variation in mineral or base concentrations between peat and marl soils corresponds to different vegetation types, with relatively high organic content and CEC in graminoid fen and sedge meadow, a combination of high Na, Mg, and total Ca in spring run and marl flat, and transitional conditions in calcareous seep. Therefore, when these substrate differences occur within fens, corresponding vegetation zones should be expected.

Until now, absence of strong evidence for an environmental-vegetation gradient within calcareous fens may have been due to focus on water samples and hydrology (Amon et al. 2002), as well as lack of gradient analysis within an environmentally heterogeneous fen. Although calcareous fens are maintained by discharge of base-rich ground water, water samples are problematic for characterizing a substrate gradient encountered by plants due to their spatial flow and sensitivity to precipitation and evaporation (Carpenter 1995). Hydrology and topographic relief probably covary with other environmental conditions (Kotowski et al. 2001) in structuring vegetation because peat accumulates in areas with weaker water flow and is eroded in marl flats and spring-runs (Miner and Ketterling 2003). Hydrologic variation also may directly affect vegetation pattern by causing differences in rates of peat oxidation and mineralization across topographic gradients, which would result in greater mineral and nutrient concentrations in areas of greater drainage and organic content. At Bluff Fen, this effect would be most important in graminoid fen habitat, which has greater water-table variation than other habitats. Indeed, graminiod fen has the greatest organic content and CEC among the Bluff Fen habitats. The strong surface-water flow of spring runs and marl flats also could select for aquatic or disturbance-adapted species. Continuous water flow also provides protection for fire-sensitive species, such as the shrub *Potentilla fruticosa* (Bowles et al. 1996).

Factors Affecting Species Richness

Data from Bluff Fen support the unimodal hump-back model (Grime 1979) for the relationship between species richness and biomass, and they correspond to other North American wetlands (e.g., Gough et al. 1994, Gough and Grace 1999, Grace 1999). Our representation of this model (Figure 3) uses vegetation height and light penetration as biomass surrogates to indicate that short vegetation and high light levels are weak predictors of species richness, apparently because of environmental regulation of the number of species capable of existing in areas of low biomass. We measured mean species richness at the small plot scale, following Grace (2001), because measures of total species present will vary with sample size or area based on the well-known species-area relationship. In this observational study, we have not tested nor compared importance of many co-varying factors (Grace 1999). For example, light penetration would be more uniform across vegetation types early in the growing season, especially after prescribed burns. At that time, below-ground resource competition could affect species richness, with the reduced light penetration becoming more important as the growing season advances. Although the low species richness in sedge meadow corresponds to increasing vegetation height and lower light penetration (as expected by the model), lower pH and prolonged surface flooding and freezing (Stoynoff 1993, M. L. Bowles, pers. obs.) could also reduce the number of species capable of occupying this habitat. Nevertheless, the great abundance in sedge meadow of *Typha*, which can exclude other species by its large canopy (Apfelbaum 1985), may be a primary factor controlling richness. For example, cattail cover and frequency increased while species richness decreased in sedge meadow at Bluff Fen during a five-year period (Bowles et al. 1996).

In European fens, relatively high N and P inputs enhance biomass and competition that reduces species richness (Wheeler and Giller 1982, Boyer and Wheeler 1989, Verhoeven and Schmitz 1991, Wheeler and Shaw 1991, Wassen et al. 1995). Although we did not measure N, we found little variation in P across the fen, and it is unknown whether excessive levels of these nutrients occur in Bluff Fen or if they are related to the increase in *Typha* in sedge meadow. The slightly lower P/Ca ratio in spring run may be due to Ca immobilizing P by forming apatite (calcium phosphate), which could reduce plant growth in areas of exposed marl or carbonates (Wilson and Fitter 1984, Boyer and Wheeler 1989, Boeye and Verheyen 1994, Wassen and Joosten 1996). However, species richness is not correspondingly high, as described by Boyer and Wheeler (1989). It is likely that lower richness in spring run and marl flat vegetation is environmentally regulated, resulting in an assemblage of few stress-tolerant species with poor competitive abilities that can withstand the skewed chemistry and base concentrations of these habitats (van der Valk 1975, 1976, Grime 1979, Wilson and Keddy 1986). Spring run represents the most extreme condition, with a combination of low organic content and CEC and high $CaCO_3$, Mg, and Na concentrations. High Na levels can cause extreme osmotic conditions in plants (Larcher 1975), but this effect may be moderated by the presence of Ca and Mg ions (Maas 1986, Brady 1990, Cooper 1996). Na was significantly lower only in graminoid fen. There is some evidence for stress tolerance among spring run and marl flat species. *Deschampsia caespitosa* colonizes toxic metal-contaminated soils of abandoned mine smelters (Cox and Hutchison 1979, 1981, Bush and Barrett 1993). This grass and the sedge *Rhynchospora capillacea* were essentially restricted to spring run habitat at Bluff Fen. In Iowa fens, *R. capillacea* was most abundant in stressed habitat but had greater biomass in adjacent habitat with greater soil nutrient levels (van der Valk 1975, 1976). Species that are also important in marl flat, such as *Eleocharis rostellata* and *Carex sterilis*, may be stronger, stress-tolerant competitors. Seischab et al. (1985) considered *E. rostellata* a stress-tolerant competitor in New York fens because it occupied both marl and organic habitats but had lower biomass in marl habitat. Similarly, *C. sterilis* also occupies open areas of organic soils in other graminoid fens (M. Bowles, pers. obs.).

Summary

At Bluff Fen, a floristic gradient occurs across sedge meadow, graminoid fen, calcareous seep, marl flat, and spring run vegetation. This distribution corresponds to gradients in substrate base concentrations, which differ primarily between organic soils of sedge meadow and graminoid fen and mineral soils of spring run and marl flat habitats, with calcareous seep at an intermediate position. A unimodal distribution of species richness across the fen gradient reflects a model in which vegetation height and light penetration are weak predictors of species richness because of the strong effect of the environmental gradient on species composition. As a result, lower species richness in sedge meadow seems to be caused primarily by greater vegetation height and its influence on light transmittance, while low richness in spring run seems to be an environmental determinant of species that can tolerate a combination of comparatively high Mg, Na, and total Ca concentrations and low organic content and CEC. Species richness in stressed habitats also may be limited by the pool of species available at the landscape level to occupy these conditions (e.g., Gough et al. 1994, Grace and Pugesek 1997, Grace 2001). Although this study indicates strong correspondence between vegetation pattern and gradients in substrate characteristics and biomass, more work is need to understand hydrologic factors that may underlie this relationship.

Causes of vegetation pattern and structure at Bluff Fen have conservation and management implications, as they help demonstrate how human impacts may affect biotic and abiotic mechanisms that regulate species composition and richness in fen habitats. Calcareous fens could be vulnerable to alteration of base-rich ground-water supplies and enhanced N and P levels (Bedford and Godwin 2003), hydrologic change or sedimentation (Wilcox et al. 1985, Werner and Zedler 2002, Woo and Zedler 2002), and increased Na and Cl from urban pollution (Carpenter 1995, Wilcox 1986, Panno et al. 1999). Maintenance of a base-rich water source can also help buffer against potential effects of increasing N and P (Verhoeven et al. 1996). Plant species adapted to spring run and marl flat appear to have the greatest vulnerability to local extinction because of their landscape rarity in the fragmented Midwest landscape, where long-distance dispersal would be required to re-colonize habitats. The only other local habitat with vegetation and edaphic characteristics similar to that of spring run and marl flat habitats is calcareous intradunal ponds (pannes) along Lake Michigan. Panne habitats have high levels of carbonate, bicarbonate, Mg, and pH, which regulate the species pool, while hydrology determines vegetation zones (Hiebert et al. 1986).

ACKNOWLEDGMENTS

This study was made possible by partial funding from the Illinois Department of Natural Resources and the Illinois Chapter of The Nature Conservancy. We especially thank Ken Johnson for assistance with data collection, Steve Byers, Maggie Cole, and the Friends of the Fen for field assistance and information on past management history of Bluff Fen, and Rita Hassert of the Morton Arboretum for library research. Helpful reviews were provided by Christopher Dunn, Noel Pavlovic, Bill Sluis, Chris Whelan, Peter White, Line Rochefort, and anonymous reviewers. We also thank Jim Miner for sharing unpublished ground-water data and for helpful review.

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Manuscript received 12 January 2004; revisions received 28 June 2004, 7 March 2005, and 5 May 2005; accepted 6 May 2005.

Appendix I. Mean (± se) soil chemistry and mineral and nutrient concentrations at Bluff Spring Fen Nature Preserve. OC = % organic content, CEC = cation exchange capacity (in cmol (+)/kg), Pbs = percent base saturation. Total Ca and P1 are in parts per million. F = ANOVA test statistic, P = probability that means differ. Communities with similar letters are not different at P < 0.05 with Duncan's multiple range test.

	Sedge meadow	Graminoid Fen	Calcareous Seep	Marl Flat	Spring Run	F ratio and Probability
pH	7.12 ± 0.06 ab	7.73 ± 0.03 c	7.35 ± 0.15 abc	7.49 ± 0.05 bc	7.70 ± 0.10 c	$F_{4,22} = 9.69$, $P < 0.0001$
OC	24.39 ± 1.09 a	31.38 ± 2.92 b	22.48 ± 1.03 a	8.76 ± 1.97 c	4.08 ± 0.63 c	$F_{4,22} = 50.76$, $P < 0.0001$
CEC	46.56 ± 1.93 a	52.72 ± 3.42 a	49.70 ± 6.23 a	30.22 ± 3.85 b	18.96 ± 2.27 b	$F_{4,22} = 15.01$, $P < 0.001$
Pbs Na	2.46 ± 0.26 ab	1.66 ± 0.21 ab	62.90 ± 0.36 ac	2.72 ± 0.14 ac	3.34 ± 0.39 ac	$F_{4,22} = 4.44$, $P = 0.009$
Pbs Ca	63.61 ± 1.40 a	63.48 ± 2.93 a	58.84 ± 4.11 a	48.60 ± 1.72 b	39.50 ± 4.47 b	$F_{4,22} = 12.32$, $P < 0.001$
Total Ca	13729 ± 1309.9 a	22060 ± 3614.6 b	21350 ± 3122.3 b	22710 ± 649.2 b	25700 ± 1037.2 b	$F_{4,22} = 4.87$, $P = 0.006$
Pbs Mg	31.21 ± 1.25 a	29.24 ± 2.31 a	35.56 ± 3.56 a	47.22 ± 1.52 b	55.20 ± 3.96 b	$F_{4,22} = 20.06$, $P < 0.001$
Pbs K	2.760 ± 0.35 ab	3.62 ± 0.73 bc	2.7 ± 0.50 ab	1.48 ± 0.12 a	1.94 ± 0.22 ab	$F_{4,22} = 3.42$, $P = 0.026$
P1	4.00 ± 1.11 a	6.80 ± 0.37 a	5.40 ± 1.54 a	4.20 ± 0.37 a	3.00 ± 0.84 a	$F_{4,22} = 2.01$, $P = 0.128$