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CALCAREOUS FENS OF WESTERN NEW ENGLAND AND ADJACENT NEW YORK STATE

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ABSTRACT

This study presents a community characterization of calcareous fens of western New England and adjacent New York State. Based on analyses of data from 24 sites, seven vegetation types are defined: *Carex lasiocarpa-Cladium mariscoides* Type, *Carex aquatilis* Type, *Betula pumila* Type, *Carex lacustris* Type, *Carex stricta* Type, *Typha angustifolia-Carex lasiocarpa* Type, and *Carex interior-Carex leptalea-Carex flava* Type. The distribution of these vegetation associations is related to hydrologic and ionic gradients. Calcareous fens of the region are similar to minerotrophically rich fens elsewhere in North America with respect to vegetation and environmental characteristics.

Key Words: wetlands, calcareous fens, vegetation classification, ordination

INTRODUCTION

Calcareous wetlands are ecologically significant communities that support numerous rare or uncommon plant species as well as several unusual animal species (McVaugh, 1957; Bernard et al., 1983; Rawinski and Rooney, 1989; Weatherbee, 1990). Historically limited in distribution and extent throughout the northeastern United States, modern development pressure continues to threaten the integrity of several sites.

Although calcareous wetlands are recognized as priorities for conservation, most previous investigations of freshwater wetlands in the northeastern United States have focused on peatlands characterized by acidic, nutrient-poor surface waters (Moizuk and Livingston, 1966; Hemond, 1980; Damman and French, 1987; among others). This research trend reflects the predominance of acidic bedrock throughout the region and has resulted in the general absence of information concerning the vegetation and environmental characteristics of circumneutral to alkaline wetlands. The present study marks the first comprehensive evaluation of calcareous fens in western New England and adjacent New York State, providing baseline information that is critical for conservation and management planning, as well as for future more detailed studies of these communities. The specific objectives of this study are to: 1) characterize vegetation associations of calcareous fens in western New England and adjacent New York

State, 2) relate variation in fen vegetation to environmental parameters, and 3) compare fens of the northeastern United States with those described from elsewhere in North America.

Calcareous fens are non-forested wetlands that are influenced by base-rich groundwater and contain calcicoles (Rawinski, 1984). In the present study, the term 'fen' is applied to both level and sloping communities with or without peat deposits. Although most studies of fens in North America have been restricted to peatlands (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Davis and Anderson, 1991), several European investigators have recognized the floristic and functional similarities between sites with peat and those that lack organic sediments (Wheeler, 1980; Boyer and Wheeler, 1989; Peterson, 1989).

STUDY AREA

In western New England and adjacent New York State, calcareous fens occur primarily as small communities (<1–50 ha) throughout the Berkshire Valley Lowland and portions of the adjacent Taconic Region where carbonate bedrock or surficial deposits occur (Figure 1). Many calcareous fens in the region occur on rocks of the Stockbridge formation, which consist primarily of marble, limestone, dolostone and other carbonate-rich rock types (Motts and O'Brien, 1981). A few fens overlie the Walloomsac and related formations that contain limestone interbedded with schists. A single fen in the Connecticut Valley of Massachusetts occurs on Mesozoic sedimentary bedrock. Although most fens occur on calcareous till deposits, several have developed on glaciofluvial or glaciolacustrine deposits.

Calcareous fens in the region occur at elevations that range from 75 to 400 m a.s.l., with most sites between 150–300 m. Climate throughout the region is continental, with cool winters and warm summers (U.S.D.A., 1988). Average annual precipitation of 110 cm is fairly evenly distributed throughout the year.

METHODS

The methods for this investigation are modified from those established for prior surveys for the Massachusetts Natural Her-

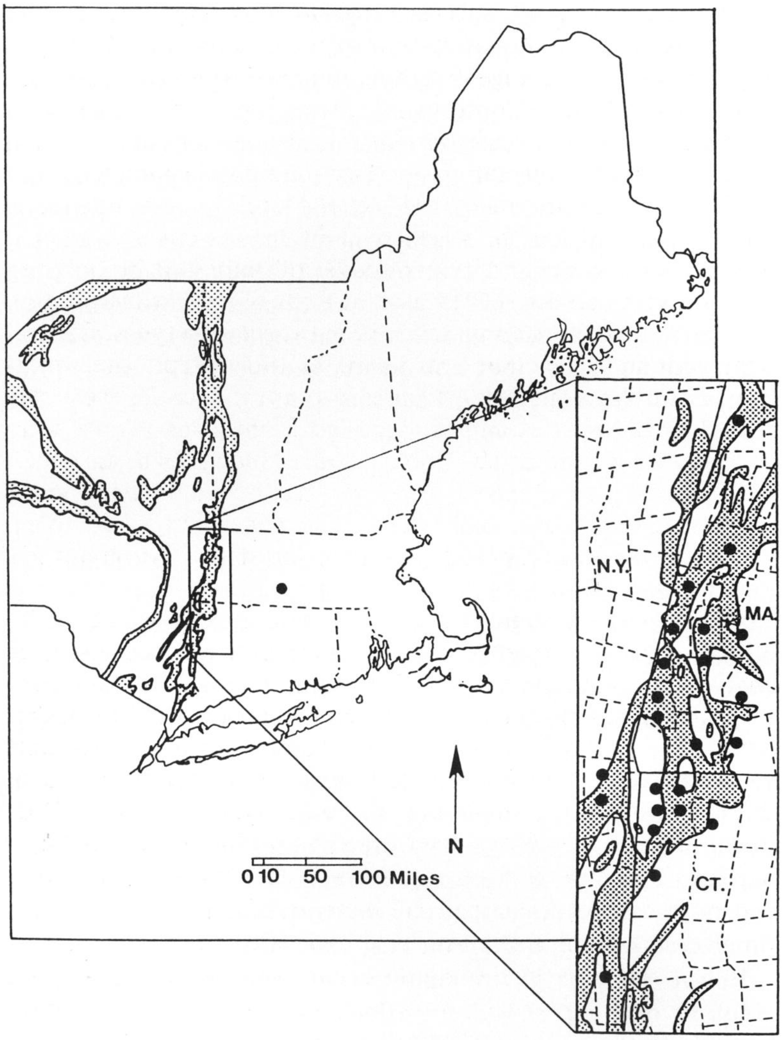

Figure 1. Map showing the location of the study area and the occurrence of carbonate bedrock (stippled) in the northeastern United States. Study sites are indicated as dots on the enlarged inset (right), except for one site in the Connecticut Valley that is indicated on the regional map (left). Modified from Moore (1935), Denny (1982), and Isachsen et al. (1991).

itage and Endangered Species Program (Motzkin, 1991). Field sites were selected in consultation with the staffs of the MA, CT, and NY Natural Heritage Programs and the Eastern Heritage Task Force of The Nature Conservancy. Twenty-four sites, believed to represent most of the undisturbed, non-forested fens in the region, were sampled for vegetation and environmental characteristics.

Fifty-five 100 m^2 relevés (Mueller-Dombois and Ellenberg, 1974) were sampled for vascular plant species-cover estimated within height strata and percent cover of dominant bryophytes. Relevés were subjectively located in areas of uniform vegetation and distributed to encompass a range of vegetation types. General observations of vegetation structure, landform type, site condition, disturbance history, and presence of rare species were also recorded. Bryophytes and unidentified herbaceous species were collected for identification. Nomenclature follows Seymour (1989) for vascular plants, except for *Carex* section Stellulatae, which follows Reznicek and Ball (1980), and *Carex stricta* complex, which follows Standley (1987). Nomenclature for bryophytes follows Crum (1976).

Surface water pH and conductivity were measured at each relevé location. Water samples were collected, refrigerated, and later analyzed at the University of Massachusetts using an atomic absorption spectrophotometer to determine concentrations of calcium, magnesium, and phosphorus. Water color of filtered samples (related to concentration of humic acids) was estimated in three classes: 'clear', 'moderate', or 'dark'. Depth of organic sediments at each relevé was determined by probing to a maximum depth of 2 m. A soil auger was used to determine the degree of decomposition of the upper one meter of organic sediments, estimated according to the Von Post scale (Clymo, 1983).

Relevé cover data were analyzed with cluster analysis and ordination techniques. Agglomerative cluster analysis (AGGLOM; Orloci, 1967) served as the basis for classifying vegetation types and detrended correspondence analysis (DCA; Hill, 1979) was useful in identifying relationships among relevés. Canonical correspondence analysis (CCA; ter Braak, 1986), correlation analysis, and Duncan's Multiple Range Tests were used to identify environmental factors influencing the distribution of plant communities.

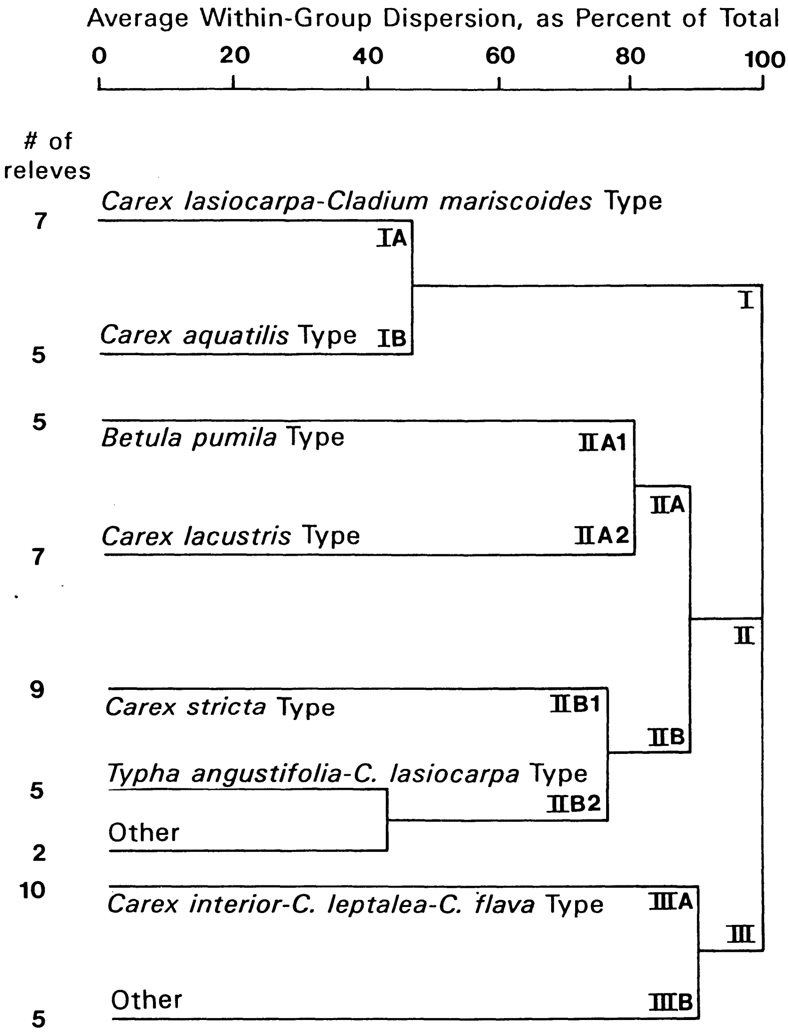

Figure 2. Simplified AGGLOM dendrogram based on absolute distances for species cover in 55 relevés. See text for description of vegetation types.

RESULTS

Vegetation Classification

Relevé data were clustered by AGGLOM using absolute distances into three main groups, composed of several smaller clusters (Figure 2). Group I is characterized by *Carex lasiocarpa, C. aquatilis, Potentilla fruticosa,* and *Myrica gale. Cladium mariscoides, Rhyncospora alba, Sarracenia purpurea, Andromeda glaucophylla, Pogonia ophioglossoides, Drosera rotundifolia, Menyanthes trifolia,* and *Utricularia* spp. occur with greater frequency in this group than in Groups II or III (Table 1). *Sphagnum* spp. and *Campylium stellatum* are the common bryophytes. Uncommon species associated with Group I include *Carex limosa, C. aquatilis,* and others.

Group II is characterized by *Betula pumila, Carex lacustris, C. stricta, Thelypteris palustris, Salix candida,* other *Salix* species, and *Spiraea latifolia. Rhus vernix, Phragmites communis, Typha angustifolia, T. latifolia, Lythrum salicaria,* and *Lysimachia thyrsiflora* are also characteristic of this group. *Galium labradoricum, Betula pumila,* and *Salix candida* are species characteristic of Group II that are regionally uncommon.

Group III is characterized by *Carex interior, C. leptalea, C. flava, C. hystericina, Larix laricina, Parnassia glauca, Solidago patula, S. purshii,* and *Thelypteris palustris,* with *Rhamnus alnifolia, Equisetum fluviatile, Equisetum* spp., *Ribes* spp., and *Cornus* spp. also important. Rare species include *Carex sterilis, C. tetanica, Equisetum scirpoides, Petasites palmatus, Lobelia kalmii,* and *Spiranthes romanzoffiana.*

Within the classification hierarchy, subgroups are characterized by a subset of the species listed for the major groups as well as by additional species. Subgroups that are distinct with respect to species composition and abundance may be considered separate vegetation types (Table 1). Group I includes two such subgroups. The ***Carex lasiocarpa-Cladium mariscoides* Type** (Subgroup IA) is a sedge-dominated association characterized by *Carex lasiocarpa, Myrica gale, Potentilla fruticosa, Peltandra virginica,* and *Cladium mariscoides.* Other frequent species include *Drosera rotundifolia, Sarracenia purpurea, Hypericum virginicum, Rhyncospora alba, Typha* species, *Vaccinium macrocarpon,* and *Utricularia* spp. The dominant bryophytes are *Campylium stellatum, Calliergonella* sp., and *Sphagnum* spp.

The ***Carex aquatilis* Type** (Subgroup IB) is structurally similar to Subgroup IA but is dominated by *Carex aquatilis* or by *Carex aquatilis* and *C. lasiocarpa* and lacks species such as *Peltandra virginica* and *Hypericum virginicum.*

Group II includes four subgroups. The ***Betula pumila* Type** (Subgroup IIA1) is characterized by a shrub layer of *Betula pumi-*

Table 1. Percent frequency of occurrence by Group and Subgroup. * = incomplete sampling of minor bryophytes; no frequencies calculated.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Trees							
Chamaecyparis thyoides	14						
Acer rubrum	14	20	100	14	57	40	40
Fraxinus spp.			20		29		20
Pinus strobus					14		70
Larix laricina			20				40
Tsuga canadensis							30
Betula alleghaniensis					14		20
Carpinus caroliniana					14		20
Populus tremuloides							20
Quercus alba							20
Betula papyrifera							10
Tilia americana							10
Shrubs							
Chamaedaphne calyculata	14						
Lonicera villosa	14						
Aronia arbutifolia	14					20	10
Andromeda glaucophylla	14	40					
Myrica gale	86	100	40		14	40	
Potentilla fruticosa	86	100	100	71	43	20	80
Alnus spp.	43	40	40	14	86	60	20
Salix discolor	14	20	40	71	14		40
Spiraea latifolia	14		40	43	71	60	40
Cornus stolonifera	14		80	14		40	50
Cephalanthus occidentalis	14		20	14	14	60	
Salix candida		20	20	57	14	80	10
Betula pumila		60	100			40	
Rhus vernix			40	14	14	20	20
Rhamnus alnifolia			20	14			40
Ribes spp.			20	14			60
Salix serissima			40	43	14		50
Salix spp.			60	14	43	20	60
Rosa palustris			40		29		10
Viburnum recognitum			20		14	20	10
Rhamnus frangula			20				
Ilex verticillata			20				
Myrica pensylvanica			20				
Cornus amomum				29	14		
Cornus racemosa				14	14		20
Spiraea tomentosa					14		10
Lyonia ligustrina					14		40
Lindera benzoin					14		20
Amelanchier sp.					14		20

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Vaccinium corymbosum						20	10
Viburnum lentago							30
Corylus spp.							10
Ulmus sp.							10
Vaccinium angustifolium							10
Hamamelis virginiana							10
Rhamnus cathartica							10
Graminoids							
Rhyncospora alba	43						10
Eriophorum gracile	14						
Scirpus acutus	43	20		14		20	
Scirpus hudsonianus	14	40					
Cladium mariscoides	86	60					
Carex lasiocarpa	100	60			14	100	
Carex aquatilis	14	100	40			20	
Phragmites communis		20	40			40	
Carex limosa		20					
Carex prairea		20	40	14	14	40	10
Calamagrostis canadensis			60	57	29	20	10
Poa palustris	14		20				
Carex lacustris			80	100		40	10
Eleocharis erythropoda		20	20	43			20
Carex stricta			40	57	100	60	20
Carex stipata					57		
Scirpus atrovirens					43		30
Carex vulpinoidea					29		
Dulichium arundinaceum						60	
Eleocharis sp.	29	40			14	60	30
Carex comosa			20	14	14	20	
Carex interior			60	29	14		100
Carex leptalea			40	29			100
Carex flava		20	40		29	40	90
Carex hystericina				29	43		80
Carex tetanica			20				30
Eriophorum viridi-carinatum	14				14		50
Glyceria striata			20	43		20	50
Juncus sp.				14	14	20	20
Muhlenbergia glomerata	14		20	14	14		50
Carex scoparia				14	14		
Phalaris arundinacea				14			
Bromus ciliatus			20		14		30
Juncus dudleyi					14		30
Juncus effusus					14		20

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Juncus nodosus					14		50
Eleocharis acicularis					14		
Leersia oryzoides					14		
Carex rostrata					14		
Poa pratensis					29		10
Carex granularis							40
Anthoxanthum odoratum							20
Festuca spp.							20
Poa compressa							10
Sphenopholis sp.							10
Carex gracillima							10
Carex laevivaginata							10
Carex spp.	14						10
Andropogon scoparius							10
Danthonia spicata							10
Herbs							
Utricularia spp.	29						
Potamogeton spp.	29						
Potentilla palustris	29		40				
Peltandra virginica	71		40		14	40	
Pogonia ophioglossoides	29	20					10
Drosera rotundifolia	86	20				20	50
Sarracenia purpurea	100	80					
Vaccinium macrocarpon	100	80	20				
Menyanthes trifolia	86	100	20			20	
Utricularia intermedia	57	80	20		14		
Typha latifolia	14	60	60	57	14		10
Equisetum fluviatile			100	43	14	40	
Lysimachia thyrsiflora			100	14		40	10
Osmunda regalis	14		40	14			10
Sagittaria latifolia			40		14	20	
Parthenocissus quinquefolia			20		14		
Rubus spp.			80	29	29		40
Polygonum sp.			20	29	29		
Acorus calamus				29			10
Lemnaceae spp.				14	14		
Galium labradoricum			40	43	14		10
Iris versicolor			40	57	14	40	20
Impatiens capensis			20	14	43		
Viola sp.			20		19		
Brasenia schreberi					29		
Solidago spp.			40		14		20
Typha angustifolia	43		40	14	29	100	

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Thelypteris palustris	29		100	86	71	100	90
Hypericum virginicum	71		20	14	57	80	
Lythrum salicaria			60	14	29	60	20
Eupatorium maculatum			40	43	43		40
Onoclea sensibilis			20	14	29	20	20
Eupatorium perfoliatum				14	14	20	20
Aesclepias incarnata			20	29		40	
Proserpinaca palustris			20	14		20	
Campanula aparinoides					29	40	
Solidago patula					43	20	90
Utricularia minor			20				
Equisetum spp.				14	14		80
Parnassia glauca				43			80
Solidago purshii	14	20	20	43			70
Symplocarpus foetidus			40	43	14	20	50
Thalictrum polygamum			40	14			40
Solanum dulcamara			20	14			
Galium spp.				29	43		40
Rumex spp.				29	14		
Ludwigia palustris				14	14		
Verbena hastata				14			
Umbelliferae spp.				29			10
Hydrocotyl americana					14		40
Achillea millefolium					14		20
Compositae spp.					29		20
Lonicera spp.					14		20
Lysimachia ciliata					14		10
Apios americana					14		10
Nuphar variegatum					14		
Boehmeria cylindrica					14		
Desmodium sp.					14		
Geum rivale							40
Senecio aureus							40
Prunella vulgaris							30
Petasites palmatus							20
Smilacina stellata							20
Potentilla simplex							20
Fragaria sp.							20
Eupatorium rugosum							10
Tussilago farfara							10
Amphicarpa bracteata							10
Geranium maculatum							10
Houstonia sp.							10
Cardamine sp.							10

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Sanicula marilandica							10
Spiranthes romanzoffiana							10
Taraxacum officinale							10
Chrysanthemum leucanthemum							10
Clematis spp.							10
Cypripedium reginae							10
Adiantum pedatum							10
Aster puniceus							10
Aster schreberi							10
Aster umbellatus							10
Dryopteris cristata							10
Epilobium leptophyllum	14						10
Equisetum scirpoides							10
Lycopus uniflora							10
Lysimachia terrestris						20	10
Mentha arvensis							
Unknown	14		20	14	29		20
Bryophytes							
Sphagnum fimbriatum	14						
Sphagnum subsecundum var. *contortum*	14						
Drepanocladus sp.	14		20	14		60	
Calliergonella sp.	71	40	60	14	14	40	10
Campylium stellatum	86	100	80	57	29	40	60
Sphagnum warnstorfii	14						30
Sphagnum spp.							20
Sphagnum magellanicum							10
Thuidium delicatulum			*				
Leptodictyum sp.					*		
Aulacomnium palustre							*
Cratoneuron filicinum							*
Scorpidium scorpioides							*
Tomenthypnum nitens							*
Helodium blandowii							*
Dicranum scoparium							*
Thuidium recognitum							*

la, Potentilla fruticosa, Acer rubrum, Cornus stolonifera, and *Salix* spp., amidst herbaceous species such as *Carex lacustris, Calamagrostis canadensis, Typha angustifolia, T. latifolia, Lysimachia thyrsiflora, Lythrum salicaria, Thelypteris palustris, Equisetum*

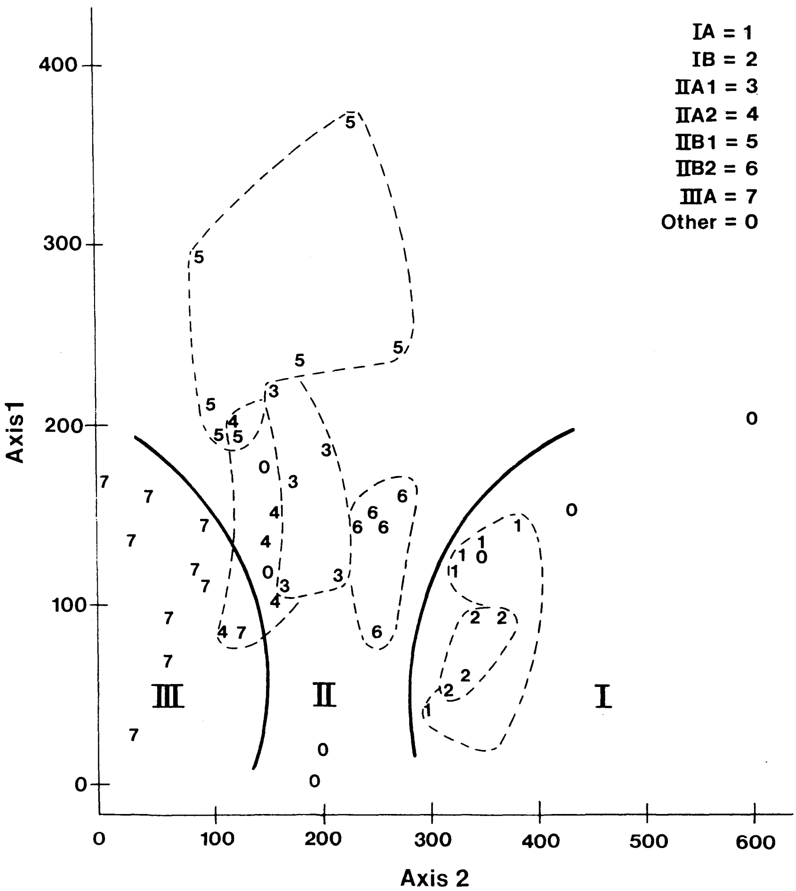

Figure 3. Plot of DCA sample ordination for axes 1 and 2. Numbers refer to groups and subgroups defined by cluster analysis (Figure 2).

fluviatile, and *Campylium stellatum. Rhus vernix* is locally abundant.

The ***Carex lacustris* Type** (Subgroup IIA2) includes some of the species found in the *Betula pumila* type, but lacks extensive woody cover. Frequent species include *Carex lacustris, C. stricta, Salix candida, Potentilla fruticosa, Typha* spp., and *Thelypteris palustris.*

The ***Carex stricta* Type** (Subgroup IIB1) has higher frequency and cover values for *Carex stricta* than other subgroups. *Acer* *rubrum, Alnus* sp., *Scirpus atrovirens, Galium* spp., *Eupatorium maculatum,* and *Thelypteris palustris* are other characteristic species.

The ***Typha angustifolia-Carex lasiocarpa*** **Type** (Subgroup IIB2) is dominated by *Typha angustifolia* and *Carex lasiocarpa,* with *Salix candida, Cephalanthus occidentalis, Dulichium arundinaceum, Eleocharis* spp., *Campanula aparinoides,* and *Hypericum virginicum* frequently encountered. *Potentilla fruticosa* is less frequent in this subgroup than in any other vegetation type identified through cluster analysis. Two plots in this Subgroup are shown as 'Other' in Figure 2. These plots are dominated by *Scirpus acutus* with only low cover of species characteristic of the *Typha angustifolia-Carex lasiocarpa* Type.

Group III includes two subgroups. The ***Carex interior-C. leptalea-C. flava*** **Type** (Subgroup IIIA) has sparse tree and shrub strata containing *Pinus strobus, Larix laricina, Potentilla fruticosa, Salix serissima, Ribes* spp., and *Rhamnus alnifolia,* and a low herbaceous stratum characterized by *Carex interior, C. leptalea, C. flava, C. hystericina, Juncus dudleyi, J. nodosus, Muhlenbergia glomerata, Parnassia glauca, Solidago purshii,* and *S. patula.* Relevés in Subgroup IIIB are shown as 'Other' in Figure 2 because these plots contain vegetation that appears transitional between two or more of the types described above.

Figure 3 presents the results of the DCA ordination, with relevés assigned according to the groups and subgroups defined by cluster analysis. The grouping of relevés along the ordination axes demonstrates the lack of overlap between types defined by cluster analysis at both a coarse (major groups) and fine level (subgroups) of classification.

Environmental Characteristics

The surface waters of the calcareous fens investigated are circumneutral to alkaline (pH: 6.0–8.1), with relatively high concentrations of calcium (8–65 mg/liter) and magnesium (4–32 mg/liter) (Table 2). Phosphorus levels are low, with only 8 out of 55 samples above the detection limit of .15 ppm (not shown in Table 2). Depth of organic sediments range from >200 cm in most Group I sites to 0–15 cm in areas with visible groundwater seepage (Group III). Where organic sediments occur, the degree of de-

Table 2. Environmental characteristics of calcareous fens of western New England and adjacent New York State (average value with range in parentheses). Groups and vegetation types numbered as in Figure 3. Color refers to filtered samples (1 = clear, 2 = moderate, 3 = dark).

	No. of Samples	pH	Conductivity (μmho)	CA (mg/liter)	MG (mg/liter)	Depth* (cm)	Von Post (0–10)	Color (1–3)
Group I	12	6.6 (6.0–7.1)	415 (87–1151)	31 (11–62)	10 (4–17)	200	3 (2–3)	2 (1–3)
Type 1	7	6.5 (6.0–7.0)	213 (87–322)	22 (11–34)	10 (4–17)	200	3 (3–3)	2 (1–3)
Type 2	5	6.8 (6.5–7.1)	697 (225–1151)	43 (26–62)	10 (7–14)	200	3 (2–3)	2 (1–3)
Group II	26	6.9 (6.5–7.7)	366 (208–581)	43 (8–65)	19 (7–32)	135 (20–200)	7 (3–9)	2 (1–3)
Type 3	5	6.8 (6.7–6.8)	391 (251–505)	43 (34–52)	19 (11–26)	171 (55–200)	5 (3–8)	2 (1–2)
Type 4	7	6.8 (6.5–7.4)	341 (225–461)	50 (30–62)	16 (10–22)	141 (65–200)	7 (3–9)	1 (1–3)
Type 5	9	7.1 (6.7–7.7)	371 (248–515)	45 (16–65)	19 (7–32)	103 (20–200)	8 (3–9)	2 (1–3)
Type 6	5	6.9 (6.7–7.2)	368 (208–581)	35 (8–50)	22 (15–29)	150 (75–200)	5 (3–9)	1 (1–2)
Group III	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)
Type 7	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)

* Maximum value of 200 cm.

composition within the uppermost one meter of sediments varies from largely undecomposed peat (Von Post scale: 2–3) in many Group I plots, to highly decomposed muck (Von Post: 7–9) in Group II sites.

Correlation analyses indicate a significant negative relationship between depth of organic sediments and pH ($R = -.63$; $P = .0001$), degree of decomposition ($R = -.45$; $P = .0017$), and Mg concentration ($R = -.33$; $P = .02$). Ca concentration is positively correlated with Mg concentration ($R = .58$; $P = .0001$), and with conductivity ($R = .49$; $P = .0004$), and both Ca and Mg are negatively correlated with hydrogen ion concentration (Ca: $R = -.39$, $P = .01$; Mg: $R = -.39$, $P = .01$). pH is positively correlated with degree of decomposition of peat ($R = .34$; $P = .03$). Water color is positively correlated with hydrogen ion concentration ($R = .36$; $P = .01$).

Relationship Between Vegetation and Environment

Canonical correspondence analysis (CCA; ter Braak, 1986), a form of direct gradient analysis in which the vegetation ordination is constrained by environmental data, was used to relate vegetation variability to measured environmental variables. In the resulting ordination (Figure 4), relevés separate primarily along gradients of depth of organic sediments, pH, and degree of decomposition of organics. Ca, Mg, conductivity, and water color account for less of the variability in the vegetation. Combined, these environmental factors account for a relatively low percentage of the total variability of the vegetation (~25%), reflecting the fact that the fens investigated are highly variable with respect to vegetation and water chemistry. ter Braak (1986) has noted this pattern for other data sets, suggesting that CCA may still be useful in cases where a relatively low percentage of the total variability is accounted for by the ordination diagram.

The hierarchical nature of cluster analysis allows one to test the hypothesis that different environmental variables are associated with vegetation variation at different levels of classification. For example, in montane systems one might hypothesize that elevation gradients are responsible for patterns of vegetation variation at a coarse level. Within a particular elevation zone, however, local edaphic factors (rather than elevation) might control patterns of vegetation variation. Duncan's Multiple Range Tests

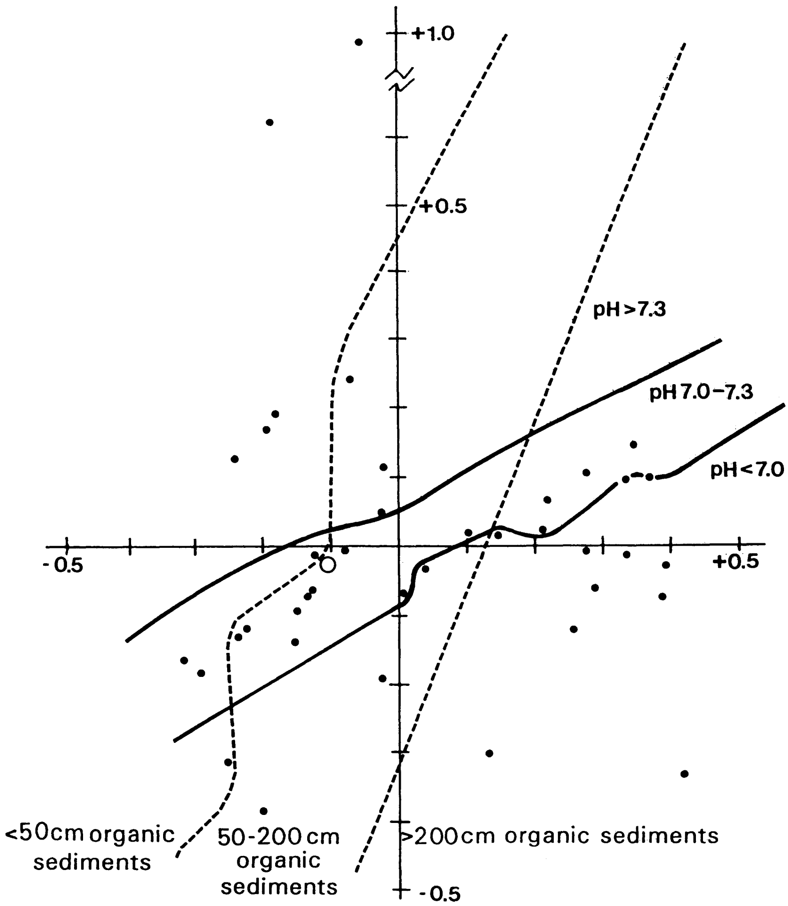

Figure 4. Plot of CCA sample ordination for axes 1 and 2. Broken lines distinguish plots with >200 cm, 50–200 cm, and <50 cm of organic sediments. Solid wavy lines separate plots with pH values of >7.3, 7.0–7.3, and <7.0. An outlier with respect to pH class (pH = 7.4) is indicated by an open circle.

were used to determine which environmental factors differ significantly with respect to major vegetation groups and subgroups defined by cluster analysis.

At the coarse level of classification, depth to mineral soil is the only variable measured that differs significantly ($P = .0001$) between all three groups. Hydrogen ion concentration, Mg, and degree of decomposition of organics (Von Post value) for Group

I are significantly different (P = .01, P = .0004 and P = .0001, respectively) from Groups II and III (which are not different from each other). Calcium levels are different (P = .07) between Groups I and III, but not between Groups I and II or between Groups II and III. Conductivity and color of filtered samples do not vary significantly among the three groups. These results suggest that Groups I and III (defined by cluster analysis of relevé data) are most different with respect to environmental parameters (e.g., depth of sediments, pH, Mg, degree of decomposition, and Ca) and that Group II is intermediate with respect to these variables. As with the CCA results, depth to mineral soil is the single variable most strongly associated with vegetation patterns at this level of classification.

Similar analyses were performed to determine environmental differences between subgroups within each major cluster group. Within Group I, Subgroup 1A differs significantly from Subgroup 1B with respect to Ca concentration (P = .0223) and conductivity (P = .0098). Within Group II, only Von Post values differ between the subgroups (P = .0767), with Subgroup IIB1 significantly different from Subgroup IIA1 (but not from IIA2 and IIB2), and Subgroups IIA1, IIA2, and IIB2 not significantly different from each other. No other environmental parameters tested differ significantly between subgroups defined by cluster analysis. Group III contains only one subgroup (IIIA) considered to be a distinct vegetation type, and so was not included in this level of analysis.

DISCUSSION

Relationship of Vegetation to other North American Fens

The coarse level of classification determined through cluster analysis of relevé data can be related to existing classifications of calcareous wetlands. Group I corresponds to a Lake Basin Graminoid Fen type described from the Northeast (Rawinski, 1984; Weatherbee, 1990), and to a Rich Graminoid Fen type of New York State (Reschke, 1990). Dominant species in this group are also recorded from minerotrophic fens of northern Michigan (Schwintzer, 1978). Group II contains elements of the Seepage Swamps of highly calcareous soils described by McVaugh (1957) and the Seepage Marsh of Rawinski (1984), which he describes as having characteristics of both fen and marsh. Rich-fen types from Britain are structurally similar to Group II vegetation (Wheeler, 1980). Group III, which corresponds to Reschke's (1990) Rich Sloping Fen and to Rawinski's (1984) Calcareous Sloping Fen, contains several species considered to be 'rich fen indicator species' in Ontario (e.g., *Carex leptalea, Eriophorum viridi-carinatum, Scorpidium scorpioides*; Sims et al., 1982).

Several of the vegetation types (subgroups) described here are also related to types found elsewhere in North America. The *Carex lasiocarpa-Cladium mariscoides* Type (Subgroup IA) has been described from a Maine peatland (Rawinski and Rooney, 1989). The vascular vegetation of the *Carex aquatilis* Type is apparently related to the *Drepanocladus revolvens-Carex aquatilis* association found in patterned rich fens in western Alberta (Slack et al., 1980), although none of the study sites investigated in our region display the physiographic patterning typical of fens in boreal climates (Foster and King, 1984; Glaser, 1987). Additional work is needed to evaluate the bryophyte composition of this type.

The *Betula pumila* Type corresponds to a 'larch-birch-sumac swamp type' described from a site included in this investigation (McVaugh, 1957) and to the Rich Shrub Fens of New York (Reschke, 1990). The *Carex stricta* Type is apparently similar to the Sedge Meadow communities found in Maine and New York (Reschke, 1990; Gawler, 1991). No published descriptions correspond closely to the *Typha angustifolia-Carex lasiocarpa* Type.

The *Carex interior-C. leptalea-C. flava* Type contains species described by numerous authors as typical of rich calcareous fens (e.g., Sims et al., 1982; Vitt and Chee, 1990), although no specific reference to this association occurs from outside the region.

Field observations suggest that two additional vegetation associations occur in fens of the region but were inadequately sampled in the current study. A *Scirpus acutus* association was observed in several of the largest peatland fens and along marl pond shores. Also, extensive *Phragmites communis*-dominated areas occur in association with several of the vegetation types described above. Additional sampling is required to relate these associations to the vegetation classification presented here and to those developed for other regions of North America.

Environmental Characteristics

Several authors have related vegetation patterns to environmental characteristics of graminoid-dominated peatland fens elsewhere in North America (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Foster and King, 1984; Vitt and Chee, 1990). Comparison of environmental characteristics reported here (Table 2) with those of previous investigations (Table 3) suggests that the groups and subgroups defined in the current study are comparable to minerotrophically rich fens sampled throughout North America. Of the types considered here, Group I is apparently the least 'rich' (with respect to surface water chemistry), Group II sites are intermediate, and Group III may be characterized as extremely rich (Table 2).

Group I represents a peatland-fen type characterized by deep organic sediments, permanently saturated conditions, and consolidated or floating, sedge-dominated organic mats. Although little is known of the developmental history of these fens in our region, preliminary observations of the macrofossil stratigraphy of two sediment cores extracted from Kampoosa Fen in Stockbridge, MA indicate that since the development of a peat mat at this site, fairly uniform sedge and shrub-sedge peat has accumulated to a depth of 270 cm. This suggests that vegetation structurally similar to the modern vegetation has occupied the site since the time of peat mat establishment. Although the time it has taken for these 270 cm of sediments to accumulate is not known, an estimate of a few thousand years seems reasonable, based on estimates of peat accumulation rates from throughout northeastern North America. Thus, the vegetation at this site appears relatively stable and there is no indication of rapid infilling or terrestrialization.

Sites supporting Group II vegetation are characterized by 50–200+ cm of moderate to well-decomposed organic sediments occurring in a variety of seasonally inundated depressions and drainages. Vegetation characteristic of this group occurs in basins that also support Group I vegetation, in canopy gaps within rich forested swamps, in drainages with current or former beaver impoundments, and in level to slightly sloping sites adjacent to Group III vegetation.

Group III sites are slightly to moderately sloping with groundwater seepage frequently visible in distinct rivulets. In areas of

Table 3. Chemical properties of waters from North American wetlands (average values with range in parentheses). From Zoltai (1988).

Wetland Class	No. of Samples	pH	Conductivity (μmho)	CA (mg/liter)	MG (mg/liter)	Source
Bog	18	4.0 (3.7–4.4)	–	2.3 (1.2–3.7)	0.4 (0.2–0.9)	Schwintzer (1981)
	13	(4.6–5.1)	(35–62)	(0.2–0.8)	(0.1–0.2)	Gauthier (1980)
	10	(3.8–4.4)	31	0.2	0.1	Foster and King (1984)
Fen (poor)	193	(4.6–5.2)	(18–59)	(0.4–4.8)	(0.1–0.7)	Gauthier (1980)
	14	(4.7–5.5)	49	0.3	0.2	Foster and King (1984)
	1	5.0	–	2.4	0.4	Vitt et al. (1975)
Fen (moderately poor)	42	5.2	65	1.1	0.2	Gauthier (1980)
Fen (intermediate to rich)	9	7.2 (6.8–7.9)	281 (140–456)	28 (18–37)	11 (4–28)	Slack et al. (1980)
	21	6.1 (5.2–6.9)	59 (33–128)	10 (4–18)	–	Glaser et al. (1981)
	5	6.5 (5.4–7.1)	–	43 (7–124)	10 (2–15)	Schwintzer (1978)
Swamp (coniferous)	12	7.2 (6.9–7.8)	–	40 (22–52)	12 (8–17)	Schwintzer (1981)

heavy groundwater discharge, mineral soil is typically exposed. Elsewhere, small hummocks develop with shallow accumulations of organic matter. Field observations suggest that the importance of woody species in seepage fens is inversely related to disturbance, with more highly disturbed sites (i.e., those that are flooded by beavers, grazed, or mowed) supporting only low, scattered shrubs. A similar pattern has been described from European fens (Regnéll, 1980; Peterson, 1989).

Environmental Gradients and Vegetation Distribution

CCA analyses indicate that depth to mineral soil is the environmental parameter that accounts for the greatest portion of the variability in the relevé data, with degree of decomposition of organics and pH also important. Duncan's Multiple Range Tests also indicate depth as a significant variable, along with degree of decomposition, pH, Ca, and Mg concentrations. In the study sites considered, depth of peat probably reflects a gradient of 'rate of groundwater-flow' ranging from 'slow' (and poorly aerated) in well-defined basins with deep peat accumulations (Group I), to relatively 'rapid' (and well aerated) in sloping (Group III) sites that lack peat. Depth of peat may also indicate the relative availability to vegetation of nutrients or cations derived from contact with mineral soil. The results of both CCA and Duncan's Multiple Range Tests suggest the importance of both hydrologic gradients (as indicated by depth of organic sediments) and ionic gradients related to alkalinity-acidity (pH, Mg, and Ca concentrations) in determining the variability between the rich fen types considered here.

Similar hydrologic and ionic gradients have been related to vegetation distribution in fen types throughout North America. Peat depth, pH, water levels, and water chemistry are related to differences between fens in Canada (Slack et al., 1980; Sims et al., 1982; Vitt and Chee, 1990). Vegetation variation in a peat and marl fen in western New York is related to complex gradients associated with hydrology, soil organic matter, and soil carbonate-carbon concentrations (Bernard et al., 1983). In one of the few detailed studies to consider non-peatland fens, Boyer and Wheeler (1989) suggest that structural and compositional variation in seepage fens in Britain is related to differences in phosphorus availability between high and low groundwater discharge areas.

At a fine level of classification, subgroups within Group II do not differ significantly with respect to most environmental parameters measured. This probably reflects the high degree of variability of the measured environmental parameters, a pattern noted by several authors (e.g., Sims et al., 1982) for rich fens elsewhere in North America.

Within Group I, relevés in the *Carex lasiocarpa-Cladium mariscoides* Type differ significantly from those in the *Carex aquatilis* Type with respect to Ca concentration and conductivity, but not with respect to depth of organics or degree of decomposition. This suggests an ionic (alkalinity-acidity) rather than hydrologic gradient, with the *Carex lasiocarpa-Cladium mariscoides* Type representing the 'poorer' type. This corresponds well with the observation that in the northeastern United States, *Carex lasiocarpa* occurs at sites ranging from poor to rich, whereas *Carex aquatilis* is restricted to minerotrophically rich sites. These results also suggest that with respect to Group I, different environmental gradients (hydrologic vs. minerotrophic) may be associated with vegetation variation at different levels of classification.

CONCLUSIONS

Calcareous fens of western New England and adjacent New York State are similar to rich peatland fens throughout North America with respect to species composition, water chemistry, and the influence of hydrologic and minerotrophic gradients on vegetation distribution. Future attempts to develop regional classifications of fens should more fully evaluate seepage and seasonally inundated types. In cases where hydrologic and ionic (alkalinity-acidity) gradients do not appear to explain observed variability in vegetation, factors such as nutrients, developmental history, response to disturbance, or biotic interactions may be significant.

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