DISSERTATION

THE ECOLOGY OF CALCAREOUS FENS IN PARK COUNTY, COLORADO

Submitted by

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In partial fulfillment of the requirements for

the degree of Doctor of Philosophy

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Committee on Graduate Work

Advisor

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ABSTRACT OF DISSERTATION

THE ECOLOGY OF CALCAREOUS FENS IN PARK COUNTY, COLORADO

Calcareous fens are wetlands which accumulate peat and have alkaline ground water as their dominant hydrologic input. This combination of environmental characteristics produces an unusual type of habitat and a large number of rare and regionally endemic plant and insect species are found within these fens. In spite of the ecological importance of calcareous fens, they have been subjected to a number of destructive land use practices, most commonly peat mining and drainage. The plant ecology and effects of disturbance in these wetlands were studied on three calcareous fens in South Park. The fens used in this study were chosen to represent the range and degrees of disturbance found within South Park wetlands.

All the fens studied were classified as extremely rich, based on species indicators and water chemistry. Detrended correspondence analysis, canonical correspondence analysis and two-way indicator species analysis (TWINSPAN) were used to evaluate fen vegetational patterns and classify vegetational assemblages. Vegetation on and between the fens reacts to five primary gradients: water table height, minerotrophy, microtopography, fen margin to expanse, and regional differences. Vegetation types resulting from these gradients were classified into five classes, eight subclasses, and twelve associations.

An evaluation of the effects of peat mining and ditching were made in a comparative study of intact and disturbed portions of each fen. Peat mining was found to significantly impact vegetational composition, species richness and vegetative cover even many years after the cessation of the disturbance. Mining was also found to affect several soil attributes and water quality. Extremely high uranium levels were found to be closely associated with peat mining activity at one of the fens. Fen drainage was found to significantly change vegetational composition, soil structure, and several water chemistry parameters.

Revegetation following experimental disruption was studied to elucidate patterns of secondary succession and evaluate the role of the soil propagule bank in fen restoration. Plots within experimental blocks were manipulated to approximate the effects of peat mining either with no restoration applied or with stockpiled peat reintroduced. Experimental manipulation had major effects on plot vegetation, although in blocks located in previously impacted areas plot vegetation rebounded quickly to near pre-treatment condition. In areas with intact wetland hydrology, seeds were found to play a minor role in revegetation with most growth originating from vegetative structures. In artificially drained areas, sexual reproduction was the dominant mode of revegetation. In essentially all cases, replacement of the upper 10cm of native soil significantly speeded revegetation by supplying the plot with native topsoil and viable sexual and asexual propagules. Based on these results, stockpiling and reintroduction of native topsoil is a recommended approach to restoring disturbed fens.

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INTRODUCTION

The region known as South Park in central Colorado is one of the few places on the continent that possesses boreal-type calcareous fens. South Park is an expansive parkland, located in a broad valley between the Front Range on the East and the Mosquito Range on the West (Fig. 1.1). The park is dominated by short-grass steppe reminiscent of Colorado's eastern plains, but it is situated at elevations between 2590 and 3050 m (8500 ft. to 10,000 ft). South Park's calcareous fens are one of the most important wetland resources in Colorado. These wetlands contain some fifteen state rare or endemic plant species, eleven rare invertebrate species and three regionally endemic vegetation types (Sanderson and March 1996). The fens form rich islands of biodiversity and unique habitat in the short-grass steppe that surrounds them and perform important environmental functions such as water quality improvement and water storage. Due to the slow accumulation of the organic matter which forms their soils, the fens take centuries to develop; as such, losses of these fens are essentially irreversible. In recognition of these facts, state and federal agencies have adopted policies to help conserve these sites, but significant threats to these systems still exist.

Investigation of South Park's fens has only recently been initiated starting with Cooper's (1991) survey. But while scientists have only recently discovered the peatlands of South Park, these sites have been of interest to ranchers and developers since the 1800's. Historically the wetlands were ditched, drained and converted to "productive land", or simply to prevent cattle from becoming bogged down in their soft soils. More recently, miners have discovered the value of peatlands as a source of horticultural "peat moss". Compared to other peatlands in the state, those in South Park readily lend

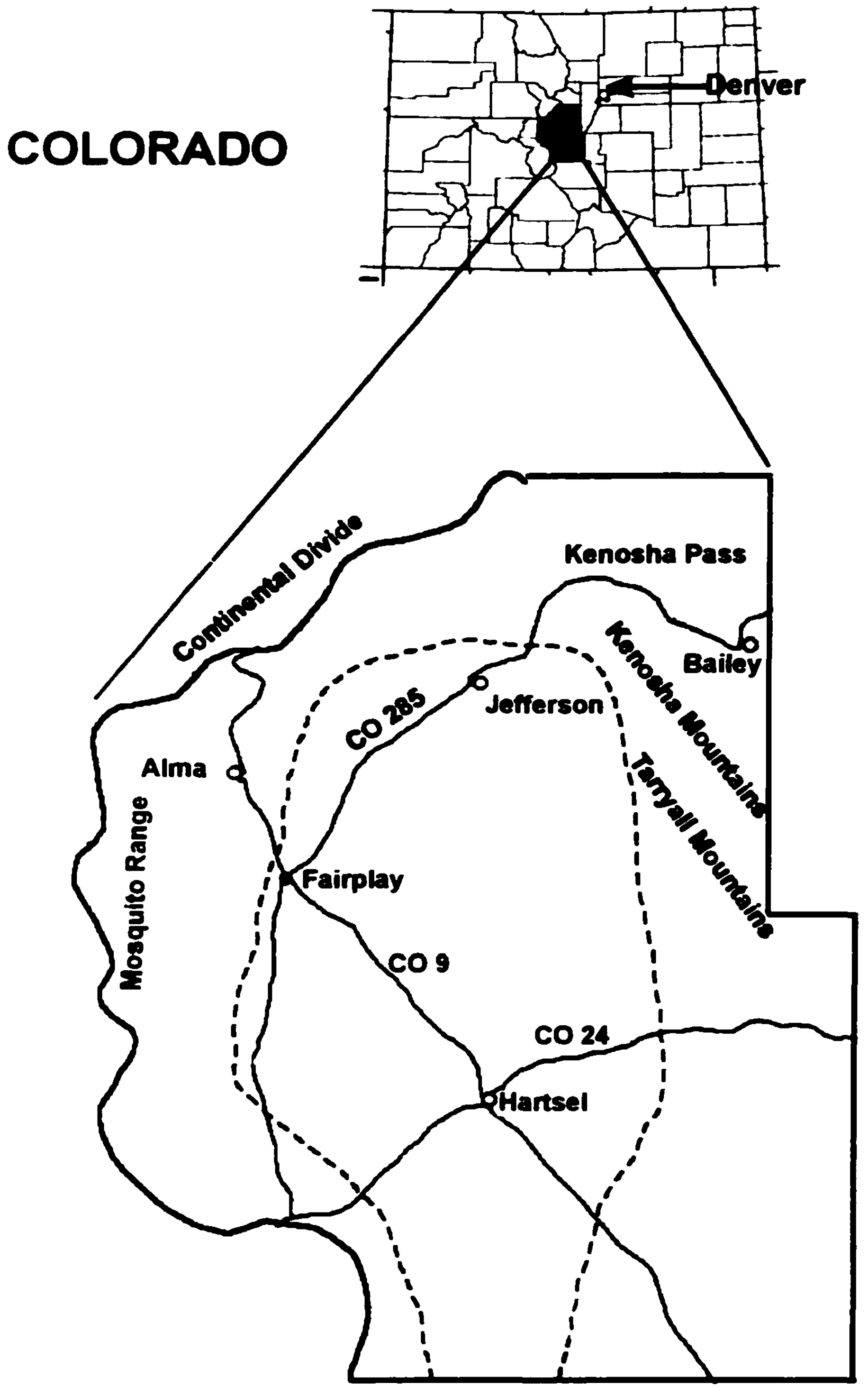

Figure 1.1. Map showing the location and landmarks of Park County, Colorado. The dashed lines indicates the approximate boundary of South Park.

themselves to peat mining. This seems the case for two reasons. First, they are usually more expansive than the typical montane fens, and second, virtually all of these fens are situated close to good roads and population centers. In 1989, 37% of all the peat mined in Colorado came from the fens of Park County, and this percentage is thought to have increased since 1989 (Stevens et al. 1990). Due to these disruptive land use practices, a large percentage of South Park's fens have been significantly impacted and many have been obliterated.

Until recently (Johnson 1996a), no information was available on the environmental and ecological functions performed by calcareous fens. Since no specific information was available as to the negative environmental impacts resulting from various fen usages, it was difficult for government agencies to objectively evaluate permits for peat mining or other destructive practices (T. Carey, pers. commun. 1996; Omaha District U.S. ACE, Tri-Lakes Project office). A primary goal of this study is to increase our knowledge of calcareous fen ecology, its environment, and its reaction to disturbance for the benefit of both the scientific and management communities.

Upon the cessation of disturbance, many fens still have intact hydrology and patches of native vegetation and soils. When wetland destruction is incomplete, it is feasible that the wetland may be restored to a state resembling natural conditions; however, successful restoration is contingent upon knowledge of impact effects and the merits of potential restoration strategies. A secondary goal of this study is to investigate the ecological impacts of destructive land use practices and evaluate the efficacy of plausible restoration approaches.

This project was initiated in 1995 as a pilot study focusing on a single fen (Johnson 1996a). In 1996, the project was expanded to include two additional fens, thereby encompassing greater variation in fen vegetation, environment, and impacts. Project fieldwork continued through the 1998 growing season. This study includes and builds upon the information compiled in Johnson (1996a) and was designed to provide scientists and managers with a broad spectrum of information about the ecology of South Park's extremely rich fens. The specific goals of this project were to: (1) characterize the species composition of major calcareous fen vegetational assemblages and the environmental factors governing their distribution; (2) assess the ecological impacts of peat mining and water diversion on these fens; and (3) evaluate vegetational recovery following disturbance and methods to enhance revegetation.

This dissertation provides background information about the nature of fens and the environmental setting of South Park, including its vegetation, geology and climate. It then relates the findings of the current study to investigations of other Colorado fens and calcareous fens around the world. It is hoped that this information will aid scientists and managers in making critical management decisions, enhance our understanding of these interesting and important habitats, and provide a foundation of information for the benefit of future investigations.

This dissertation is divided into five major sections. Chapter 1 presents a preliminary overview of the vegetation, geology, climate, and study sites in South Park. Chapter 2 describes a study which investigated the vegetation and factors influencing species composition on calcareous fens. Chapter 3 contains a discussion on the impacts which peat mining and draining have on fen ecology, while Chapter 4 contains the results of an experiment which examined vegetational recovery after simulated peat mining. A number of appendices are included at the end of the dissertation. The first presents a detailed account of methods of community analysis and the author's critical evaluation of such techniques. Included appendices contain the raw data obtained during this study.

CHAPTER I

SOUTH PARK, COLORADO: AN OVERVIEW OF VEGETATION, GEOLOGY, CLIMATE, AND STUDY SITES

THE VEGETATION OF SOUTH PARK AND FENS

Until recently there was little interest in the biology of South Park except as it affected agricultural pursuits. As a result, there have been no systematic surveys published on the upland vegetation of which I am aware. Information on community types included in this introduction originates from personal experience and unpublished data, GIS resources supplied by the Colorado Natural Heritage Program, and references to similar vegetational types occurring in regions other than South Park.

South Park contains a mosaic of vegetation types which are distributed primarily according to differences in soil moisture. Soil moisture is controlled in the park by various factors such as slope, aspect, and soil texture. Within and adjacent to South Park there are several major vegetational units including short-grass steppe, aspen forest, spruce-fir forest, bristlecone pine woodlands, fens, wet meadows, cinquefoil shrub lands, beaver complexes, playas and riparian corridors. Each of these units may be further broken down into a myriad of sub-types, but this introduction will only cover the major vegetational units, with the exception of fens which will be considered in more detail due to the central role they play in the current study. Also, only vegetational types occurring in middle to northern South Park are considered.

Upland Vegetation

Short-grass steppe dominates the majority of South Park. The vegetational character and flora is quite similar to that found on the plains of eastern Colorado, even though South Park's steppe resides about 1500 m higher than that of the central plains. This vegetation is dominated by grasses, such as *Bouteloua gracilis*, *Buchloë dactyloides*, and *Koeleria macrantha*. Forbs such as *Artemisia frigida*, *Andromeda* spp., and *Physaria* spp. are also common. Moisture seems to be the key limiting factor in South Park, although soil composition is also influential. Grazing, which is ubiquitous in short-grass areas, also plays a role in defining the vegetational structure of this region.

Other than the pervasive short-grass steppe, the next most prevalent upland vegetation type is quaking aspen (*Populus tremuloides*) forest. These areas are found on the hills and ridges distributed throughout South Park and on the bordering mountain foothills. The forests generally have a closed single-layer canopy that allows enough light penetration to permit rich understory growth. In many areas, *Picea engelmannii*, *Abies lasiocarpa*, and *Pseudotsuga menziesii* can be found scattered throughout the canopy. Common understory species include *Ribes* spp., *Muhlenbergia* spp., *Fragaria ovata*, *Potentilla* spp., *Erigeron peregrinus* and *Anemone* spp. Most or all of these forests have been cut at least once for fuel wood or other purposes. They are frequently grazed as well.

An interesting upland vegetation type is bristlecone pine (*Pinus aristata*) woodland. This vegetation is typically found on steep, rocky, south-facing slopes. Soil only thinly covers these sites and there is generally a high percentage of exposed rock (Brunstein and Yamaguchi 1992). Such sites are dry due to their slope, exposure, and soil texture. Because of the thin soil and prevalence of exposed bedrock, understory vegetation is patchy and often scarce. Common species in the understory are *Juniperus communis, Ribes* spp., *Festuca arizonica, F. thurberi,* and *Trifolium dasyphyllum* (Alexander 1987). Bristlecone pine is a long-lived species, and some of the oldest non-clonal plants alive in Colorado are found in this community (Brunstein and Yamaguchi 1992).

The Wetlands of South Park

Meadows

The wetlands of South Park are in contrast to the dominant semi-arid vegetation of the region. Numerous wetland types and many vegetational associations are represented within these areas. The most widespread of the wetland types are the meadow systems.

Meadows, as defined here, are graminoid dominated wetlands situated on mineral soils. Meadows dominate many thousands of acres in South Park. Virtually all of South Park's meadows have been, or currently are, hayed and/or grazed. The majority have also been hydrologically altered during some point in their history through irrigation or draining. These management practices have occurred since South Park was settled during the mid 1800's, resulting in large scale changes in meadow vegetation. To further complicate ecological interpretation, recent water right acquisitions by Front Range cities have diverted much of the available irrigation water. Many of these formerly irrigated meadows are now experiencing significant changes in species composition due to such withdrawals. Consequently, it is difficult to infer the exact natural conditions of these wetlands based on contemporary studies. Because historical studies of this vegetation are not available, contemporary patterns of vegetation will be described here.

Meadows in South Park can be divided into four broad classes: wet meadow, mesic meadow, dry meadows, and cinquefoil meadow, although there is no sharp distinction between the classes.

Wet Meadows:

Wet meadows are located in areas that are currently irrigated, receiving ground water discharge, along water courses, or in sheltered depressions. They are most expansive in the relatively cool and moist northern region of South Park near the Town of Jefferson. These meadows have seasonally high water tables that are subject to draw downs as the growing season progresses (City of Thornton, unpubl. data.). The soils generally remain moist throughout the growing season and, during wet years, may remain saturated to the surface. Walter et al. (1990) showed that winter recharge of soil moisture is critical in such areas, and that on the average soil moisture recharged during the winter is consumed in the upper 30 cm after about 100 days into the growing season. The average growing season length reported by Walter et al. (1990) is between 135 and 141 days. Because of the oxidizing conditions that occur during water table draw downs, wet meadows do not form organic soils, although a thick O horizon is commonly present.

Wet meadow vegetation is dominated by graminoids with forbs scattered throughout. Shrubs are scarce or absent. Common graminoid species are *Deschampsia cespitosa*, *Calamagrostis stricta*, *C. canadensis*, *Alopecurus alpinus*, *Agrostis* spp., *Juncus balticus*, and *Carex aquatilis*. Forb species include *Caltha leptosepala*, *Pedicularis groenlandica*, *Primula incana*, *Lomatogonium rotatum* and *Parnassia parviflora*. If shrubs are present, they are almost exclusively *Salix planifolia*, *S. brachycarpa*, or *Pentaphylloides floribunda*.

Microtopography in the form of hummocks and hollows is common in these areas. Hummocks are created from a combination of the effects of cattle grazing (Lesica and Kannowski 1997) and autogenic processes (e.g. Johnson 1997). Microtopography creates a heterogenous soil environment and often channelizes surface flow. Wet meadows commonly intermingle with the more hydric fens and it is not always trivial distinguishing between the two wetland types. In fact, mineral soil meadows are an important component of most fen complexes in Colorado and elsewhere. In these cases distinction between fen and meadow approaches irrelevance. The term "mire" takes into account the heterogenous edaphic nature of these systems (see Terminology Section, p. 12), and a recent peatland policy document wisely addresses this fact (U.S. Fish and Wildlife Service, 1999 Region 6, Regional Policy on the Protection of Fens).

Mesic Meadows:

Mesic meadows are similar to wet meadows except they are more subject to water table draw downs and lack species which cannot tolerate soil desiccation or successfully compete under such conditions. Walter et al. (1990) indicated that these sites have used all the winter-recharged soil moisture in the upper 30 cm after only 60 days into the growing season. These sites are often found on the fringe of irrigated areas or in locales receiving some natural sub-irrigation (i.e. ground water flow). Sedges are less common in mesic meadows compared to wet meadows and tend to only occur in depressional areas that maintain high soil moisture; *Deschampsia cespitosa* also has a lower coverage. Common grasses are *Phleum alpinum, Elymus trachycaulus, Hordeum brachyantherum, H. jubatum, Festuca idahoensis, Muhlenbergia* spp., *Juncus balticus, Triglochin maritimum*, and *Alopecurus alpinus.* Herbs such as *Iris missouriensis, Potentilla subjuga, P. plattensis, Achillea millefolium, Aster occidentalis,* and *Polygonum bistortoides* are common.

Hummock - hollow microtopography may be present on these sites, although it tends to be less well developed than in wet meadows. This is probably due to the decrease in soil organic matter which comprises the majority of hummock material. In mesic meadows hummocks can be formed by cattle grazing or autogenic processes as in the wet meadows. Hummocks in mesic and dry meadows can also begin as abandoned ant mounds that become colonized by plant species (Lesica and Kannowski 1997).

Dry Meadows:

Dry meadows lie in areas that receive only marginal amounts of sub-irrigation, that were formerly irrigated, or on topographical rises within wetter meadow or fen complexes. Large expanses of this community may lie in areas that are not actually jurisdictional wetlands (*sensu* US ACE 1987). In a marginal wetland habitat such as this, “uplands” frequently coalesce and inter-digitate with jurisdictional wetlands forming a upland-wetland complex.

Distinction between upland and wetland in these situations is quite difficult and, from an ecological standpoint, somewhat arbitrary.

Species composition in dry meadows resembles that of mesic meadows, although sedges are generally absent and there may be a higher proportion of forbs. Additional species, or species with a higher cover than in wetter meadows are *Argentina anserina*, *Antennaria microphyllum*, *Poa* spp., *Aster* spp., *Muhlenbergia richardsonis*, and *Cirsium coloradense*.

Cinquefoil Meadows:

Cinquefoil meadows are something of a hybrid between meadow and shrub land vegetation. It is unclear as to whether this is generally a natural community type in South Park, or whether it is largely transient and dependent upon anthropogenic environmental changes. These sites are found in a variety of landscape positions, on a range of soil types, and may have disparate species compositions in the herbaceous layer. Cinquefoil meadows are found on both mineral soils and organic soils that have been de-watered. They are frequently found in long, broad, shallow swales leading to the intersection of mountain valleys and the floor of the park but can be found in other areas such as gentle hill sides, as well.

These meadows have an open shrub layer canopy dominated by shrubby cinquefoil (*Pentaphylloides floribunda*) and a herbaceous layer comprised mostly of grasses. Understory species composition can vary according to the site history and soil conditions. A quantitative examination of one such meadow is provided in this study (see Chapter 3).

Vegetation plots were placed in examples of all the above meadow types during this study, but since meadow vegetation was not the focus of this study, the range of field conditions exhibited by the community types was not sampled.

Willow Dominated Systems

Two types of willow- (*Salix* spp.) dominated systems will be discussed – carrs and tall-willow riparian corridors. Carrs are shrub-dominated wetlands that are located predominately on organic soils (Tansley 1939, Cottrell 1993). Carr soils may only be marginally organic, however, when associated with channelized surface flow due to sediment deposition and the erosion caused by channel meandering. Mineral soil inclusions are also not uncommon.

Carrs:

Carrs are frequently associated with flowing water – both diffuse surface and channelized flows. In many systems they seem to depend on sediment deposition from flowing water to supply mineral nutrients (Dix 1974). Carrs may be expansive, such as in beaver complexes or near stream headwaters, or they may be localized as on the margins of large graminoid-dominated fens. In all of these systems the water table is at, or near, the surface perennially. Willow carr vegetation was sampled on the margin of Crooked Creek Fen during this study. The reader is directed to Chapter 2 for details about floristic composition and ecology.

Tall-Willow Riparian Corridors:

Tall-willow riparian vegetation lines many of the larger perennial channels in South Park forming long, narrow corridors of wetland habitat. This habitat is important to a variety of wildlife species as it provides ample cover, forage, nesting sites and travel corridors. It is also an important component of fisheries maintenance since the overhanging branches and undercut banks provide shade and structure to the channels.

The shrub canopy of the wetlands is often closed and reaches heights of three meters or more. In South Park the shrub flora is generally comprised of *Salix monticola, S. brachycarpa,* and *Salix planifolia*. The understory is heterogeneous with lush vegetation in light gaps, interspersed with nearly barren patches in densely shaded areas. In the understory, graminoids such as *Carex aquatilis, C. utriculata, C. microptera, Calamagrostis canadensis, Elymus trachycaulum, Alopecurus alpinus, Juncus balticus,* and *J. longistylis* are common. *Fragaria* spp., *Thermopsis montanum, Thalictrum alpinum, Pedicularis crenulata, Sedum rhodantha, Conioselinum scopulorum* and *Swertia perennis* are common understory forbs. *Pentaphylloides floribunda* and *Ribes* spp. may also be found scattered below the upper canopy. The tall-shrub riparian vegetation of South Park seems similar to riparian association 11 detailed in Baker (1989), the main exception being that *S. brachycarpa* has replaced *S. geyeriana* in South Park.

Fens

This section will provide background on the study of peatlands, fen ecology, and classification, focusing especially on aspects relevant to Colorado fens.

Terminology

The history of peatlands study, coupled with the many cultures involved with these studies, has created a confusing array of terms, most of which have both scientific and colloquial definitions. Colloquial definitions are troublesome because they often misrepresent the nature of a site when the term is taken in a specific sense. The terminology used in this dissertation is widely agreed upon throughout the world. In some cases more regional definitions may be employed, but they will be specifically defined.

Peatland is broad term for any wetland that possesses organic soils, regardless of hydrology or vegetational composition (Gore 1983). **Mire** is a term that is closely related to peatland (Cajander 1913), and the two often they are taken as synonyms, but mire is a bit less crisply defined. It is taken to encompass both peat-producing areas and associated mineral soil areas that are part of the same wetland complex (Sjörs 1961a, Pakarinen 1995). In this sense mire is a somewhat broader term than peatland, which was devised to account for the mosaic nature of these wetland systems.

At the most basic level, there are two types of peatlands – bogs and fens. **Bogs** are peatlands whose biota has become isolated from ground water flow due to peat accumulation. They frequently possess a domed shape. Because of the peat accretion, plants only receive nutrients and moisture from precipitation and dust (Du Rietz 1949, Sjörs 1950b, Moore and Bellamy 1974). Bogs are therefore said to be ombrotrophic (*ombro* = precipitation, *trophic* = nourished). Owing to such limited inputs, and the cation exchange of the dominant plant *Sphagnum*, bogs have a low pH (less that 4) and are quite poor in nutrients (Du Rietz 1949, Sjörs 1950b, Gore 1968, Moore and Bellamy 1974, Gore 1983). Ericads are usually present and numerous, and trees may or may not be present.

Fens on the other hand are influenced to varying degrees by ground water. Because of this, fens are termed minerotrophic (*minero* = mineral, *trophic* = nourished)(Du Rietz 1949, Sjörs 1950b, Vitt et al. 1975, Slack et al. 1980). They are also geogenous because their vegetation and soils are formed under minerotrophic conditions, i.e., they are influenced by ground water that has been in contact with the underlying parent material (Gore 1983). Fens are generally more nutrient rich and alkaline than bogs and fen species require comparatively high nutrient levels. Witting (1949, in Waughman 1980) has suggested that 1 mg/l of calcium is the lowest concentration in which fen vegetation can occur, while Glaser et al. (1990) found that at the Lost River Peatland in Minnesota, bogs were located in sites with pH < 4.5 and pore water calcium < 2 mg/l. Fens are typically dominated by sedges and other graminoids; shrubs are often common. Using this broad definition, trees may also be present, although the name should be modified to reflect this fact, for example "treed fen" (e.g. Sjörs 1950b, Sjörs 1961a, Sjörs 1963, Johnson 1996b). Note that using this broad definition of fens, carrs can be included as a specific type of fen.

Classification and Ecological Gradients

Fen classification is based on the concept that certain assemblages of species can be predicted to occur under a given set of environmental conditions, i.e., many species have a high fidelity for a certain habitat type. In this regard, classification cannot be separated from investigation into the ecological and environmental situations within which species grow. Species composition, and therefore presumably the environment also, has been found to vary in peatlands along 4 interrelated gradients (Malmer 1986), or directions of variation (sensu Sjörs 1950b). The four primary directions of variation are due to: (1) minerotrophy; (2) microtopography; (3) position within the peatland, i.e. mire margin to expanse gradient; and (4) biogeography. Fens are frequently classified according to their position along one or more of these gradients.

Minerotrophy

The minerotrophy gradient is perhaps the most widely known of the four. It is also the most frequent gradient on which regional and international classifications are based. The amount and character of water entering a fen highly influences species composition by affecting species richness, the type of species present, and the amount of biomass produced by those species. Some fens may be nearly insulated from ground water due to the accumulation of peat; others may be influenced by topogenous ground water that is low in nutrients, such as that percolating through siliceous parent material, while still others may be subject to both receiving little and nutrient poor ground water. In such cases, fens are typically low in species diversity, contain a high coverage of *Sphagnum*, and numerous oligophilic species.

At the other extreme, fens may be highly influenced by ground water, exposed to a high volume of flowing (soligenous) water, subjected to ground water high in cations due to contact with calcareous or dolomitic parent material, or a combination of such factors. In these cases, fens will typically be vegetated by numerous, minerophilic species and brown mosses – especially those in the Amblystegiaceae.

Due to the cosmopolitan nature of the minerotrophy gradient, it has been widely used to classify fens with the most common divisions being poor, moderate, rich, and extremely-rich fens (Du Rietz 1949, Sjörs 1950a). These terms allude to several related fen attributes. Originally the terms referred to the species richness of a site (Du Rietz 1949, Sjörs 1961b, Sjörs 1963), but later workers also tied them to nutrient status, which is one of the driving factors of species diversity on fens (Gorham and Pearsall 1956, Gorham 1967. Sjörs 1983, Malmer 1986). The concentration of calcium and pH are especially important in this sense (Sjörs 1950a, Heinselman 1970, Vitt et al. 1975, Sjörs 1983, Wassen et al. 1989, Glaser et al. 1990, Malmer et al. 1992). These terms have also been used to imply the relative number of calciphilous species residing at a site (Vitt and Slack 1975, Slack et al. 1980). These workers have found bryophytes to be especially indicative of stand environment (see also Malmer et al. 1992), although bryophytes can also have surprisingly broad ecological tolerances to pH and calcium content (Kooijam and Westhoff 1995). It should be noted that this gradient is usually manifested as a regional gradient, between fen sites, but minerotrophic gradients can also be exhibited within sites.

Commonly, one or more of the above criteria are used in conjunction to classify fens. Chee and Vitt (1989) provide a comprehensive review of the water chemistry criteria used in defining these fen types. Table 1.1 shows water chemistry summaries for fen classes. As is evident from the overlap in parameters, these criteria provide only an approximate indication of the overall fen nutrient condition. Roughly speaking, typical poor fens have a

Table 1.1. Water chemistry values for the four minerotrophic fen classes. EC is specific conductivity reported as microsiemens.

Reference	Study Area	pH	EC µS	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)
POOR FENS							
Zoltai & Johnson (1987)	West-Central Canada	4.8	53	2.9	1.2	3.9	1.3
Zoltai & Johnson (1985)	Alberta	4.7	45	2	0.8	4	0.9
Comeau & Bellamy(1986)	Eastern Canada	4.3	-	7	2	4	0.4
Karlin & Bliss (1984)	Alberta	3.5-6.1	-	2	1-3	-	-
Glaser et al. (1981)	Minnesota	4.0-4.6	25-50	2.0-2.1	-	-	-
Vitt et al. (1975)	Alberta	5.2	-	2.3	0.4	3.0	-
Bellamy (1968)	Western Europe	4.5	-	20	5	7	2
Sjörs (1963)	Ontario	4.1-5.4	16-22	2	0.5	0.3	0.1
Sjörs (1948)	Sweden	4.2	-	6	2	2	0.4
MODERATE AND MODERATE-RICH FENS							
Chee & Vitt (1989)	Alberta	5.3-7.1	18-240	19-22	4-5	4-7	1.6-1.7
Zoltai & Johnson (1987)	West-Central Canada	5.8	212	25.0	10.2	4.7	1.4
Zoltai & Johnson (1985)	Alberta	6.0	249	28	11	5.1	1.8
Comeau & Bellamy (1986)	Eastern Canada	5.5	-	15	6	7	1
Karlin and Bliss (1984)	Alberta	4.6-7.1	-	4-51	2-12	-	-
Yefimov & Yefimov (1973)	U.S.S.R	6.1	-	18	8	1	0.3
Persson (1961)	Sweden	5.4-7.0	-	40-50	30	85-93	10
Sjörs (1948)	Sweden	6.0	-	68	12	2	0.4
RICH							
Glaser et al. (1981)	Minnesota	5.1-7.0	23-82	3-56	-	-	-
Bellamy (1968)	Western Europe	6.6	-	183	19	11	2
Sjörs (1963)	Ontario	5.8-7.4	48	9	2	1	0.3
EXTREMELY RICH FENS							
Glaser et al. (1990)	Minnesota	6.6-7.5	16-30	-	-	-	-
Zoltai & Johnson (1987)	West-Central Canada	6.5	374	54	14	6.54	0.1
Karlin & Bliss (1984)	Alberta	7.2-8.2	-	31-120	10-53	-	-
Slack et al. (1980)	Alberta	6.8-7.9	140-456	18-37	4-18	-	1.4-8.0
Sjörs (1961a)	Ontario	7.9	207	32	7	5	0.6

pH of 4.0-5.5 and calcium concentrations of 2-7 mg/l. The pH of moderate fens is generally 5.5-7.1, while calcium concentration ranges between 10-50 mg/l, rich fens are pH 6.0-7.5 with calcium between 25 - 80 mg/l, while extremely-rich fen pH is between 6.5 - 8.5 and calcium is greater than 30 mg/l.

Many species have a high fidelity for one of the minerotrophic classes. Based on this relationship, such species have often been used as indicators of peatland trophic conditions. This approach has been used to reduce the amount of environmental sampling necessary at a site by inferring environmental conditions through the flora. For instance, it is common for researchers to refer to poor or rich fen species.

Caution must be applied when using either floristic or chemical indicators alone, however, as specific site conditions or biogeographical constraints can muddle many classifications (Bridgham et al. 1996). Glaser et al. (1981), for instance, found the use of indicator species to be of questionable utility in their studies of the Red Lake Peatlands in Minnesota. They found that poor fen sites often had a species composition closely resembling that of both rich fens or ombrotrophic bogs. Explanations given for this discrepancy include insufficient sampling, an "unstable" vegetation composition and the absence of several indicator species from the study area's flora. Gorham (1950) also noted difficulties using minerotrophic indicator species. Lack of commonly cited indicator species in the regional flora must always be considered when using the indicator species approach (see below).

Similarly, using cation concentration criteria, Malmer et al. (1992) found it difficult to distinguish between moderate and extremely-rich fens, nor could they separate poor fens from bogs; although the latter situation was explained as a geographical effect. Differences in the rate at which water flows through a fen significantly affects effective minerotrophy. In highly soligenous fens, water moves rapidly through the active peat layer, or actrotelm, causing a large flux in nutrients across root uptake zones. It may also bring well oxygenated water into the root zone. This phenomenon has the effect of making such soligenous fens effectively "richer" than their water chemistry alone would suggest. The effect this has on fen flora has been noticed in several studies (e.g. Gorham and Pearsall 1956, Sjörs 1963).

Clearly, species' physiological tolerances and complex chemical interactions muddy attempts at developing a discrete classification. Therefore as many indicators as possible should be used when developing classifications; optimally both environmental and species characteristics should be used, although this is not always possible for practical reasons.

Microtopography:

Microtopography has a marked effect on fen vegetation (e.g. Sjörs 1950b, Sjörs 1961a, Sjörs 1963, Heinselman 1970, Vitt et al. 1975, Slack et al. 1980, Sjörs 1983, Malmer 1986, Charman 1993, Johnson 1996b, Johnson 1997). Unlike minerotrophic gradients, this one acts exclusively within sites. In its most common forms, microtopography can exist as stings and flarks (elongated ridges perpendicular to water flow and similarly oriented troughs, respectively), hummocks and hollows, or elevated peat islands such as palsas (i.e. tree peat islands with ice cores).

The effects of microtopography have been known for at least 70 years (Lewis et al. 1928, in Slack et al. 1980). In most cases, microtopography influences species composition by changing the water table relative to ground's surface, altering soil and pore water chemistry, or both (e.g. Bellamy and Rieley 1967). The environmental heterogeneity imparted by these surficial features greatly enhances site alpha, or within-habitat diversity. Within a matter of less than a meter, nearly complete species turnover can occur due to microtopographical effects alone (Vitt et al. 1975, Karlin and Bliss 1984, Charman 1993, Johnson 1996b).

Mire Margin to Expanse:

Like the microtopographical gradient, this one is manifested within individual sites. Its importance has been known at least since the early 1900's (Cajander 1913), but Sjörs (1948, 1950b) presented the first explicit treatment of the topic. The margin to expanse gradient is thought to arise primarily due to changes in ion content of the ground water as it filters though the actrotelm, or upper layer, of the peat. As the water flows through the peat, minerals are lost through absorption by living plant roots and adsorption to organic acids and root exteriors (e.g. Gorham 1957, Moore and Bellamy 1974, Vitt et al. 1975, Karlin and Bliss 1984). In other words, this is essentially a within-site minerotrophy gradient whose manifestation is a change in vegetational structure. Most commonly this gradient shows up as a change from high production mire margin areas rich in tall shrubs and many times trees, to lower production mire expanses dominated by graminoids, mosses, and stunted shrubs. The importance of this gradient has been noted in Rocky Mountain fens (Cooper and Andrus 1994, Johnson 1996b).

Biogeographical Considerations:

The regional flora dictates which plant species can inhabit any given area. While this seems essentially tautological, it has significant ramifications for ecological investigations (Malmer 1986, Chee and Vitt 1989, Cooper 1990, Bridgham et al. 1996). As discussed above, indicator species are often used to infer site environmental conditions since they have a high fidelity to a particular suite of environmental factors. However, the lack of recognized indicator species within a region can hinder investigations and reduce study comparability. Absence of indicator species can also make conclusions about fen characteristics uncertain since their absence could signify either inappropriate fen conditions or a more general lack of the species in the regional flora. This issue is especially important in the southern Rockies which lack many of the common circumpolar indicator species. As can be seen from the above discussion, the main gradients of peatland variation can be used as a basis for regional wetland classification, but each may also be found within a single fen. It is important to note that none of the gradients are mutually exclusive, and more often than not are juxtaposed atop one another. Such gradient superimposition provides ample challenges for peatland ecologists.

Colorado Peatlands and Their Classification

Little has been published on Rocky Mountain peatlands. Colorado's peatlands have been referred to using a number of different terms such as bogs, fens, swamps, or marshes. Because of the primary role of groundwater in their hydrology and the accumulation of organic matter, these peatlands are technically fens. No extensive bogs have ever been found in the state due to insufficient precipitation, and previous references to Colorado "bogs" have been based only on the colloquial meaning of the term. It has been proposed, however, that in Colorado, as elsewhere, large peat hummocks can form areas environmentally equivalent to miniature bogs in peatlands which are otherwise fens (Sjörs 1961a, Sjörs 1965, Bellamy and Rieley 1967, Zoltai and Johnson 1985, Pakarinen 1995, Johnson 1996b).

In Colorado, fens are found above about 2600 m (8500 ft.), but are most common in the subalpine zone and above (>2750 m). Subalpine fens are generally found in valley bottoms and mountain parks. They may also be associated with river systems, usually occurring at slope breaks such as where valley sides or terrace shoulders intersect relict floodplains. In general, fens can occur anywhere in the subalpine zone where enough ground water emerges to perennially saturate the soil. A shallow grade also helps to increase the residence time of the discharged water and aids in soil saturation. Many such locations occur in the mountains of Colorado and fens are not uncommon, but subalpine fens are generally small and easily damaged. The exact extent of fens in Colorado is not precisely known, but it certainly seems to be less than one percent of the total land area.

For the most part, mires in Colorado's Front Range have been described as poor or moderate fens (Bierly 1972, Cooper 1986, Cooper 1990, Johnson 1996b), but true poor fens in the original sense may not actually exist in Colorado. Mountain fens are often difficult to classify using the established poor-moderate-rich scheme. The difficulty lies in the discrepancy between ionic and pH indicators of fen type. Often ground water pHs are only slightly acidic to circumneutral, which indicates a moderate or rich fen environment. At the same time, cation concentrations may be extremely low (e.g. calcium concentrations of 1-2 mg/l), thus indicating poor or extremely poor fen conditions (Table 1.2). Similarly, species indicators may suggest the range of poor to rich fen conditions.

The classification difficulties seem attributable to three factors: (1) the different hydrologic settings of mountain fens compared to the boreal fens in which this classification was devised; (2) the different geologic settings; (3) and the different floristic settings. Siliceous rocks are the predominant soil parent material in this region (Marr 1961, Richmond 1974) and this has led to the formation of mineral-poor soils. Further, these soils are heavily leached by the acidic litter produced by conifers (Marr 1961). Such traits have led to ion poor ground water and therefore only weakly minerotrophic fens. In addition to soil differences, snow melt greatly influences aquifer and surface water sources in the mountains (Rink and Kiladis 1986, Cooper 1990). Snow melt water in this area is deficient of mineral nutrients and slightly acidic. The large and sudden flush of this water during the early summer greatly dilutes any ionicly rich water sources, and imparts a circumneutral pH to soligenous water. This is in contrast to the poor fens of the boreal zone where pH and cation content are largely biogenically mediated and the level of minerotrophy determined by the degree to which vegetation is isolated from ground water sources (Gorham 1957, Vitt et al. 1975, Glaser et al. 1981, Nicholson and Vitt 1990).

Countering the effects of the nutrient poor water is the relatively large nutrient flux caused by flowing water, resulting from steep hydrologic gradients. As discussed above, this can effectively increase the amount of nutrients available for plant growth and so allow the growth of a more minerotrophic flora than expected based on water chemistry alone. The

Table 1.2. Published water chemistry data on subalpine fens in the southern Rocky Mountains.

Reference	Study Area	pH	CND MS	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)
Cooper (1990)	Rocky Mountain National Park, CO	>5.0	13-15	4.18	-	~2.5 - 3.5	-
Walton-Day (1991)	Lake County, CO	4.6	-	31	11.7	2.6	<1 - 4.0
Cooper (1994)	Wind River Mountains, WY	2.1-6.5	-	1.4 - 14.6	0.3 - 1.0	0.9 - 2.3	-
Johnson (1996)	Rocky Mountain National Park, CO	6.4	38 - 52	2.5	52.0	2.1	0.60

circumneutral pH also affects the effective minerotrophic environment because many cations are more bio-available at such pHs (Sjörs 1963).

Finally, as considered earlier, many species commonly used as minerotrophy indicators in boreal regions and Europe are not present in the southern Rocky Mountain flora. This necessitates the generation of region-specific indicators to be used in conjunction with species of known ecological preference.

While moderate fens are far and away the most common fen type in this region, divergent types also occur. For instance acidic "iron fens", generally called iron bogs, may be found in areas with unusual geology, frequently in mineral-bearing volcanic deposits. These sites may have pHs in the threes and a high coverage of *Sphagnum* mosses, which is uncommon in this region (Johnson, unpublished data). Another fen type are the rich and extremely rich fens, which occur in South Park and near North Park. These sites, found in areas with calcareous or dolomitic parent material, are rich in base cations, and have a pH that is usually greater than seven. Such sites are the topic this dissertation and will be covered in detail in the following chapters.

GEOLOGY AND GEOMORPHOLOGY OF SOUTH PARK

Physiography of South Park

South Park is one of the four major inter-mountain basins in Colorado formed during the Larimide Orogeny (Lozano 1967). The park is bounded by the Front Range on the east, on the west and north by the Mosquito Range, and by the Buffalo Peaks in the south. Roughly speaking, the park encompasses 2330 km^2 (900 $mi.^2$), and is 80 km^2 (50 mi.) long and 56 km^2 (35 mi.) wide at its widest points (Stark et al. 1949).

The primary topographical features of South Park are several prominent north-northwest oriented ridges of exposed bedrock, Quaternary alluvial terraces, and scattered moraines. The park slopes to the east in the northern regions and progressively more to the southeast moving south (Stark et al. 1949). The average slope of the valley floor is near one degree.

Based on physiography, South Park can be divided into three regions: the Elkhorn Uplands in the northwest; the plains in the north, center and west; and the southern volcanic region (Fig. 1.2). This study focuses on the plains region and western foothills. Therefore, the remaining two regions will be discussed only incidently.

Although in a local area of low relief, South Park lies at an elevation of between 2590 m and 3050 m (8,500 to 10,000 ft.), which places it within the subalpine vegetation province (Marr 1961). During the Quaternary, most of South Park served as an outwash plain for glacial rivers originating in the Mosquito range (Tweto 1974). This accounts for much of the Park's relative flatness. Most of the topographical relief in South Park consists of Quaternary fluvial terraces and bedrock ridges.

While all of the inter-mountain parks are unrepresentative of typical montane conditions, South Park is unique. Most of the inter-mountain parks are underlain with outwash primarily composed of granitic or volcanic material. South Park in contrast, has a

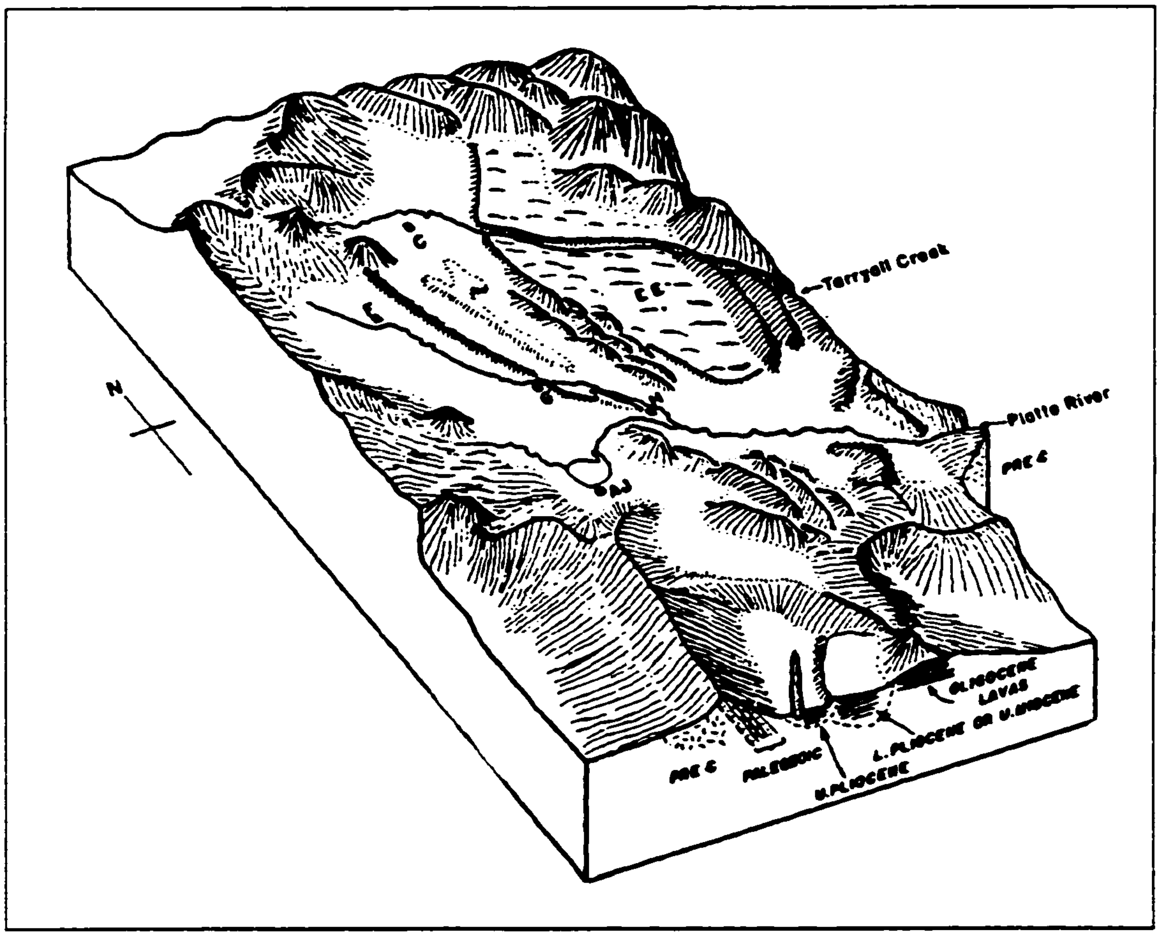

Figure 1.2. A block drawing showing the physiography of South Park. The key to symbols is: C - Como, EE - Elkhorn Upland, F - Fairplay, G - Garo, H - Hartsel, AJ - Antero Junction. The rise due west of Garo is Little Black Mountain. From Stark et al. (1949).

till with a high proportion of calcareous and dolomitic material (Tweto 1974, Appel 1995). The geology of this area is complex and not precisely known, but according to the description of Lozano (1967) and Valdes (1967), this till was mainly derived from the Pennsylvanian-aged Maroon Formation and the till is associated with the Pinedale and Bull Lake glacial intervals (Tweto 1974). The calcareous and dolomitic nature of the these strata causes groundwater flowing through them to become quite alkaline, and pH can be as high as 11 (Appel 1995). In contrast, water flowing through granitic outwash is nearly neutral to slightly acidic. The highly basic, minerally rich ground water is a primary cause of the unique species composition found in South Park's fens.

Geologic History of South Park

Structural geology and historical erosional cycles have shaped South Park's current physiography. The park is a complexly faulted, asymmetrical, north-northwest trending syncline which has been filled with Tertiary sediments and Quaternary glacial outwash (Lozano 1967, De Voto 1971).

The formation of South Park began in the late Cretaceous and Paleocene during the mountain building of the Laramide Orogeny (De Voto 1971). Differential uplift occurred along the north-northwest trending faults of South Park's basement blocks creating the Sawatch and Front Ranges. The uplift laterally compressed and deformed South Park's floor. Through this differential uplift, the primary syncline of the valley was formed, as well as the major faults of the region, the Elkhorn, Mosquito, and London faults (De Voto 1971). These faults essentially define the boundaries of the park as we see it today.

The newly created mountain ranges surrounding the park began their first erosional cycles during the lower Tertiary Period, including the Paleocene and Eocene Epochs. This was a time of sedimentation within the South Park syncline. In the southern areas around the Buffalo Peaks, extensive volcanic activity also occurred beginning around the Oligocene.

In subsequent periods, erosion dominated the valley floor processes as rivers carved their way into the newly deposited sediments. During erosional periods, cycles of river downcutting and planation alternated with terrace and pediment formation. These cycles were especially pronounced during the Pleistocene as the climate cycled between glacial and interglacial periods. The glaciers did not reach the park floor and the greatest glacial extent was just west of Fairplay during the Fairplay glacial interval (Singewald 1950).

Geology of South Park and the Mosquito Range

Much of the unique character of South Park's wetlands stems from the nature of the underlying parent material, the geology of the adjacent Mosquito Range, and their combined effect on the regional geochemistry. The Mosquito Range was formed during the Sawatch Uplift of the Laramide Orogeny. Figure 1.3 shows a typical stratigraphic section through the range. The park has a similar stratigraphy, although, some units may be missing. The central core of the Mosquito Range is comprised of Precambrian granites, primarily, metamorphosed granites, gneiss and schist (Chronic 1964). Over these granites are laid Cambrian to Pennsylvanian sediments. Of primary concern here are the upper four strata: the Leadville Limestone, and the Belden, Coffman and Maroon Formations. It should be noted that

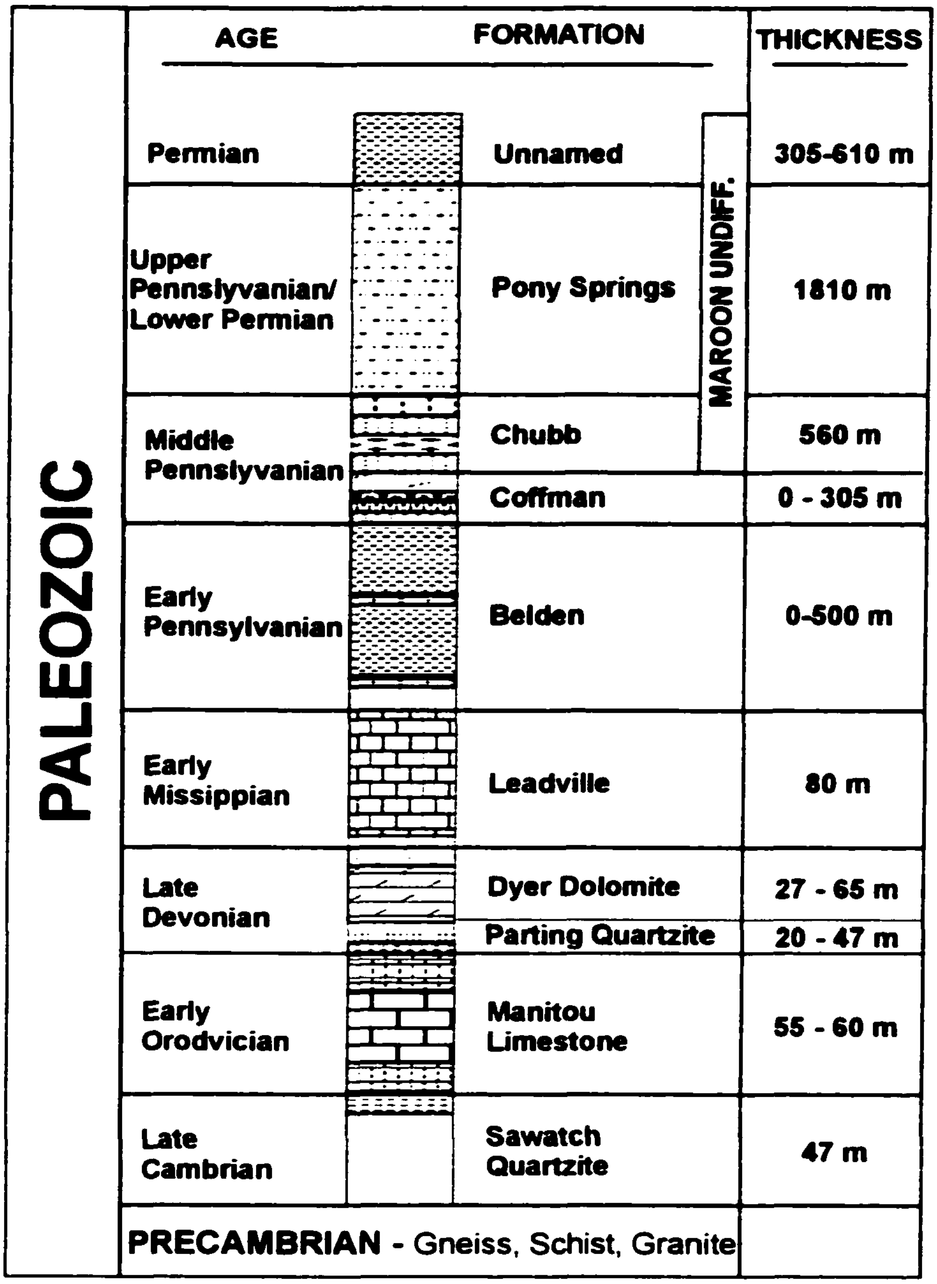

Figure 1.3. A typical stratigraphic cross section through the Paleozoic and Lower Permian rocks in South Park. The right column gives the approximate thickness of each stratum. The central column shows the major formations with members shown but not named. Important formations and their comprising members are described in the text (after Chronic 1964 and de Voto 1971).

inconsistencies abound in the nomenclature of these units (Lozano 1967, De Voto 1971). This is especially true of stratigraphic units within the park itself. Difficulties seem to arise due to the complex folding that has occurred and the locally complete erosion of certain units. Table 1.3 provides a key to the Paleozoic and Mesozoic stratigraphic terms used by various authors. This paper uses the terminology of De Voto (1971).

What follows is a brief description of the formations mentioned above. Figures 1.4a-c are geological maps of South Park in the vicinity of the three study sites. The site locations and approximate extents are shown on each map.

Leadville Limestone:

The Leadville Limestone member was deposited during the early Mississippian. Although called a limestone, in many areas it is essentially pure dolomite, while in other regions it is actually limestone (Stark et al. 1949, Chronic 1964). The reason for the dolomitization is uncertain but is perhaps due to Laramide tectonism and mineralization. The thickness of this formation ranges from 45 to 100 m.

Belden Formation:

The Belden Formation was probably deposited during the early Pennsylvanian, although good index fossils for this period have not been found (Chronic 1964). The formation consists of dark gray to black shales, thin limestones and fine sandstones, although the shales dominate the profile (Stark et al. 1949). The total formation thickness ranges between 150 to more than 900 m.

Table 1.3. A key to stratigraphic nomenclature used by various investigators. This study uses the nomenclature of De Voto (1971). Table after De Voto (1971).

<table>
<tr><th colspan="2">Johnson, 1934</th><th colspan="2">Gould 1935</th><th colspan="2">Stark et al. 1949</th><th colspan="2">Brill 1952</th><th>Chronic 1958</th><th colspan="2">De Voto 1971*</th></tr>
<tr><td colspan="2" rowspan="3">Maroon</td><td rowspan="5">Maroon</td><td>Maroon Undiff.</td><td rowspan="4">Maroon Undifferentiated</td><td>Unnamed</td><td colspan="2" rowspan="2">Maroon</td><td rowspan="2">Maroon</td><td rowspan="4">Maroon formation Undifferentiated</td><td>Unnamed</td></tr>
<tr><td>Pony Springs Member</td><td>Pony Springs</td><td>Pony Springs</td></tr>
<tr><td rowspan="2">Chubb Member</td><td rowspan="2">Chubb Member</td><td rowspan="3">Minturn</td><td rowspan="3">Jacque Mt. Is. Member & unnamed</td><td rowspan="3">Minturn</td><td rowspan="2">Chubb Member</td></tr>
<tr><td rowspan="3">Weber(?)</td><td rowspan="3">Upper Zone</td></tr>
<tr><td>Coffman Mem.</td><td rowspan="4">Weber (?)</td><td>Coffman Member</td><td colspan="2">Coffman</td></tr>
<tr><td colspan="2" rowspan="3">Weber (?)</td><td rowspan="2">Middle Member</td><td colspan="2" rowspan="3">Belden</td><td rowspan="2">Belden</td><td colspan="2" rowspan="3">Belden</td></tr>
<tr><td></td><td>Middle Zone</td></tr>
<tr><td></td><td>Lower Zone</td><td>Lower Member</td><td>Kerber</td></tr>
</table>

Figure 1.4a. Geologic Map of central and northern South Park. The location and approximate extents of Crooked Creek and Fremont's Fens are indicated. A key to relevant geologic units follows (from Stark et al. 1949).

Pm= Undifferentiated Maroon Formation.
ls = Limestone beds of the Maroon Formation.
Kp =Pierre Shale.
Kf = Fox Hills Sandstone.
Td = Denver Formation.
Tep = Eshe Porphyry.

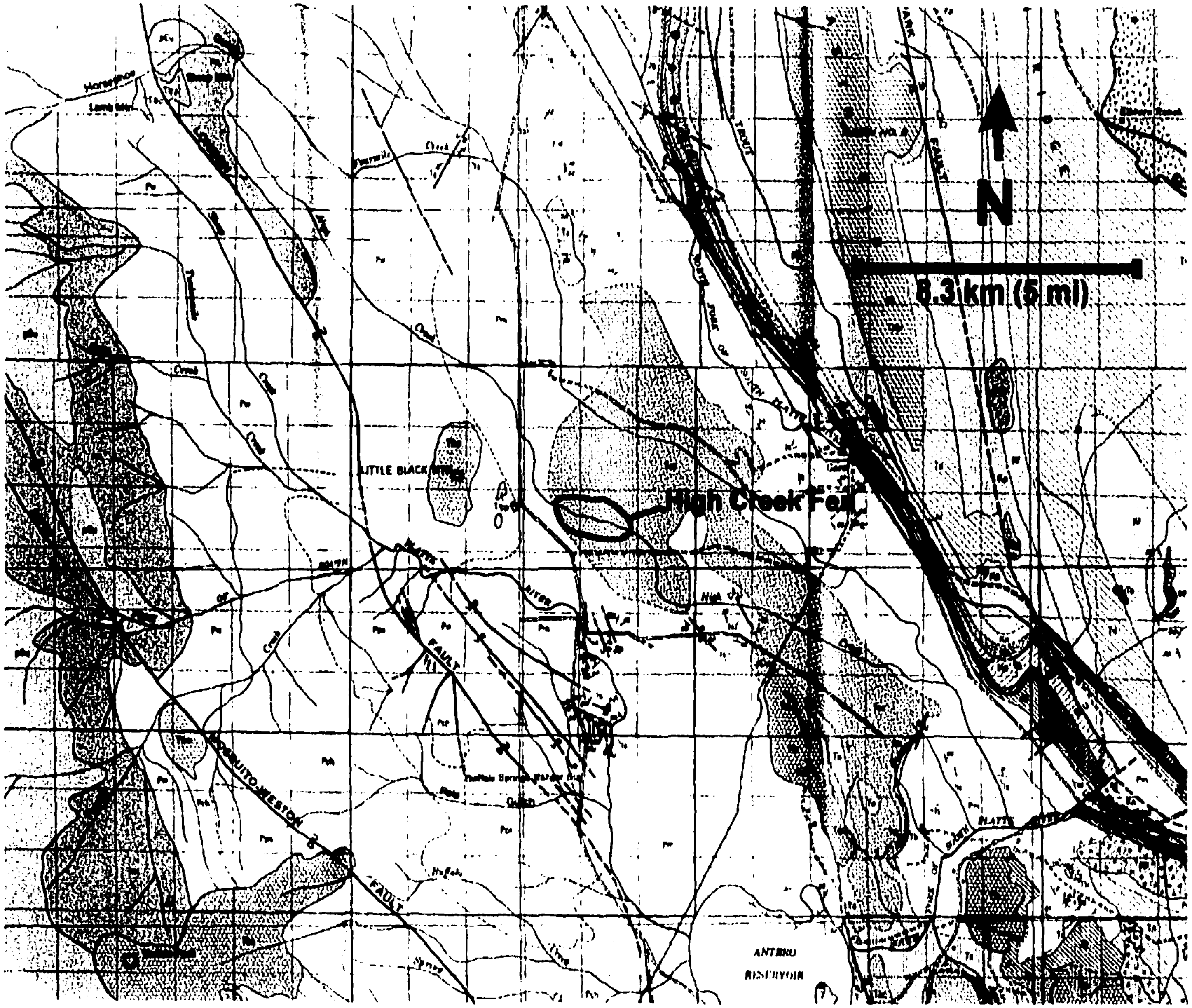

Figure 1.4b. Geologic map of south-central South Park. The location and approximate extent of High Creek fen is shown. A key to relevant geological units is shown below (From Stark et al. 1949).

Pw = Belden and Coffman Formations (Weber (?) of Stark et al. 1949)
Pm = Undifferentiated Maroon Formation.
ls = Limestone member of the undifferentiated Maroon Formation.
Pch = Chubb Member of the Maroon Formation.
Pps = Pony Spring Member of the Maroon Formation.
Tlbp = Little Black Mountain Porphyry
Tac = Quaternary Outwash from Pinedale and Bull Lake intervals.

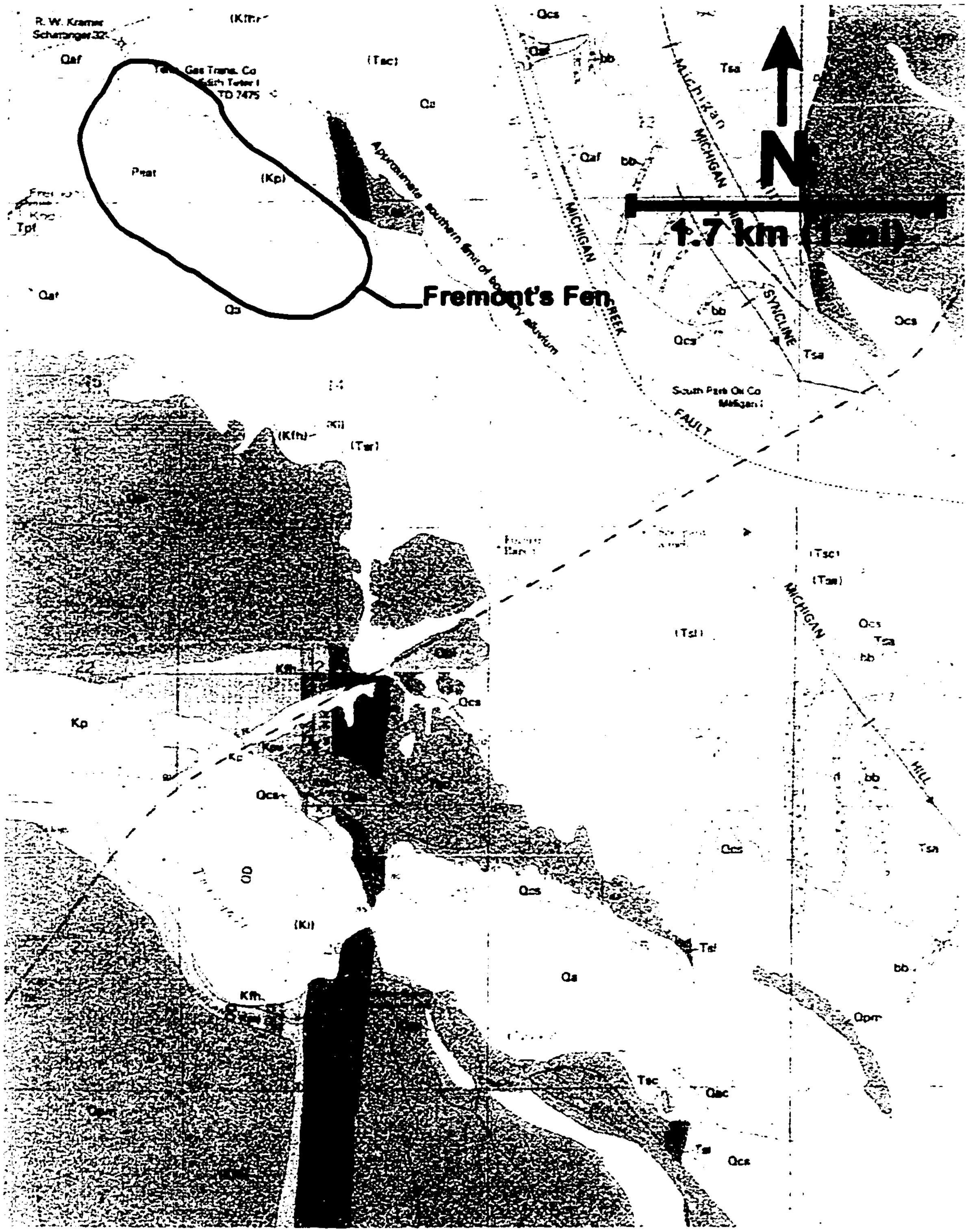

Figure 1.4C. Portion of the Geology of the Milligan Lakes Quadrangle. The location of Fremont's Fen is indicated. Geological unit symbols are as follow: Qaf - alluvial fan; Qa - glacial alluvium (mostly Pinedale); Kp - Pierre shale; Tsc - conglomerate member of the South Park (Denver) Formation; Kl - Laramie Formation; Tsr - Reinecker Ridge Volcanic Member.

Coffman Formation:

The Coffman formation consists of "crossbedded, siliceous, buff, gray, to red, arkosic conglomerates and micaceous, arkosic sandstones" of Des Moinesian age (De Voto 1971). This formation is interbedded with the shales of the Belden Formation and lies below the Maroon Formation. Also reported are the presence of Des Moinesian fusulinids imbedded in a limestone matrix in direct contact with Precambrian granite knolls (Chronic 1964). Chronic (1964) suggests that based on this evidence portions of South Park were previously an island shoreline.

Maroon Formation:

The Maroon is a massive formation, up to 3000 m thick, formed during the mid-Pennsylvanian through the Permian (De Voto 1971). In the southwestern areas of South Park, the Maroon Formation has been divided into the Chubb and Pony Springs Members. In other areas, these units are unmappable and so are left undifferentiated. This is the case in the study area, so the undifferentiated Maroon Formation will be described.

North of Antero Reservoir the Maroon formation is dominated by red arkosic sandstones, conglomerates, siltstones and shales (Stark et al. 1949, Ettinger 1964, De Voto 1971). Interbedded in these strata are irregular beds of limestone. Near Fairplay the limestone beds appear as mappable strata (Stark et al. 1949). Also reported are gypsiferous layers up to 15 m thick, although it is unclear whether these strata occur in the study area. Appel (1995) asserts that the gypsiferous beds occur in the immediate vicinity of High Creek Fen and play a role in defining its geochemistry.

The most common unit in South Park is the undifferentiated Maroon Formation; however, within the study area this unit may be overlain with Quaternary sediments (see below). Several Tertiary units not found in the surrounding Mosquito Range are present in South Park. Only those units found in the vicinity of the study area will be described.

Pierre Shale:

The Pierre Shale is comprised almost entirely of black fissile shale with occasional sandstone and calcareous beds (Stark et al. 1949, Ettinger 1964). The Pierre Shale was deposited during the Cretaceous and reaches thickness of 1,100 m (Ettinger 1964).

Fox Hills Sandstone:

The Fox Hills Sandstone is nearly pure, fine-grained, highly friable yellow to light gray sandstone. In many places the layer is so poorly cemented that it is practically loose sand (Stark et al. 1949, Ettinger 1964).

Eshe Porphyry:

The Eshe Porphyry was so named due to its prominence around the Eshe ranch in northern South Park. This is the ranch on which much of the Fremont's Fen lies. The Porphyry is an intrusive quartz monzonite and quartz diorite corresponding to Tertiary intrusive events. The ground mass of the porphyry is finely granular with phenocrysts of feldspar, biotite, hornblende and quartz. The Eshe Porphyry sits conformably atop the Pierre Shale.

Quaternary Deposits:

The Wisconsin glaciers did not reach the South Park valley floor, although terminal moraines are found as near as the South Platte valley west of Fairplay (Singewald 1950). The primary Paleocene deposits in South Park are glacial outwash plains and alluvial terraces. Most of these deposits are due to the Pinedale glacial interval, however, Bull Lake aged deposits are not uncommon. The depth of till varies considerably across the park, from thin deposits 4.5 m thick, to terminal moraines over 120 m high. Across the plain areas, 15 m is approximately the average till thickness.

CLIMATE OF SOUTH PARK

South Park is a cool and semi-arid region located in the rain shadow of the Mosquito Range. There are two weather stations in South Park relevant to this study, one at Antero Reservoir and one formerly located in Fairplay. There have also been several shorter-term studies which have examined climate as it relates to evapotranspiration in South Park. Information from each of these sources will be used to characterize the regional climate.

Temperature

The only long-term annual temperature data available come from the Antero Reservoir Station (1961-1997). Mean annual temperature at this station is 1.9 °C (Table 1.4). Spahr (1981) and Walter et al. (1990) also took temperature measurements in South Park, but only during the growing season (Table 1.4). Spahr reports that the average temperature differed significantly between his three stations ($p<0.01$), with Antero Reservoir being the warmest and Fairplay the coldest. Figure 1.5 shows the annual temperature distribution for Antero Reservoir.

Precipitation

Precipitation data are also provided in Table 1.4. Antero Reservoir is the only station with long-term and contemporary data, but a station also was maintained in Fairplay from 1954 -1956. Figure 1.6 shows the monthly precipitation for Fairplay and Antero Reservoir. On an annual basis Fairplay receives more precipitation than Antero Reservoir. However, Spahr (1981) reported that during the growing season neither Fairplay, Antero Reservoir, nor Jefferson received statistically different precipitation amounts ($p<0.01$). This suggests that the difference in precipitation between Fairplay and Antero Reservoir occurred during late fall, winter, and early spring. The precipitation distribution in Figure 1.6 corroborates this assertion. Fairplay receives its greatest monthly precipitation in April during the spring snows. Antero Reservoir receives its greatest precipitation during August, primarily in the form of convective showers. Fairplay also shows a peak in rain fall during this period. Figure 1.7 shows the fourteen-day precipitation distribution for Antero Reservoir from 1995 - 1997, the years during which this study was completed.

Table 1.4. Air temperature and precipitation data from weather stations and published data.

Station	Antero Reservoir	Fairplay	Jefferson	Hartsel	Measurement Period	Record	Source
Mean Air Temperature (°C)	1.92	n.a.	n.a.	n.a.	Jan - Dec	1961-1997	Reservoir Weather Station
	12.8	10.4	11.0	n.a.	May - Oct.	1977-1979	Spahr 1981
	10.72	n.a.	7.8	9.4	May - Sept	1961-1986	Walter, et al. 1990
Mean Total Precipitation (cm)	25.81	40.21	n.a.	n.a.	Jan - Dec.	1961-1997 (Antero) & 1954 - 1966 (Fairplay)	Weather Station Data
	17.9	n.a.	23 7	21.8	May - Sept	1962 - 1986 (Antero), 1982-1985 (Other stations)	Walter, et al. 1990
	15.0	15.8	16.83	n.a.	May - Sept.	1977-1979	Spahr 1981

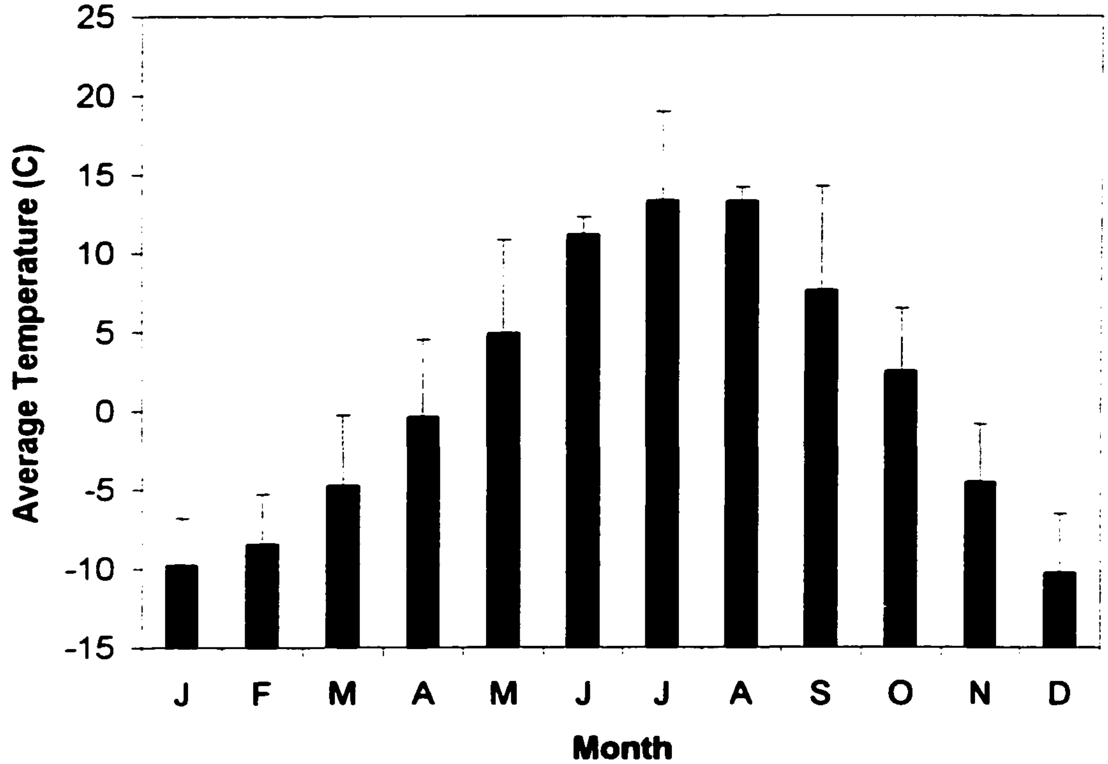

Figure 1.5. Average monthly temperature as measured at the Antero Reservoir weather station between 1964 and 1996. Bars show the standard deviation of monthly temperature.

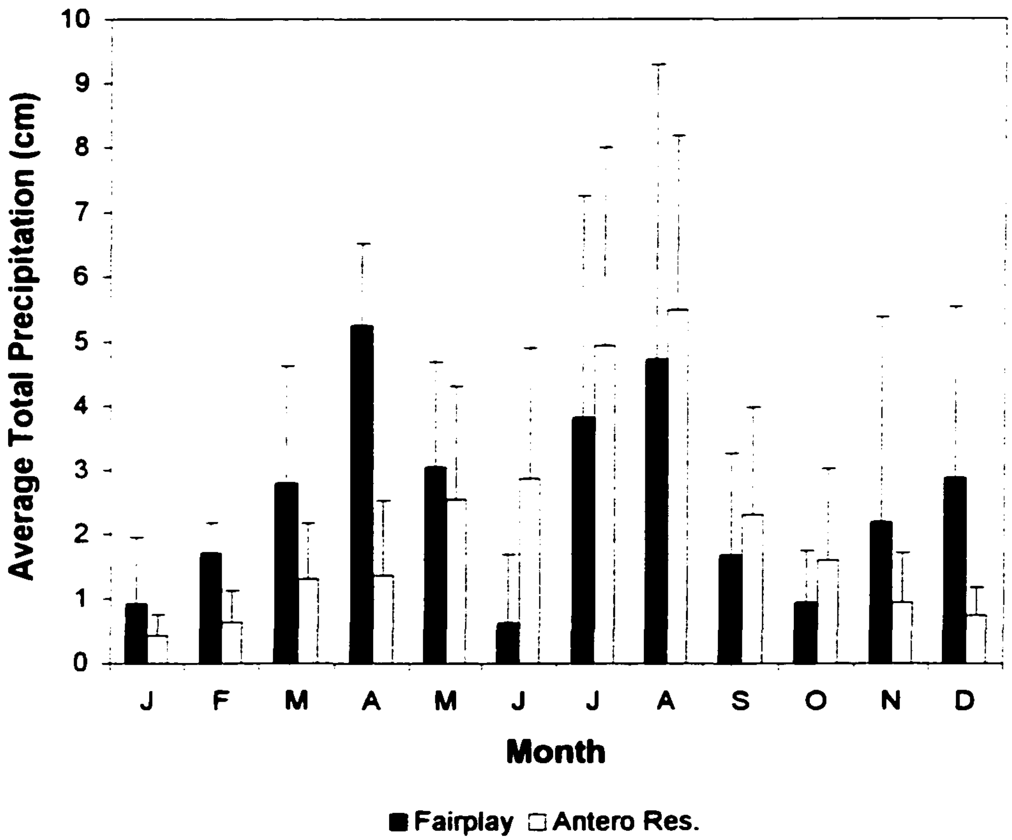

Figure 1.6. Average monthly precipitation measured at the Antero Reservoir and Fairplay weather stations. The data are from 1964 - 1966 at Fairplay and 1964-1996 at Antero Reservoir. Bars show the standard deviation of the mean.

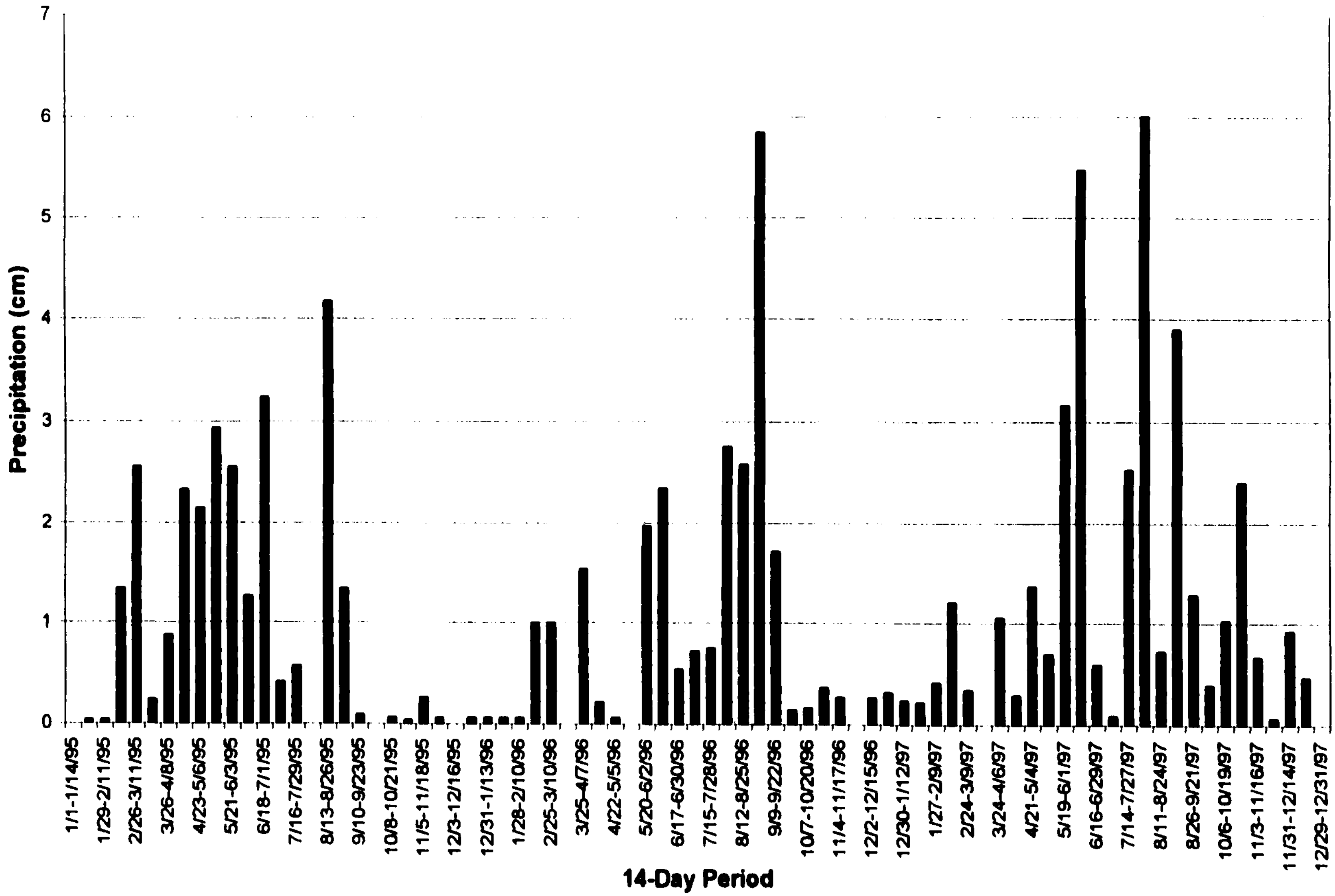

Figure 1.7. Fourteen-day total precipitation from 1995 to 1997 as recorded at the Antero Reservoir weather station.

Evaporation and Evapotranspiration

Table 1.5 presents evaporation and evapotranspiration data compiled by Spahr (1981) and Walter et al. (1990). In the rows containing pan evaporation (PE) data, total pan evaporation is given, followed parenthetically by potential evapotranspiration (PET) calculated from this number. PET was determined by multiplying total PE by an empirically derived pan coefficient (Dunne and Leopold 1978). Kruse and Haise (1974) determined the average pan coefficient for South Park to be 0.89. Later studies obtained values similar to this, as well (Walter et al. 1990).

Spahr (1981) reports that during his study, Jefferson had less PE than either Fairplay or Antero Reservoir, but Antero Reservoir and Fairplay had statistically similar PEs ($p < 0.01$). In Walter et al's. (1990) extensive study, they installed an evaporation pan, several lysimeters, and a weather station at each climate station. Table 1.5 reports the data from their evaporation pans, and flooded and damp lysimeters located in near Jefferson and Hartsel. The flooded and damp lysimeters were chosen for inclusion here because their experimental conditions are similar to the wetland conditions being studied. Walter et al. also calculated PET based on energy budget methods. Included in Table 1.5 are PET values calculated through the Pennman and Jensen-Haise methods.

The average ET measured in the three lysimeters at each site was very close to PET calculated from the pans. The difference between these measures is 2.6 cm and 0.8 cm for Jefferson and Hartsel, respectively. Of the two synthetic methods, the results of the Jensen-Haise method most closely corresponded to the PET measured in the pans and the actual ET

Table 1.5. Evaporation and evapotranspiration data from published reports. The numbers in parentheses are potential evaporation as measured by pan evaporation multiplied by an empirical pan coefficient of 0.89 (Kruse & Haise 1974).

Station	Antero Reservoir	Fairplay	Jefferson	Hartsel	Measurement Period	Record	Source
Mean Daily Pan Evaporation (cm)	0.70	0.71	0.56	n.a.	May 1 - Sept 30	1977-1979	Spahr 1981
Pan Evaporation (cm)	108.54 (96.6)	111.4 (99.1)	86.44 (76.1)	n.a.	May 1 - Sept 30	1977-1979	Spahr 1981
	n.a.	n.a.	83.2 (74.0)	99.0 (88.1)	April 26-Oct. 31	1982-1983	Walter et al. 1990
Flooded/Saturated Lysimeters	n.a.	n.a.	77.6	88.9	April 26-Oct. 31	1982-1983	Walter et al. 1990
Penman	n.a.	n.a.	68.53	74.2	April 26-Oct. 31	1982-1983	Walter et al. 1990
Jensen-Haise	n.a.	n.a.	77.6	81.2	April 26-Oct. 31	1982-1983	Walter et al. 1990

measured in the lysimeters. These results suggest that actual ET is at, or slightly higher than, calculated PET.

Of primary concern to this study is the interplay between PET and precipitation. Figures 1.8 - 1.10 show the relationship between precipitation and pan PET as measured by Spahr (1983). For all months during the growing season, and at all stations, there is a moisture deficit of up to 19 cm. This relationship underscores the importance of ground water inputs and soil moisture recharge during the colder months for maintenance of wetland conditions.

Wetlands exist only where there is a net surplus of water for an extended period of the year. Fens require a stable and high water table level table (see Chapter 2). The moisture deficits shown in Figures 1.8 - 1.10 clearly show that additional hydrologic inputs are necessary for the maintenance of fens in this area. These inputs primarily come in the form of ground water. Without maintenance of ground water levels, fens, and many other wetland types, could not exist in such an arid climate.

STUDY SITES

Three sites on the west side of South Park were chosen for this study – High Creek Fen, Crooked Creek Fen, and Fremont's Fen (Fig. 1.11). The sites span the majority of the park from north to south. These sites were chosen because they encompassed a range of sizes, landscape positions, and disturbance levels. Each is described below.

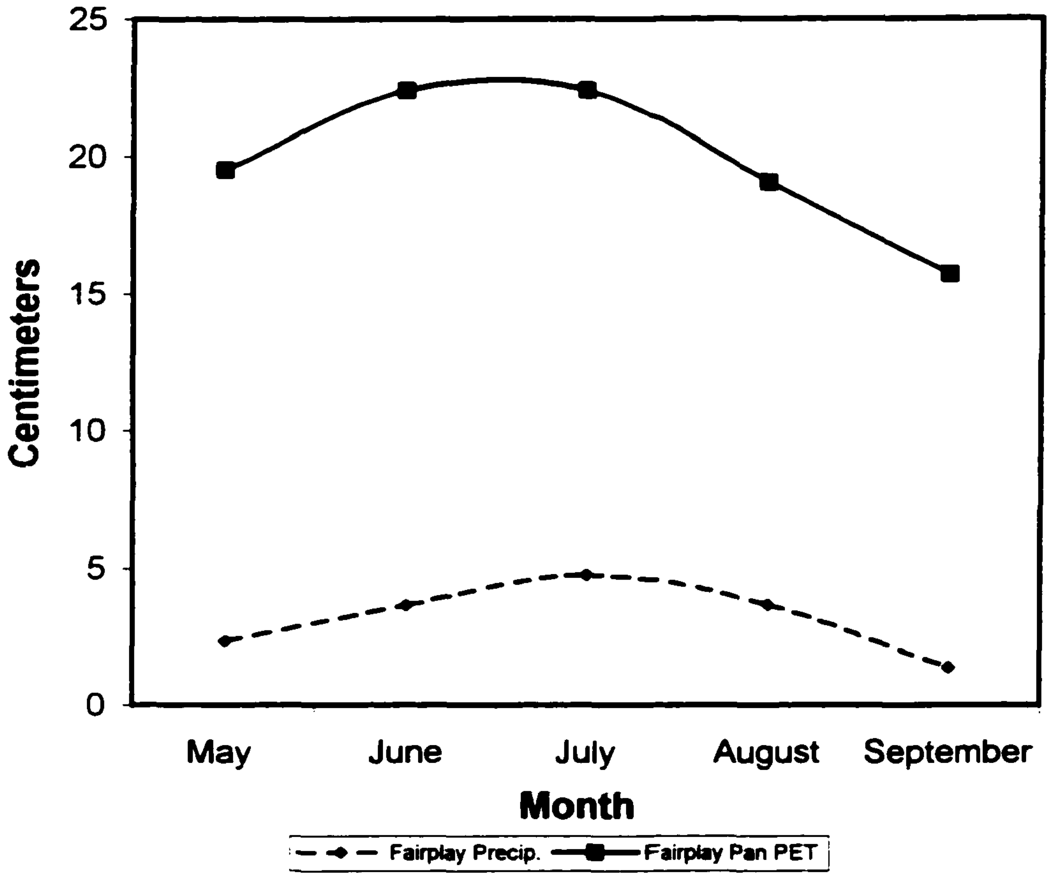

Figure 1.8. Precipitation vs. potential evaporation from 1977 - 1979 at Fairplay. Data from Spahr 1981.

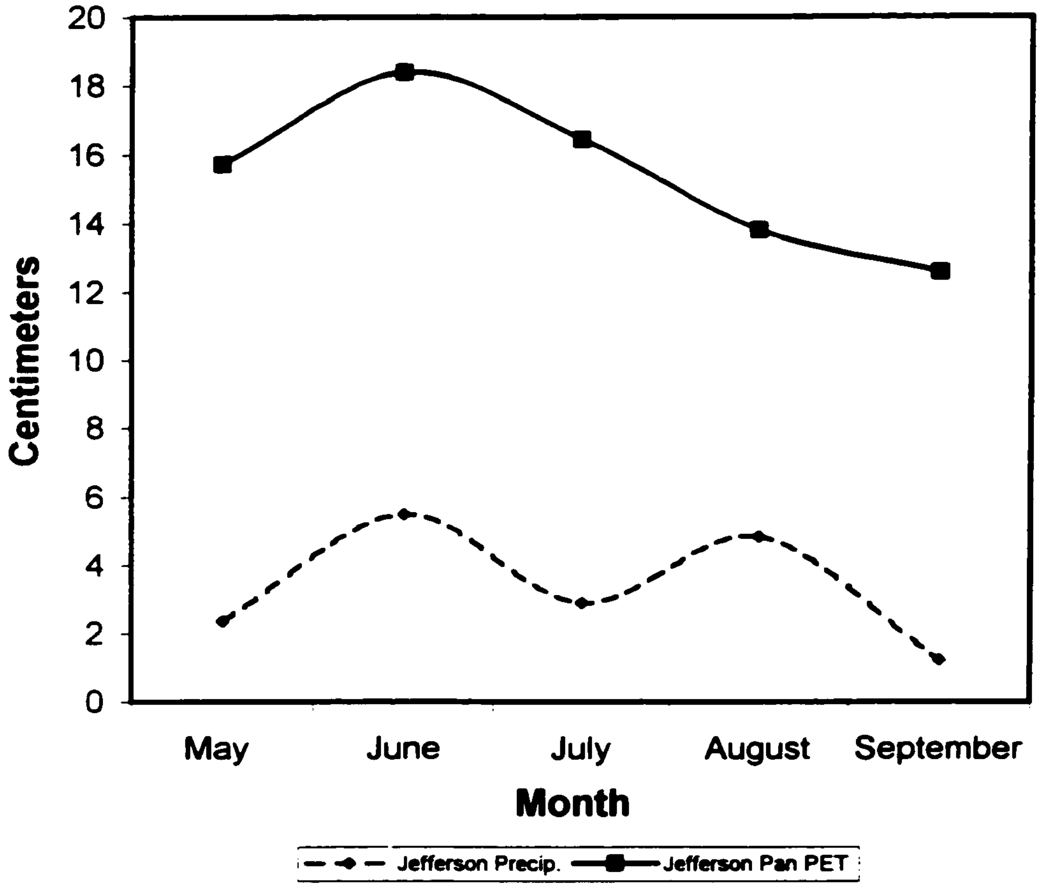

Figure 1.9. Precipitation vs. potential evaporation from 1977 - 1979 at Jefferson. Data from Spahr 1981.

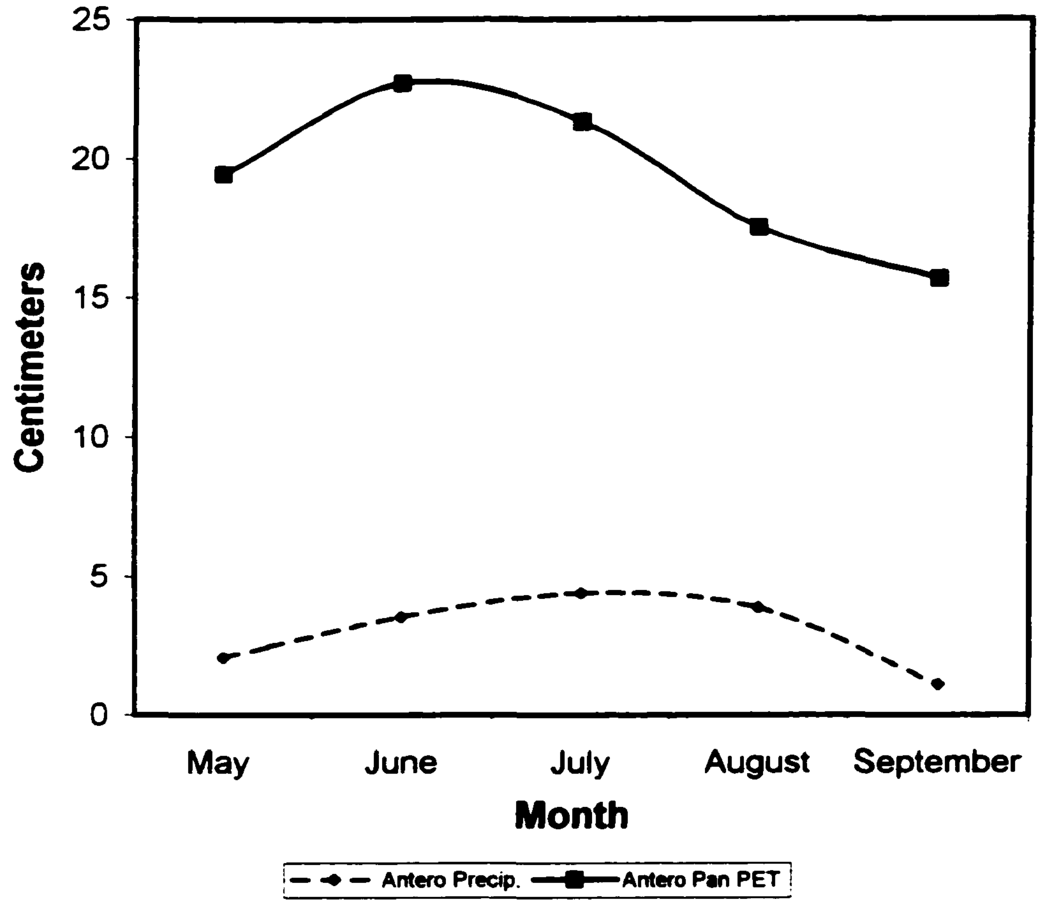

Figure 1.10. Precipitation vs. potential evaporation from 1977 - 1979 at Antero Reservoir. Data from Spahr 1981.

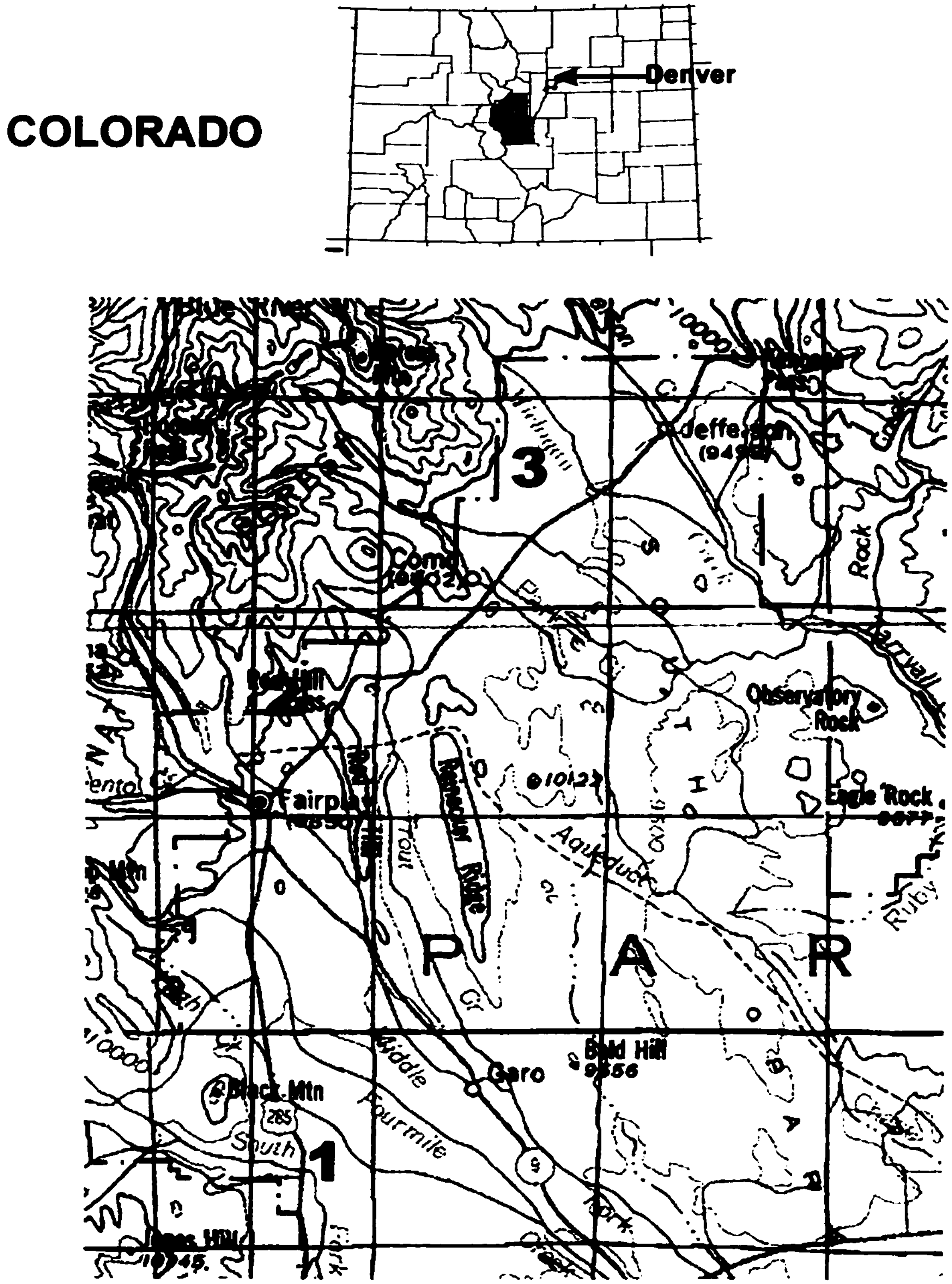

Figure 1.11. Map of Colorado showing the location of Park County (shaded). The detail shows the portion of Park County that includes South Park and the study sites. The study site locations are labeled: 1 - High Creek Fen; 2- Crooked Creek Fen; 3 - Fremont's Fen.

High Creek Fen

High Creek Fen is a Nature Conservancy preserve located about 13 km (8 miles) south of Fairplay, Colorado at an elevation of 2,830 m (Fig. 1.12). Although the whole wetland complex is regarded as High Creek "Fen", it is important to note that not all of the wetland possesses organic soils. In this regard, the wetland might more appropriately have been named High Creek Mire. The main fen with predominantly organic soils covers about 150 hectares (370 acres), while the entire wetland complex encompasses more than 300 hectares (740 acres). A technical wetland delineation has not been performed, however, so these figures are estimates.

Typically, the fen is covered with a dense canopy of sedges and grasses (Fig. 1.13). Within this graminoid matrix, slightly raised islands of willows exist; in even drier areas grow stands of blue spruce (*Picea pungens*). Dissecting the entire wetland is a maze of water-tracks. These water-tracks are characterized as having flowing surface water and somewhat sparse vegetation comprised primarily of spike-rushes (*Eleocharis* spp.) and sedges (*Carex* spp. and *Kobresia* spp.). The water-tracks may be underlain by relatively solid peat, but are more often floating vegetation mats. These vegetation mat areas are frequently referred to as quagmires, alluding to their tenuously soft nature. Peat depth ranges between 0.5 and 1 meter thick.

Portions of High Creek Fen were first purchased by The Nature Conservancy (TNC) in 1991. At present TNC owns about 480 hectares (1,185 acres) of land including High Creek Fen and the surrounding short-grass steppe. The fen has been grazed since the 1860's

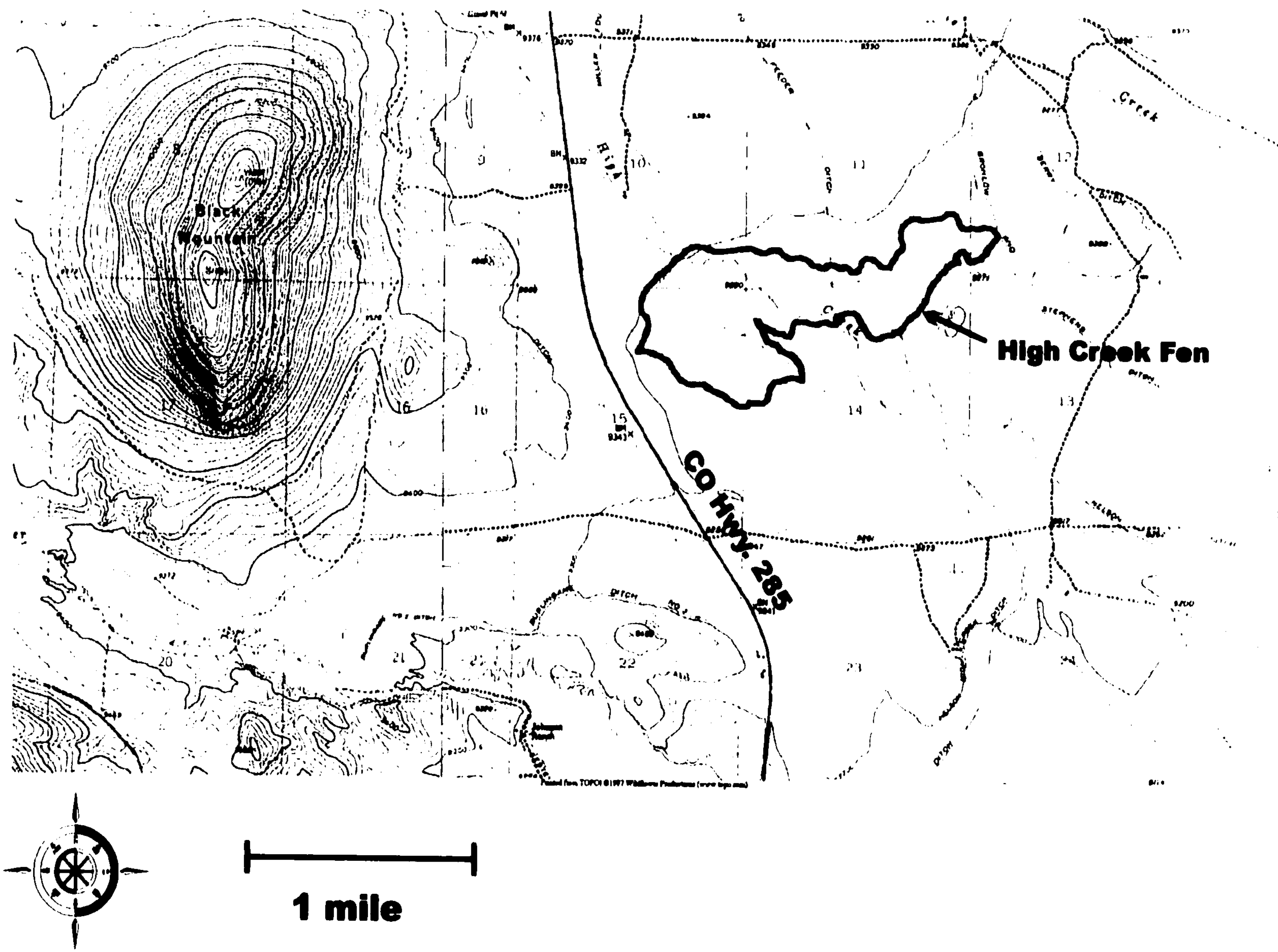

Figure 1.12. Portion of the U.S.G.S. Garo Quadrangle. The extent of organic soils at High Creek Fen is outlined in black.

Figure 1.13. View south across High Creek Fen.

(Appel 1995). During the 1970's and 1980's portions of the northern and western areas of the fen were mined for peat. A portion of the peat extracted by miners was mishandled and devalued, consequently, the miners abandoned it as spoils near the mine pit. After the acquisition of the fen by TNC, the mine was regraded using the spoiled peat, and returned to roughly the same grade as prior to mining (Allen Carpenter, TNC, 1995, pers. comm.).

Crooked Creek Fen

Crooked Creek Fen is located in the Pike National Forest on the periphery of South Park at an elevation of 3,080 m and covers 21.5 hectares (Fig. 1.14). It is surrounded by shrubby marginal wetlands to the east, aspen forest on the west, and trails north up Crooked Creek's narrow valley in the form of scattered beaver ponds and willow carrs. The fen is located on a fan-shaped slope at the foot of an extant beaver pond complex (Fig. 1.15). The fen has a relatively steep slope at its head near the ponds, but the slope decreases as it opens out to South Park. Vegetation at the fen head in the north is dominated by graminoids and tall to medium willows. This vegetation grades into open fen having only low, scattered shrubs and a carpet of sedges.

Crooked Creek Fen is generally undisturbed by human activities. The exception to this is a single ditch that transverses the fen near its foot. This ditch intercepts virtually all ground and surface water flow to a depth of about 1.5 m. The vegetation beyond the ditch is comprised of mesic grass and shrub species. Although the vegetation of the ditch-impacted area is not typical of fens, the soils of the area consist of deep peat remaining from when the

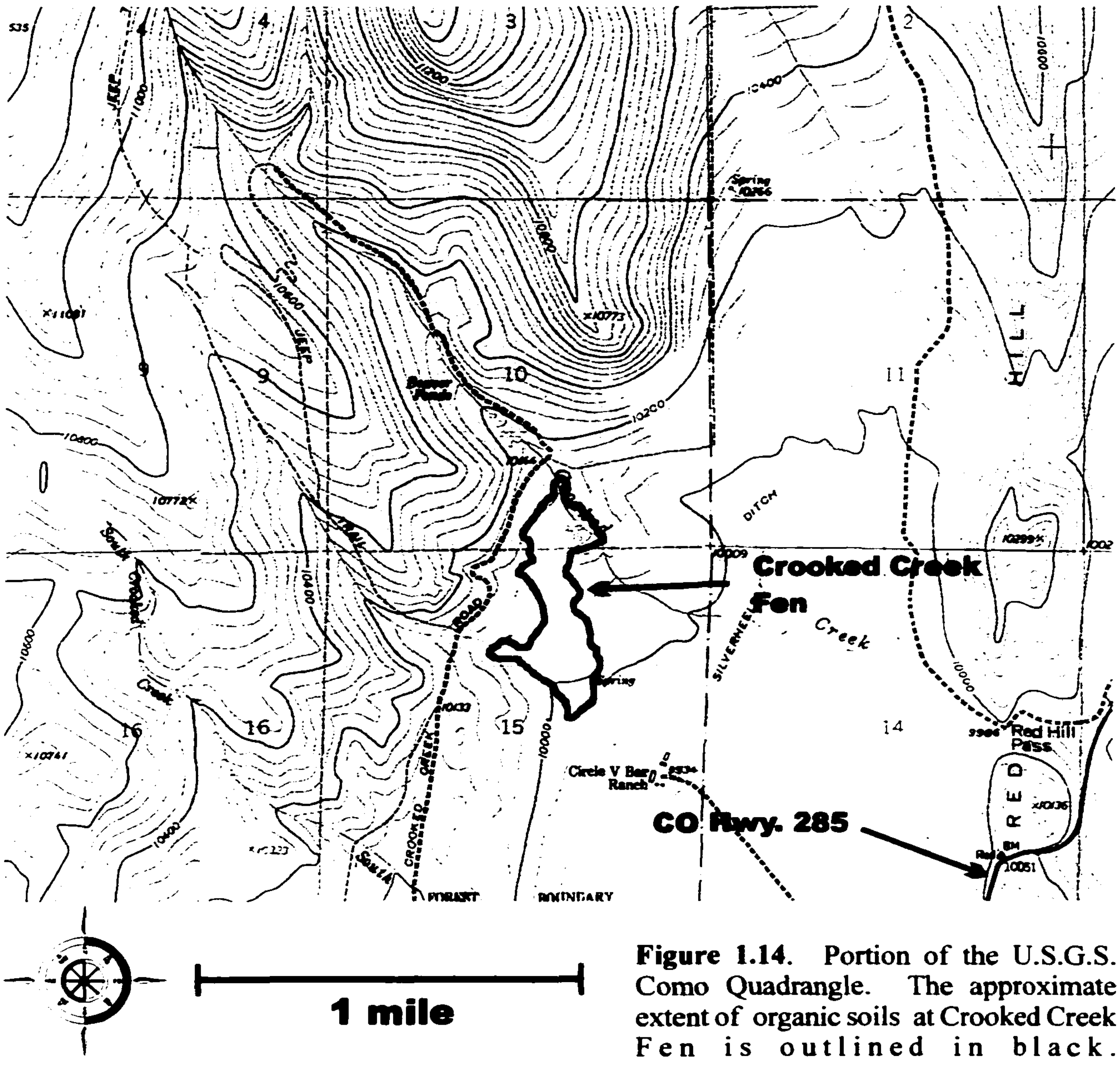

Figure 1.14. Portion of the U.S.G.S. Como Quadrangle. The approximate extent of organic soils at Crooked Creek Fen is outlined in black.

Figure 1.15. View southwest overlooking Crooked Creek Fen. The fen is located in the treeless area above and to the left of the ponds.

fen hydrology was intact. The year of ditch construction is unknown, but anecdotal accounts suggest that it is at least 20 years old.

Fremont's Fen

Fremont's Fen lies at the foot of the Mosquito Range at 2,930 m of elevation and forms an expansive fen-meadow complex (Fig. 1.16 and 1.17). It is the largest and most heavily altered of the three fens studied. The peat areas of the complex cover 97 hectares (240 acres), while the total wetland expanse is more than 526 hectares (1300 acres). The fen lies on both private land and land owned Colorado Division of Wildlife. The fen begins at a colluvial fan and slopes shallowly to the east. A series of drainage ditches cris-cross the fen and an expansive peat mine covers much of the fen where the deepest peat deposits once were. The exact age of the mine is not known, nor is the date that it was abandoned, but residents accounts indicate that mining ceased at least 15 years ago.

The vegetation of Fremont's Fen is dominated primarily by graminoids with a relatively little shrub cover. The whole wetland complex is still grazed by cattle.

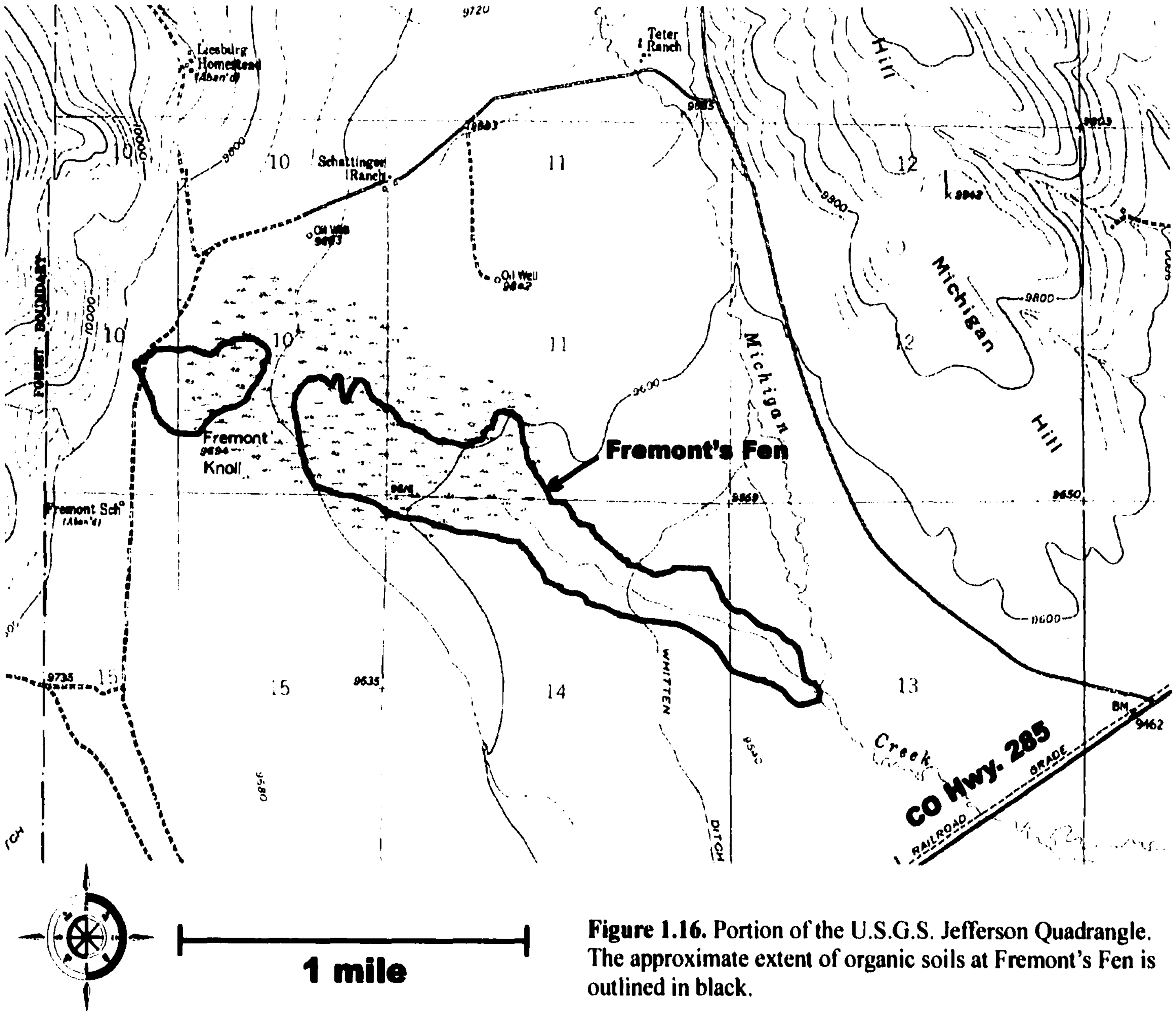

Figure 1.16. Portion of the U.S.G.S. Jefferson Quadrangle. The approximate extent of organic soils at Fremont's Fen is outlined in black.

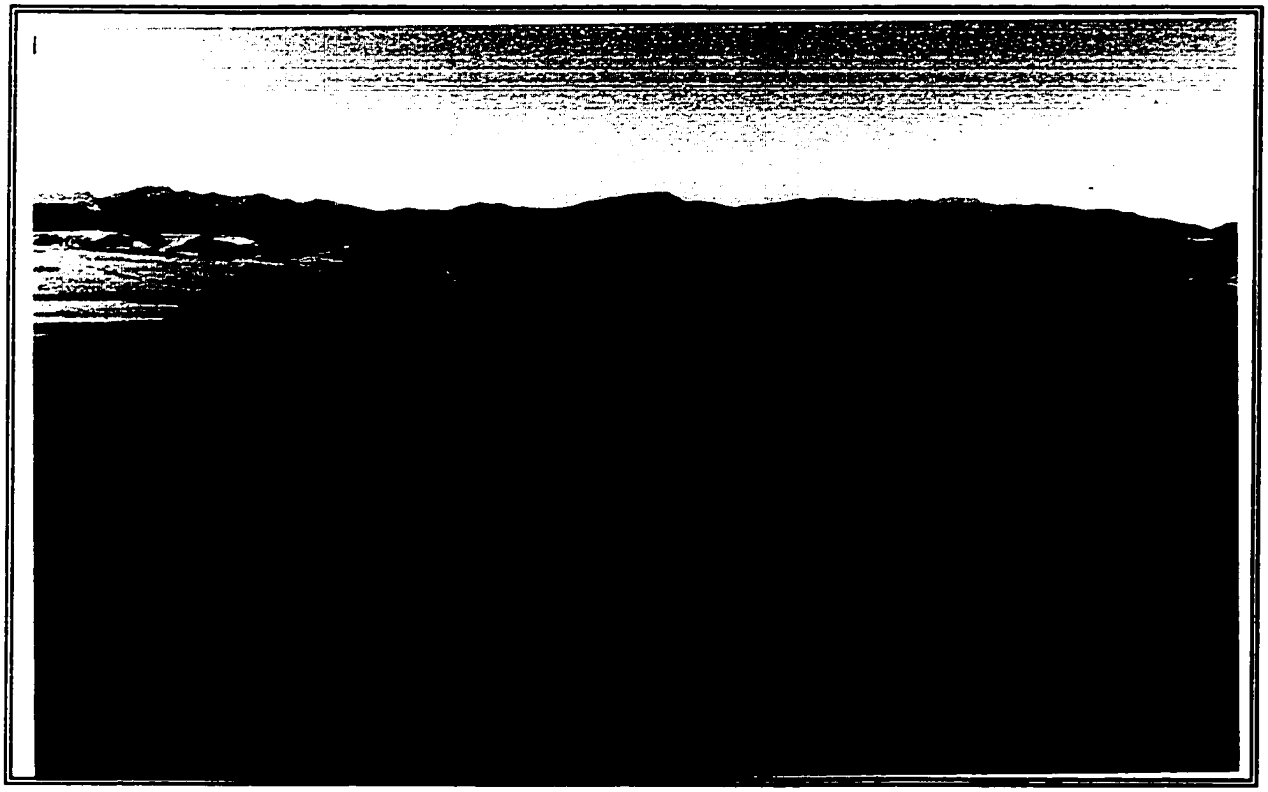

Figure 1.17. View east overlooking Fremont's Fen. Dark areas are remaining peat mine scars. Two areas of mining can be seen with a mineral soil meadow area between them.

CHAPTER II

VEGETATIONAL ASSEMBLAGES AND ECOLOGICAL GRADIENTS IN THE CALCAREOUS MIRES OF SOUTH PARK, COLORADO

ABSTRACT

The vegetation, environment and ecological gradients present on three calcareous mires were investigated. Vegetation was classified into five classes, eight subclasses, and twelve associations using two-way species indicator analysis (TWINSPAN). Vegetation samples were ordinated using detrended correspondence analysis (DCA). The first two DCA axes represented three primary gradients: water table height, mire-margin to expanse, and region. Canonical correspondence analysis (CCA) was used to directly relate environmental factors to vegetation. Water table depth, microtopographical development, soil and water pH and nutrient level, soil organic matter, and hydraulic head were significantly correlated with vegetational gradients. Mean pore water calcium concentration on these mires is 115 mg/l, electrical conductivity averages 575 µS, and mean pH is 7.4. The mires also contain a number of highly minerophilic species. Based on these criteria each site was classified as a rich to extremely rich fen complex.

INTRODUCTION

Fens are a common, although relatively minor feature of the subalpine zone of the Rocky Mountains. In Colorado and the southern Rocky Mountains most of these fens are located in cirques and glacial valleys above about 2650 m (8500 ft.), although fens can be found occasionally at somewhat lower elevations due to local conditions. The vegetation and environment of these fens has been described in a handful of publications and theses (Bierly 1972, Cooper 1986, Cooper 1990, Cooper and Andrus 1994, Johnson 1994, Johnson 1996b, Johnson 1997). The Rocky Mountain fens found in granitic basins are generally described as being transitional or moderate rich fens based on water quality and floristic criteria.

Recently, fens in South Park, a large, subalpine inter-mountain park, were found to be distinct from the typical subalpine fens (Cooper 1996). The fens of South Park have a large number of calciphilous fen species such as *Salix candida, Trichophorum pumilum,* and *Scorpidium scorpioides*. Many of the calciphilous species had never, or only historically, been reported in Colorado (Weber 1990). The calcareous environment of these fens is due to large limestone and dolomite deposits found in the Mosquito Range to the west. Such deposits are generally rare in these mountains and calcareous fens have only been identified in two other areas in the region: Pine Butte Fen in northwestern Montana (Lesica 1986) and the Swamp Lake Peatlands in northern Wyoming (Fertig and Jones 1992). Additional calcareous fens may be located in the Laramie Mountains in northern Colorado, as well (J. McKee, U.S. Fish and Wildlife Service; unpubl. data). Elsewhere throughout North America, calcareous fens are quite uncommon, having only been described in small regions within California (Major and Taylor 1988), Minnesota (Glaser et al. 1990, Almendinger and Leete 1998), Alberta (Slack et al. 1980), Ontario (Sjörs 1961a, Sjörs 1963) and Alaska (Racine and Walters 1994). Calcareous fens have also been reported in the Midwestern United States, but these fens have environments and floras unlike the boreal and subalpine fens (Curtis 1959).

Because of the unusual habitat provided by these wetlands, a large number of rare or regionally endemic species are found growing within their confines. In South Park's fens for instance, fifteen state rare or endemic plant species and at least ten rare invertebrate species have been found (Sanderson and March 1996). Due to their biological significance, in most areas calcareous fens have been given special conservation consideration, either through regulatory means (e.g. U.S. Fish and Wildlife Service Region 6, 1999 Peatlands Policy Document, Almendinger and Leete 1998) or purchase by conservation groups such as The Nature Conservancy (TNC).

Fens are a type of peatland, that is, a wetland with organic soils. Specifically, fens are peatlands whose vegetation is influenced to varying degrees by ground water. This is in contrast to bogs, in which vegetation is isolated from the effects of groundwater due to the accumulation of *Sphagnum* peat. When describing wetland complexes which possess a mosaic of both peat and mineral soils the term mire is most appropriate (*sensu* Sjörs 1961a, Pakarinen 1995). Because non-peat accumulating areas are included in the current study, these wetlands will generally be referred to as mires unless peat areas in particular are indicated.

Several primary gradients, or directions of variation (*sensu* Sjörs 1950b) have been attributed to mires including gradients due to minerotrophy, microtopography, position within the wetland, and biogeography. The nature of each of these gradients was discussed in detail in Chapter 1 (pg.15). Although the biological significance of these fens has been reported, little detailed investigation into their ecological and environmental characteristics has been undertaken. In a study of High Creek Fen (a Nature Conservancy preserve), Cooper (1996) described the wetland's vegetational assemblages. During the study, a limited number of water samples were taken and speculations made on possible water sources, but these data could not be directly related to vegetational patterns. Other studies (Cooper 1991, Sanderson and March 1996) surveyed many different calcareous fens to identify their distribution and generally characterize their vegetation, but detailed investigation of fen ecology was not a focus.

This study was designed to build upon these earlier works and broaden our knowledge of these calcareous mires by describing their vegetation, environmental characteristics and how these two attributes relate to one another. The specific goals of this study were to: (1) describe vegetational assemblages and gradients found on representative fens throughout South Park; (2) describe the environmental conditions found at these fens; and (3) directly relate mire vegetation to local environmental conditions to assess the factors influencing species composition on Colorado calcareous mires.

METHODS

STUDY SITES

Three calcareous fens, High Creek Fen, Crooked Creek Fen, and Fremont's Fen, located in South Park, Colorado were examined in this study. The general environment of South Park and these fens was described in Chapter 1. Average yearly precipitation measured at the Antero Reservoir from 1964 to 1994 is 25.1 cm (Fig 2.1). During the growing season, from May 15 to Oct 15, Antero Reservoir receives an average of 17.8 cm of precipitation, mostly in the form of rain. Total precipitation and growing season precipitation during 1995 and 1996 was not statistically different from the mean, based on a one-sample t-test comparing sample-year totals to long-term data. 1997 was significantly wetter than the norm ($p = 0.00$), receiving a total 35.2 cm of precipitation, 25.04 cm of which fell during the growing season.

ENVIRONMENTAL SAMPLING

Each site was equipped with a matrix of sampling stations consisting of a shallow ground water well and one or more piezometers. High Creek Fen had 35 stations, Crooked Creek 27, and Fremont's Fen 23. Fifteen of these stations will not be considered in this chapter since they were sites of heavy disturbance. These stations will be discussed in Chapter 3. Stations were subjectively located in the major geomorphic, hydrologic and vegetative zones which occur on the fens. A more objective sample placement was not practicable due to the large number of samples that would be required to encompass the

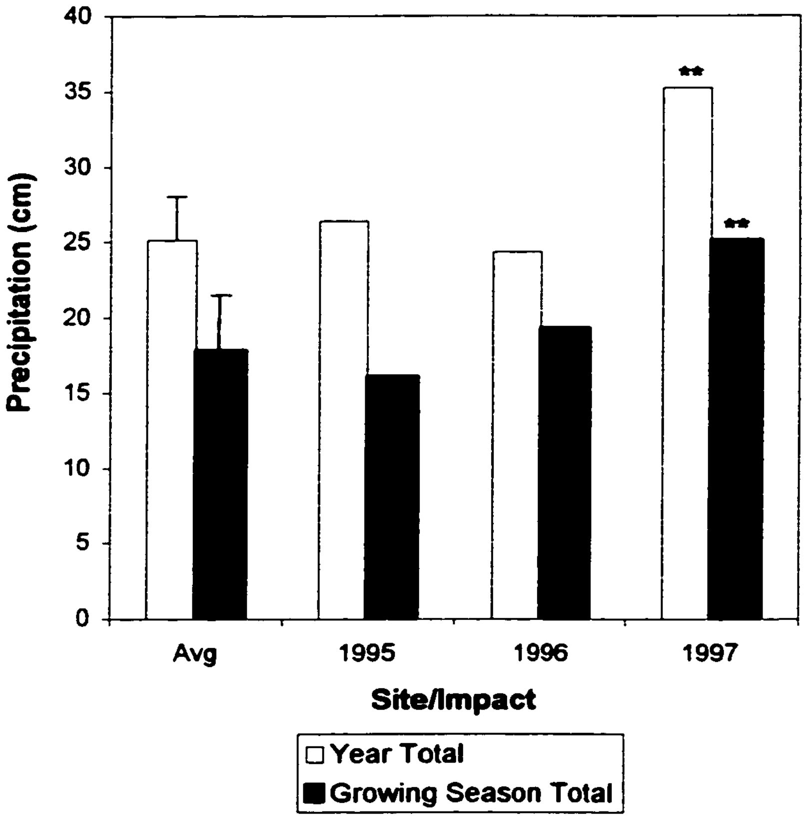

Figure 2.1. Average precipitation from 1964 to 1994 at Antero Reservoir (Avg) and precipitation during the years of this study. White bars are total yearly precipitation, black bars are precipitation during the growing season from May 15 to October 15. Error bars show the standard deviation from the mean. ** indicates a significant difference from mean precipitation with $p < 0.01$.

diversity of wetland habitats present and the consequent over sampling of common situations. Sample stations were also spatially arrayed across wetlands to ensure representation of habitats throughout the sites. Special attention was given to locating sample stations in the range of organic soil habitats, along hydrological pathways and gradients, and in characteristic vegetation types (Fig. 2.2 - 2.4).

Wells were constructed of 2.54 cm inside diameter (I.D.) polyvinylchloride (PVC) pipe, approximately 1.5 m long. Wells bottoms were capped, and the bottom 30.5 cm of the wells were perforated. Wells were driven into the peat until the top of the well was approximately 20 cm above the ground's surface or until they reached an impermeable mineral layer located below the peat. Wells were not driven deeper than an impermeable layer, even at the risk of having them go dry, because well water samples were to be used to characterize the chemistry of water flowing through the peat. Once installed, wells were allowed to recharge and then were drained several times to ensure proper functioning.

Piezometers were made of 2.54 cm I.D. PVC pipe. Piezometer bottoms were left uncapped and the pipe unperforated. Piezometers were installed to a uniform depth of 75 cm

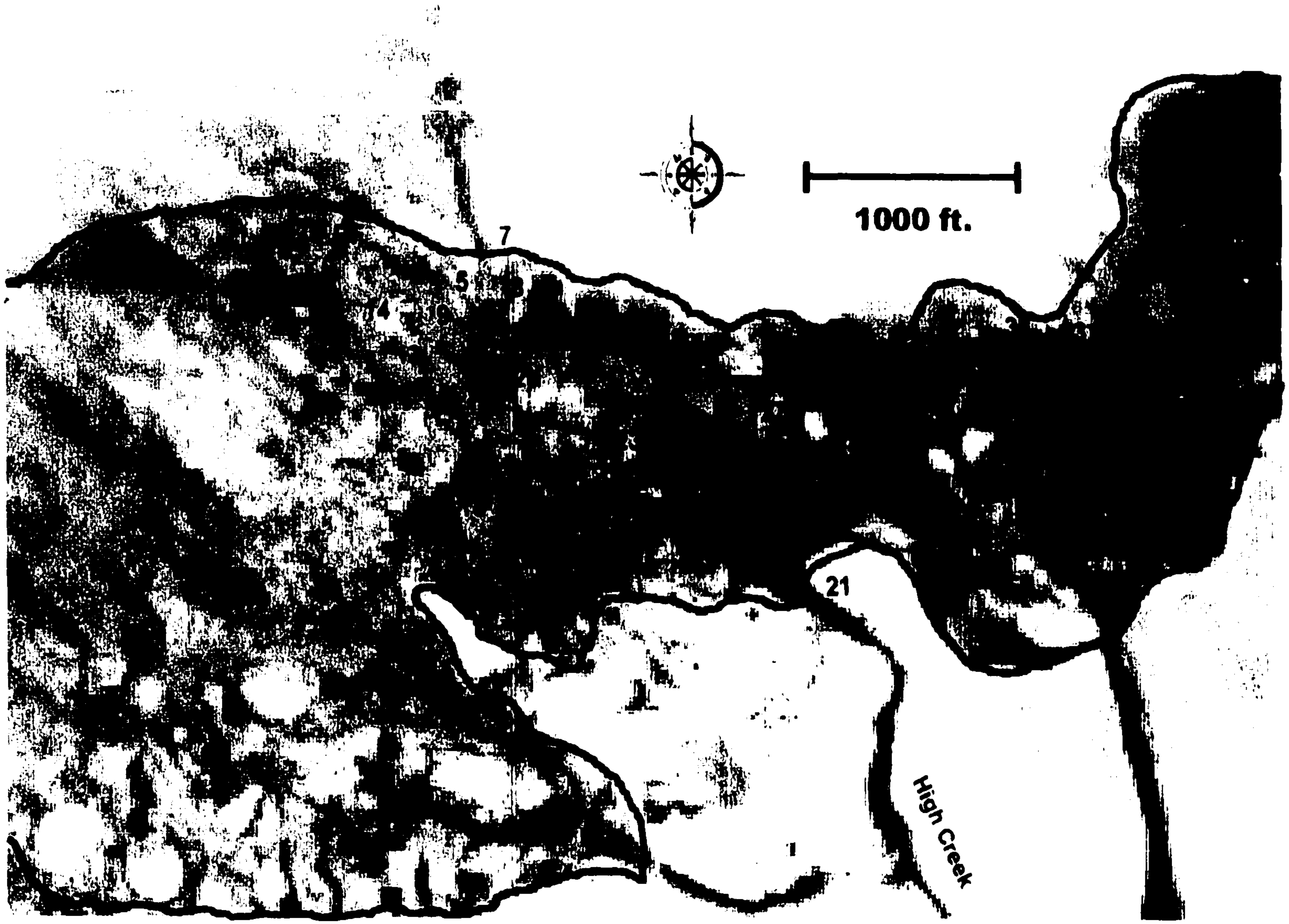

Figure 2.2. Color infrared photograph of High Creek Fen taken in June 1995. Numbered points are sampling stations. The black outline indicates the approximate extent of organic soils, although note that the boundaries continue off the figure. Dark grey areas have been mined for peat..

Figure 2.4. Color infrared photograph of Fremont's Fen taken in June 1995. Numbered points are sampling stations. Dark grey and black areas in the photograph indicate the extent and nature of peat mining at the site. The black outline indicates the approximate extent of predominately organic soils. Grey lines are the major mining roads, additional minor grades can be seen in the photograph. Blue lines show ditches and channels. Michigan Creek can be seem in the upper right corner.

at High Creek Fen and variable depths at the other fens depending on peat depth and depth to an impermeable layer. Piezometers were installed by placing a small diameter pipe, slightly longer than the piezometer, inside the piezometer and driving the two pipes into the ground simultaneously with a small sledge hammer. Once the piezometer was driven to its final depth, the inner pipe was removed, leaving the piezometer pipe clear.

Sample stations were surveyed by Tom Burnett of the Park County Mapping Department using a theodolite. At High Creek Fen, two wells previously surveyed (Appel 1995) served as elevation bench marks, and a global positioning system (GPS) unit was used to generate the horizontal coordinates of the bench marks. At Crooked Creek and Fremont's Fen, quarter-section markers were used to tie land surveys to geographic coordinates. Site maps were produced by digitally overlaying surveyed sample station and landmark coordinates onto color infrared aerial photographs taken in June, 1995 and resizing the photograph until surveyed points registered on the photograph.

Well and piezometer water depths were measured every 10 to 14 days from the beginning of June through September or early October, which roughly corresponds to the local growing season length. Measurements were taken from 1995 - 1998 on High Creek fen and 1996 - 1998 on Crooked Creek and Fremont's Fen. Water depth was measured by inserting a steel tape measure into the pipes and recording the depth at which the tape contacted the water. The height of the well protruding above the ground's surface was then subtracted from this value. The vertical water gradient, or hydraulic head, was calculated by subtracting the height of the water table surface from the height of the piezometric surface (Walton-Day 1991). Positive head values indicate ground water discharge and negative values indicate ground water recharge. Head values equal to zero that neither process is occurring at that locale.

Soil and Water Characterization

Peat depth was measured by inserting a 5 cm piston corer through the peat until it hit underlying alluvium or bedrock. Soil depth was measured off the extracted corer. The soil core was removed and examined to characterize peat decomposition and stratigraphy. To assess physical and chemical soil properties, an additional set of soil samples was taken at each site from the upper 20 cm using a hand trowel. Soil samples were taken in 1995, 1996, and 1997 at High Creek Fen, and in 1996 and 1997 at the other two sites. Samples were kept chilled and transferred to the Colorado State University Soil and Water Testing Lab (CSU). Samples were analyzed for pH, electrical conductivity, and percent organic matter, and concentration of nitrate, phosphorous, potassium, zinc, iron, manganese, calcium, magnesium, sodium, and calcium carbonate.

Pore water samples were collected on August 22 - 23, 1995 at High Creek Fen and September 13, 1997 at all fens. Samples were extracted from wells using a Teflon bailer. All samples were filtered through 0.45 μm nitrocellulose filters using a vacuum aspirator, placed in polyethylene bottles, and preserved with nitric acid. Samples were analyzed for concentrations of calcium, magnesium, sodium, potassium, phosphorous, iron, manganese, and calcium carbonate at the CSU Soil Testing Lab using inductively coupled ion spectrophotometry (ICP).

VEGETATION SAMPLING

Vegetational composition was determined at High Creek Fen on July 7 - 9, 1995, and at Crooked Creek and Fremont's Fen on July 28 - August 3, 1997. At each sampling station, a 5 m diameter (15.71 m^2) sampling plot, or releve, was centered on the ground water well. The plot size was based on preliminary a study wherein a 5 m diameter plot was found to generally fit within the patch size of plant associations and was large enough to represent the variation within associations (Johnson 1995). Within releves the cover of each plant species was visually estimated (Mueller-Dombois and Ellenberg 1974). Releves were positioned at each environmental sampling station so that vegetational composition could be directly related to measured environmental conditions. Due to the practical limitations inherent in such a goal, releves and sampling stations could not be placed in every conceivable vegetation association; however, the most significant associations were sampled. The percent cover of hummocks within each releve was visually estimated, and the heights of 12 hummocks, when present, were measured.

DATA ANALYSIS

Three related multivariate statistical techniques were used to analyze the data obtained in this study: Two-way Indicator Species Analysis (TWINSPAN); Detrended Correspondence Analysis (DCA); and Canonical Correspondence Analysis (CCA). Each approach provides a somewhat different view of data structure; when employed together each technique can be used to complement, supplement, and evaluate the other analyses (Gauch 1982, Økland 1996). For a detailed consideration of these techniques, the reader is directed to Appendix 1 where I provide an overview and critical evaluation of each technique.

Before analysis, species data were log transformed to reduce the influence of very abundant species. Mosses were made passive in all analyses since presence-absence data was collected on these species, and little bryophyte data was collected at High Creek Fen. TWINSPAN (Hill 1979) as contained in the PC-ORD program (McCune and Mefford 1997) was used to classify releves based on species composition. TWINSPAN is a divisive, polythetic classification technique which is based on correspondence analysis (Gauch and Whittaker 1981, van Tongeren 1996). The result of a TWINSPAN analysis is a dichotomized dendrogram. At each level of division, groups of releves with similar vegetation are created and one or more species are identified as being key to the separation of the two groups. These species are commonly known as "indicator species", since their presence, in part, defines group membership. It should be noted that the indicator species defined by the TWINSPAN are only used to separate releve groups; they may be of limited usefulness as actual community type indicators in the field (Hill 1979, Gauch 1982). Default settings were used during the TWINSPAN, except cut levels were 0.0, 0.3, 0.7, 1.0, 1.3, i.e., the log of the default cut values.

TWINSPAN provides discreet community groupings which are of significant descriptive heuristic utility; however, classification of vegetation along a continuum contains inherent arbitrariness and may actually obscure vegetational gradients. Two related techniques were applied to elucidate these gradients – detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). Canoco 4 was used to perform gradient analyses (Ter Braak and Smilauer 1998). DCA is an indirect gradient analysis or ordination technique, while CCA is a method of multivariate direct gradient analysis. In CCA initial sample and species placement is based on the correspondence analysis algorithm, but sample and species scores are secondarily constrained to be linear combinations of environmental variables (Ter Braak 1986).

In the DCA, detrending by segments was performed with the default 26 segments. For the CCA, the inter-sample scores option was chosen to optimally configure releve placement in the diagram (Ter Braak and Smilauer 1998), and bi-plot scaling was used. In plotting releves, scores that are linear combinations of environmental factors were used (LC scores). Before employing CCA, a step-wise selection of environmental variables was performed using the Monte Carlo permutation test available in Canoco. This was done to remove superfluous environmental variables which would have had little descriptive power, but would have introduced additional statistical error to the analysis (Ter Braak and Smilauer 1998). The product of hummock height and hummock cover was used as a variable in CCA to synthesize the effects of both microtopographical attributes (Ter Braak and Smilauer 1998).

To gauge the axis distortion inherent in CCA, Spearman's rank correlation was used to compare DCA and CCA scores (Allen and Peet 1990, Prentice and Cramer 1990, Johnson 1996b, Økland 1996). A standard product-moment test of correlation was used to determine significance of the axis correlations (Sokal and Rohlf 1981).

RESULTS

VEGETATION ASSEMBLAGES

The TWINSPAN classification separated mire vegetation into five classes: tall-hummock fen/meadow; meadow/dry fen; willow carr; fen lawn; and quagmire (Fig. 2.5). The fen lawn class was divided into three subclasses: one hummocky fen lawn and two fen lawn communities with low hummocks. Quagmire vegetation was broken down into two subclasses, also related to differences in microtopography – one growing in somewhat hummocky areas, the other where little microtopography is present. Table 2.1 contains the species composition found in each of these subclasses. The flow of community types from left to right across the TWINSPAN diagram (Fig. 2.5) primarily corresponds to a moisture gradient going from drier to wetter releves, although, other environmental factors such as water chemistry also play a role in distributing vegetation types along this gradient (see below).

The tall hummock fen/meadow communities (cluster *000, Fig. 2.5) reside in seasonally wet areas of the wetlands dominated by grasses and sedges (Fig. 2.6). Shrub cover is generally absent. Releves representing this vegetation type were located on the margin of High Creek Fen. Such sites may be situated in areas with or without organic soils. These tall hummock areas are characterized by the presence of *Deschampsia cespitosa, Elymus trachycaulus,* and *Juncus balticus* in addition to characteristic species such as *Carex aquatilis, C. simulata, C. scirpoidea* and *Primula incana.* The high production and cespitose growth form of a dominant sedge, *Carex scirpoidea*, helps produce the large hummocks

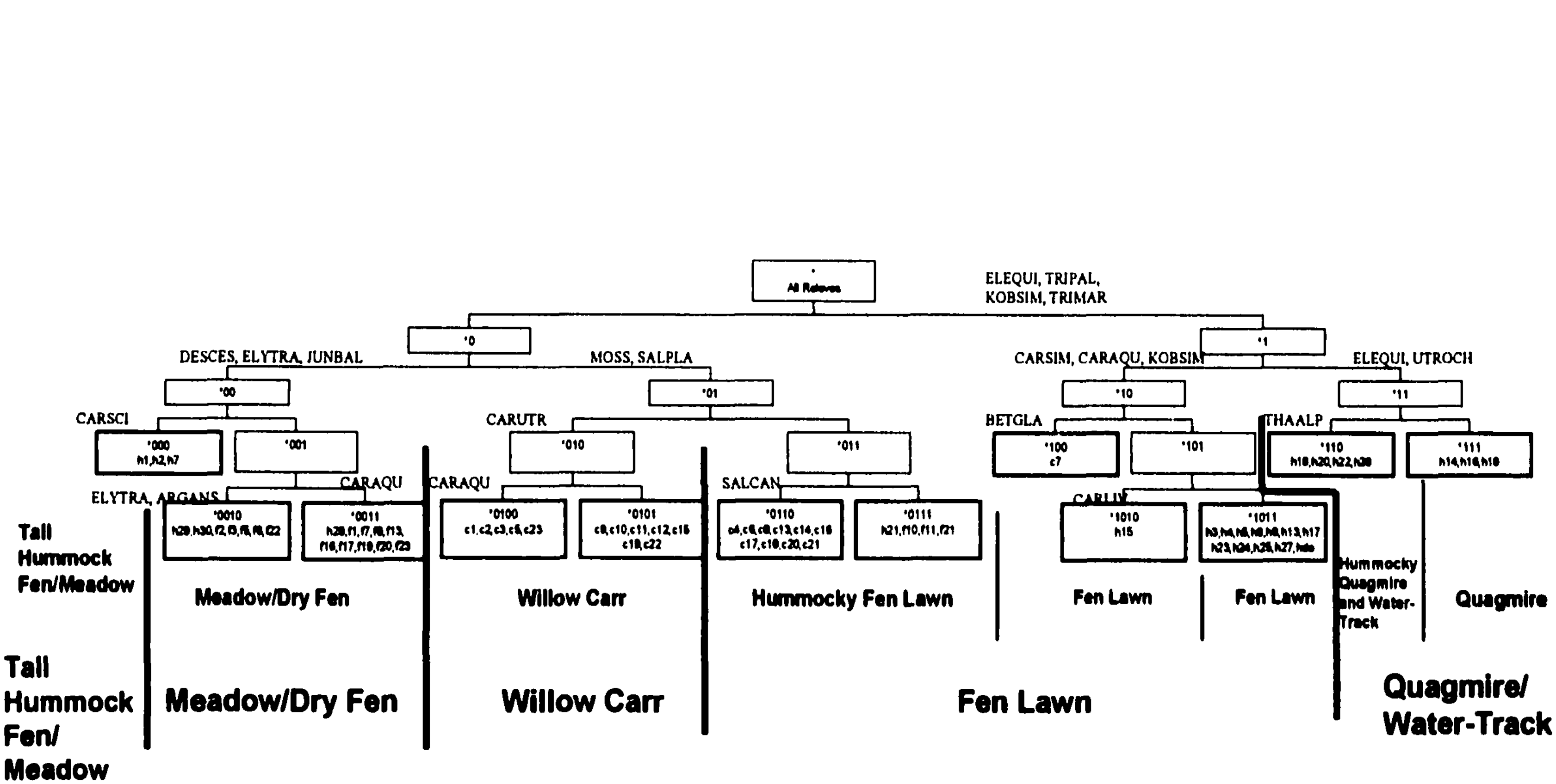

Figure 2.5. TWINSPAN dendrogram of intact releves. At each division abbreviations for diagnostic species are given. See Table 6 for a key to abbreviations. Within each box is its diagram address and in the final groupings are lists of the vegetation plots included. H indicates releves from High Creek Fen, C those from Crooked Creek Fen, and F from Fremont's Fen. Vegetational classes are separated by bold lines and names are given in large type. Subclasses, when present, are divided by thin lines with names indicated in small bold faced type. Vegetational associations are not named, but are indicated by heavy box lines.

Table 2.1. Species composition of vegetational associations. Values are percent species coverage converted into Braun-Blanquet cover classes where + = <1%, 1 = 1- 5%, 2= 6-25%, 3= 26-50%, 4=50-75%, 5=76-100%. P indicates species presence when abundance data are not present.

Class		Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Fen Lawns					Quagmire and Water-track	
Subclass		Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Hummocky Fen Lawn		Fen Lawn			Hummocky Quagmire and Water-track	Quagmire
Species Abbreviation	Association	Tall Hummock Fen/Meadow	Meadow	Dry Fen	Tall Willow Carr	Dwarf Willow Carr	Hummocky Fen Lawn	Hummocky Fen Carpet	Fen Lawn	Fen Lawn	Fen Lawn	Hummocky Quagmire and Water-track	Quagmire
ACHMIL	*Achillea millefolium*		1	1									
AGRSCA	*Agrostis scabra*			1				+					
AGRSTO	*Agrostis stolonifera*		+										
ANTSPP	*Antennaria sp.*	+	1										
ALOBOR	*Alopecurus borealis*		1	+									
ARGANS	*Argentina anserina*	1	1	1		1				+	+		
ARTFRI	*Artemisia frigida*			+									
ASTAGR	*Astragalus agrestis*		2										
ASTOCC	*Aster occidentalis*		1	+									
BETGLA	*Betula glandulosa*				1	1			+				
CALCAN	*Calamagrostis canadensis*	+	2	2	+	1	1	1			+		
CALSTR	*Calamagrostis stricta*			1				1					
CALLEP	*Caltha leptosepala*			+									
CAMPAR	*Campanula parryi*		+										
CARAQU	*Carex aquatilis*	4	1	3		2	3	3	5	+	1	1	
CARAUR	*Carex aurea*				+	+	+		+				
CARCAP	*Carex capillaris*		1	+									
CARHAL	*Carex hallii*		+				+						
CARLIM	*Carex limosa*						1		1				
CARLIV	*Carex livida*									1			
CARMIC	*Carex microptera*						+				+		
CARMIG	*Carex microglochin*										+		
CARSCI	*Carex scirpoidea*	2	1	1			1			+		+	
CARSIM	*Carex simulata*	1		2		2	3	3	+	2	2	1	

	Class	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Fen Lawns					Quagmire and Water-track	
	Subclass	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Hummocky Fen Lawn		Fen Lawn			Hummocky Quagmire and Water-track	Quagmire
Species Abbreviation	Association	Tall Hummock Fen/Meadow	Meadow	Dry Fen	Tall Willow Carr	Dwarf Willow Carr	Hummocky Fen Lawn	Hummocky Fen Carpet	Fen Lawn	Fen Lawn	Fen Lawn	Hummocky Quagmire and Water-track	Quagmire
CARUTR	*Carex utriculata*	+	2	2	3	3	1				+		
CIRARV	*Cirsium arvense*		+	+									
CIRCOL	*Cirsium coloradense*	+	+	+									
CONSCO	*Conioselinum scopulorum*		+	+	1								
CRERUN	*Crepis runcinata*	1	2	1							+		
DESCES	*Deschampsia cespitosa*	1	2	3	1	1	2	1					
DISINV	*Distegia involucrata*				1								
DODPUL	*Dodecatheon pulchellum*	+		+		+	+			+			
ELEQUI	*Eleocharis quinqueflora*	+			+		2	1	1	1	2	3	3
ELYTRA	*Elymus trachycaulus*	1	2	1				+					
EPILAC	*Epilobium lactiflorum*		+								+	+	
EPISPP	*Epilobium spp.*		1	+	+								
EQUARV	*Equisetum arvense*				1		+						
ERILON	*Erigeron lonchophyllus*	+											
ERISPE	*Erigeron speciosus*		+	+									
ERIANG	*Eriophorum angustifolium*										1		
ERIGRA	*Eriophorum gracile*					1							
GALBOR	*Galium boreale*		1		+								
GENFRE	*Gentiana fremontii*	+	+				+			+			
GENSPP	*Gentian spp.*		2	1		+	+	1					
HIEHIR	*Hierochloë hirta*	1		+									
HORBRA	*Hordeum brachyantherum*		2										
HORJUB	*Hordeum jubatum*		2	+									
HETPUM	*Heterotheca pumila*		1										
JUNALB	*Juncus albescens*								+				
JUNALP	*Juncus alpinoarticulatus*								+				
JUNBAL	*Juncus arcticus ssp. ater*		2	1	1	+	1	1		+	1	+	
JONLON	*Juncus longistylis*					+							

	Class	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Fen Lawns					Quagmire and Water-track	
	Subclass	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Hummocky Fen Lawn		Fen Lawn			Hummocky Quagmire and Water-track	Quagmire
Species Abbreviation	Association	Tall Hummock Fen/Meadow	Meadow	Dry Fen	Tall Willow Carr	Dwarf Willow Carr	Hummocky Fen Lawn	Hummocky Fen Carpet	Fen Lawn	Fen Lawn	Fen Lawn	Hummocky Quagmire and Water-track	Quagmire
KOBMYO	*Kobresia myosuroides*		2	3		1	2		+		+		
KOBSIM	*Kobresia simpliciuscula*	+	2	2			2	1	1	2	1	1	+
KOLMAC	*Koeleria macrantha*		2	1	+								
LAPRED	*Lappula redowskii*												
LEPRAM	*Lepidium ramosissimum*												
LIMHYP	*Limnorchis hyperborea*					+	+			+	+		
MAIAMP	*Malanthemum amplexicaule*				+								
MOSSPP	*Moss sp.*		+	1	3	3	3	+	4	1	1	1	+
MUHRIC	*Muhlenbergia richardsonis*		2										
PARPAR	*Parnassia parviflora*					+	+						
PASSMI	*Pascopyrum smithii*												
PEDCRE	*Pedicularis crenulata*			+									
PEDGRO	*Pedicularis groenlandica*			+	1	+	1		1	1	1	+	
PENFLO	*Pentaphylloides floribunda*		1	1	1	2	1		+	1	1	1	
PLAERI	*Plantago eriopoda*	+											
POACOM	*Poa compressa*			1									
POAGLA	*Poa glaucifolia*												
POAPRA	*Poa pratensis*		2	1		+							
POLBIS	*Polygonum bistortioides*		+	1	+	1	1						
POLVIV	*Polygonum viviparum*		+							+		+	
POLFOL	*Polemonium foliosissimum*			1									
POTPEC	*Potamogeton pectinatus*											1	1
POTPLA	*Potentilla plattensis*		1										
POTSUB	*Potentilla subjuga*		+	+									
PRIEGA	*Primula egaliksensis*	+					+			+	+	+	+
PRIINC	*Primula incana*	+	+	+									
PTIPOR	*Ptilagrostis porteri*			2									
RANCYM	*Ranunculus cymbalaria*						1						

Species Abbreviation	Association	Tall Hummock Fen/Meadow	Meadow	Dry Fen	Tall Willow Carr	Dwarf Willow Carr	Hummocky Fen Lawn	Hummocky Fen Carpet	Fen Lawn	Fen Lawn	Fen Lawn	Hummocky Quagmire and Water-track	Quagmire
	Class	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Fen Lawns					Quagmire and Water-track	
	Subclass	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Hummocky Fen Lawn			Fen Lawn		Hummocky Quagmire and Water-track	Quagmire
RUMSPP	*Rumex spp.*		1	+									
SALBRA	*Salix brachycarpa*		1	1	2	2	1			1	+	+	
SALCAN	*Salix candida*				1	+	1		1	1	+	+	+
SALMON	*Salix monticola*				2	2							
SALMYR	*Salix myrtillifolia*			+		+	1			1			
SALPLA	*Salix planifolia*		1		3	2	1		+	+		+	
SAXHIR	*Saxifraga hirculus*												
SEDRHO	*Sedum rhodanthum*			+									
STELON	*Stellaria longipes*			1				+					
SWEPRE	*Swertia perennis*				1	+	1						
SISPAL	*Sisyrinchium pallidum*						+						
TAROFF	*Taraxacum officinale*	1	1	1									
THAALP	*Thalictrum alpinum*		1	1	+	1	1			+	1	1	
TRIPUM	*Trichophorum pumilum*					1	1					1	
TRIMAR	*Triglochin maritima*	1		1		+	1		1	1	1	1	2
TRIPAL	*Triglochin palustris*										1	1	1
UTROCH	*Utricularia ochroleuca*											1	1
VALEDU	*Valeriana edulis*		1	+									
VIOADU	*Viola adunca*	+											
ZYGELA	*Zygadenus elegans*									+		+	
BARGRO	Bare ground	1	1	1				1		2	2	2	2
HUMMOK	Hummocks	3	4	3	4	2	3	2	2	3	2	1	1
Mosses													
BRANEL	*Brachythecium nelsonii*			P	P	P							
CALGIG	*Calliergon giganteum*			P	P	P							
CALSTR	*Calliergon stramineum*				P	P							
CALTRI	*Calliergon trifarium*												
CAMSTE	*Campylium stellatum*				P	P	P		P				
DISCAP	*Distichum capillare*					P	P						
DREADU	*Drepanocladus aduncus*				P	P	P						

	Class	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Fen Lawns					Quagmire and Water-track	
	Subclass	Tall Hummock fen/meadow	Meadow/Dry Fen		Willow Carr		Hummocky Fen Lawn		Fen Lawn			Hummocky Quagmire and Water-track	Quagmire
Species Abbreviation	Association	Tall Hummock Fen/Meadow	Meadow	Dry Fen	Tall Willow Carr	Dwarf Willow Carr	Hummocky Fen Lawn	Hummocky Fen Carpet	Fen Lawn	Fen Lawn	Fen Lawn	Hummocky Quagmire and Water-track	Quagmire
DREREV	*Drepanocladus revolvens*			P	P	P	P		P				
PHIFON	*Philonotis fontana*						P						
MNIABL	*Mniobryum albicans*						P						
RHIPSE	*Rhizomnium*			P	P								
SCOTUR	*Scorpidium turgescens*						P		P				
SCOSCO	*Scorpidium scorpiodes*						P		P				P
WAREXA	*Warnstorfia exannulata*			P		P	P	P					

Figure 2.6. View south across Fremont's Fen showing typical tall hummock meadow/fen habitat.

Figure 2.7. View southeast across Fremont's Fen showing the driest meadow vegetation in the foreground, and the abrupt transition to hummocky fen. Station F5 can be seen right of center.

found in these areas. Cattle grazing and ant nesting activities may also contribute to the development of these hummocks (e.g. Lesica and Kannowski 1997).

The meadow/dry fen vegetation class contains open areas dominated by graminoids. The class has a single subclass with two associations. The first (cluster *0010; Fig. 2.5) contains the driest of the meadow communities examined and is exposed to seasonal water table drawdowns (Fig. 2.7). These sites are located on mineral soil. Shrub cover is generally absent, although releve H29 possess an open canopy of *Salix brachycarpa* and *Potentilla fruticosa*. Diagnostic species are *Argentina anserina* and *Elymus trachycaulus*, with *Juncus arcticus*, *Poa pratensis*, and *Deschampsia cespitosa* being dominant.

The second association in this community type, like that above, generally has a high coverage of *D. cespitosa* and *J. arcticus*, but additional coverage by hydrophilic sedges, particularly *C. aquatilis*, is diagnostic. These sites are located on either peat or mineral soil and are also frequently located on fen margins.

The willow carr vegetation class also contains one subclass with two associations. This vegetational type was only found on Crooked Creek Fen, but it has been noted at numerous other subalpine fens (Johnson, unpubl. data). Both associations have somewhat open to densely closed canopies of *Salix planifolia* and *S. monticola* one to three meters in height. The prevalence of shrubs separates these sites physiognomically from other fen community types. A lush carpet of mosses covers the understory.

Sites in the first association (cluster *0100) are located near rivulets and relatively quickly flowing sheet-flow along the fen margin. The canopy is composed of tall willows and may be somewhat open to closed (Fig. 2.8). The understory is dominated by *Carex utriculata* and mosses. These sites have the highest moss cover of any communities surveyed. Common mosses are *Calliergon giganteum, C. stramineum, Campylium stellatum, Depanocladus revolvens,* and *Rhizomnium pseudopunctatum*.

The sites in the second association (cluster *0101) are found inside the fen margin and at the base of large bedrock hills located in the interior of the fen. These sites have an open canopy of low willows, primarily *S. planifolia* and *S. brachycarpa*, and *Pentaphylloides floribunda. Carex aquatilis* and *C. utriculata* dominate the herbaceous layer (Fig. 2.9). The moss coverage is nearly as prevalent as in the previous association with *Brachythecium nelsonii, Calliergon giganteum, C. stramineum, Campylium stellatum, Depanocladus revolvens, Rhizomnium pseudopunctatum, Warnstorfia exannulata* being common.

The fourth class contains the fen lawn sites. These sites are generally found within the fen expanses and are dominated by sedges and low shrubs are common. The class is divided into three subclasses containing a total of five associations. The first subclass includes hummocky fen lawn sites located exclusively on organic soils (cluster *0110). Small hummocks are plentiful in this vegetation, which is dominated by sedges and low, sparsely distributed shrubs (Fig. 2.9). Mosses such as *Scorpidium scorpiodes* and *S. turgescens* may carpet the field layer in the hollows between hummocks, while *Campylium stellatum, Warnstorfia exannulata* and *Drepanocladus aduncus* are found on the hummocks themselves. Sedges such as *C. aquatilis* and *C. simulata* dominate the herb layer. Hummocks have a vegetation that is slightly less hydrophilic than that of the hollows, comprised of stunted *S. candida, S. planifolia,* and *Potentilla fruticosa* in the shrub layer, and *Thalictrum alpinum, Kobresia myosuroides, K. simpliciuscula* and *C. scirpoidea* in the herb layer. Hummocky

Figure 2.8. View west at Crooked Creek Fen station 23 showing the character of the tall willow carr community. Shrubs are mainly *Salix monticola, S. planifolia,* and *S. brachycarpa*.

Figure 2.9. View west at Crooked Creek Fen showing the nature of open carr vegetation and a peat apron near the center of the photograph bearing hummocky fen lawn vegetation. Shrubs are mainly *S. planifolia, S. brachycarpa,* and *P. floribunda*.

lawns are perennially wet and are frequently found on peat aprons. Peat aprons are landforms that are generally sites of ground water discharge, roughly circular in shape with a slightly domed surface. Aprons and their surrounding vegetation will often form small mire margin-expanse situations wherein the open aprons are similar to typical fen expanse sites which grade into low shrub carr along their margins (Fig. 2.9). Mosaics of peat aprons and their marginal vegetation within the greater fen expanses and marginal areas greatly increased the amount of vegetational heterogeneity found within these fens.

The second association in subclass four (cluster *0111), is a lawn-type of vegetation, dominated by *C. simulata* and *C. aquatilis* (Fig. 2.10). This community type is found on perennially wet, quaking soils with poorly developed microtopograhy. Mosses are not common and their coverage sparse.

Subclasses five and six (cluster 1010 and 1011) are nearly identical vegetationally and environmentally, and so will be described together. These communities are typical of the fen lawns of High Creek Fen, forming communities with sparse, low hummocks and are dominated by *Carex simulata, Carex aquatilis, Kobresia simpliciuscula* and *Eleocharis quinqueflora* (Fig. 2.11). Species such as *Pedicularis groenlandica, Primula egalikensis, Thalictrum alpinum, Triglochin maritimum, T. palustris* are common and diagnostic but do not reach high cover values. Mosses are frequent, although species composition data were not collected at High Creek Fen.

Vegetation class five consists of quagmire and water track communities (Fig. 2.12). These sites are continually covered by shallow standing water except where small rises occur. Water tracks are more or less linear features with flowing surface water and quaking soils

Figure 2.10. View southeast across an expanse at Fremont's Fen station 11 showing *C. simulata-C. aquatilis* dominated fen expanse.

Figure 2.11. View south across a fen lawn in an expanse on High Creek Fen. Station 25 can be seen in the foreground.

while quagmires are amorphous expanses of quaking soils covered by shallow, slowly flowing water. The soils at these sites are tenuously thin, hardly holding the weight of a biologist. Dominant species in both vegetation types are *Eleocharis quinqueflora, Utricularia* spp., *Triglochin* spp. and mosses such as *Scorpidium scorpioides* can form expansive carpets in many areas. Marl and algae coat virtually all surfaces and may form soil strata. Hummocky quagmires (group *110) are generally found interspersed within water tracks (Fig. 2.13). In addition to the above attributes, these sites possess scattered hummocks of various sizes, but most are under 10 cm in height. On these hummocks, slightly less hydrophilic plants such as *Thalictrum alpinum, Trichophorum pumilum, Salix candida,* and *Kobresia simpliciuscula* can survive.

ORDINATION

Figure 2.14 shows axes 1 and 2 of a detrended correspondence analysis (DCA) of vegetation releves. Figure 2.15 shows axes 1 and 3 of the same ordination. The graph symbols correspond to the eight different community types parsed out by TWINSPAN. As is evident in Figs. 2.14 and 2.15, releves grouped by TWINSPAN have a high fidelity for one another in the DCA diagrams.

Table 2.2 contains ordination diagnostics for the DCA. The first three DCA axes accounted for 21.3 % of the total variance in the species data. Eigenvalues for the first three axes are 0.62, 0.34, and 0.19, respectively. Gradient lengths were high for these axes, and complete species turnover occurs across the first axis. Along the second axis, turnover is nearly complete, while approximately 50% turnover occurs along the third axis.

Figure 2.12. Closeup of the nature of quagmire and water track vegetation. Taken at High Creek Fen near station 19.

Figure 2.13. View southwest from water track vegetation at High Creek Fen station 20.

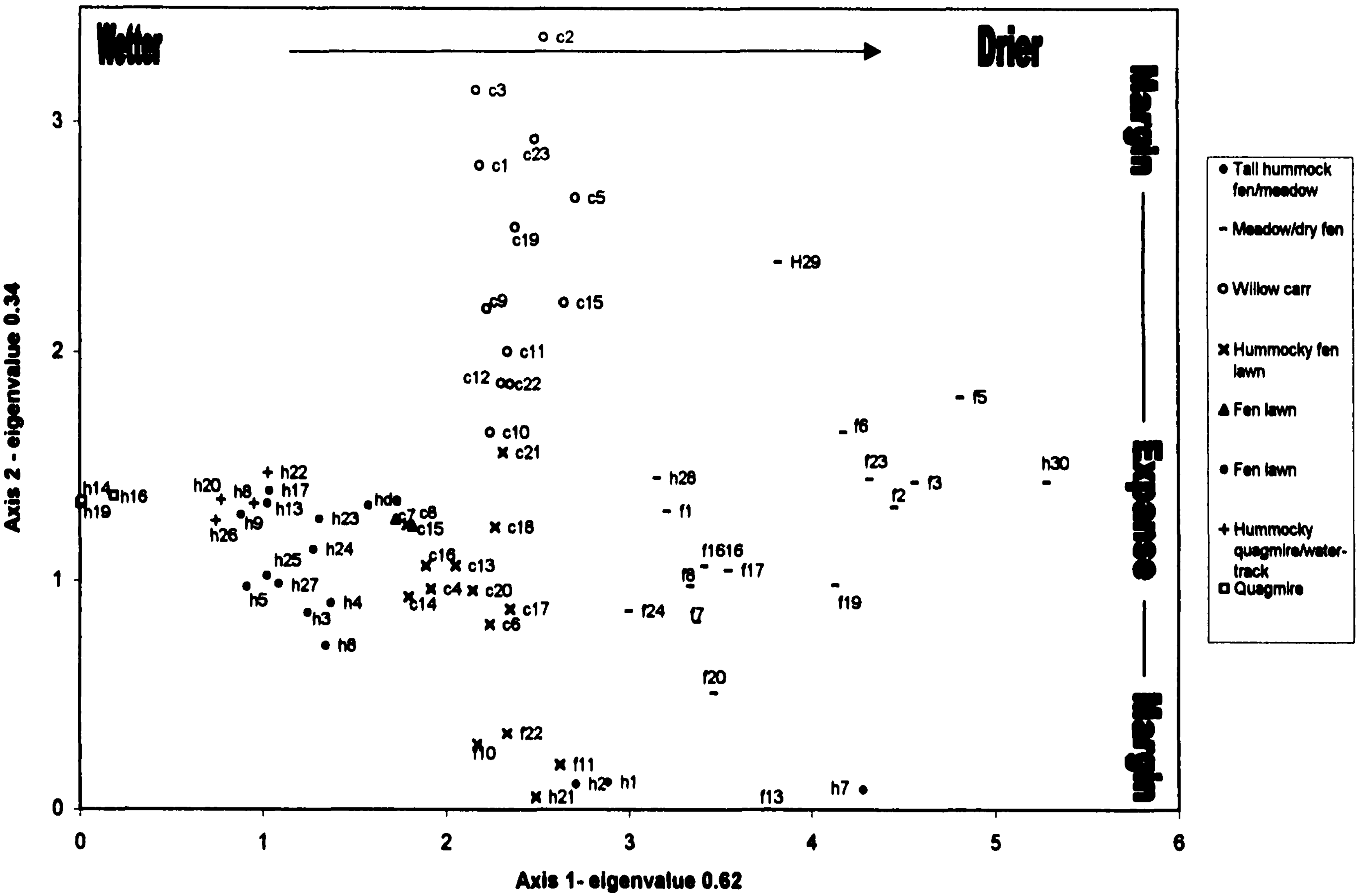

Figure 2.14. Axes 1 and 2 of a DCA ordination of releves. Symbols indicate the TWINSPAN subclasses to which the releves belong. See text for additional details.

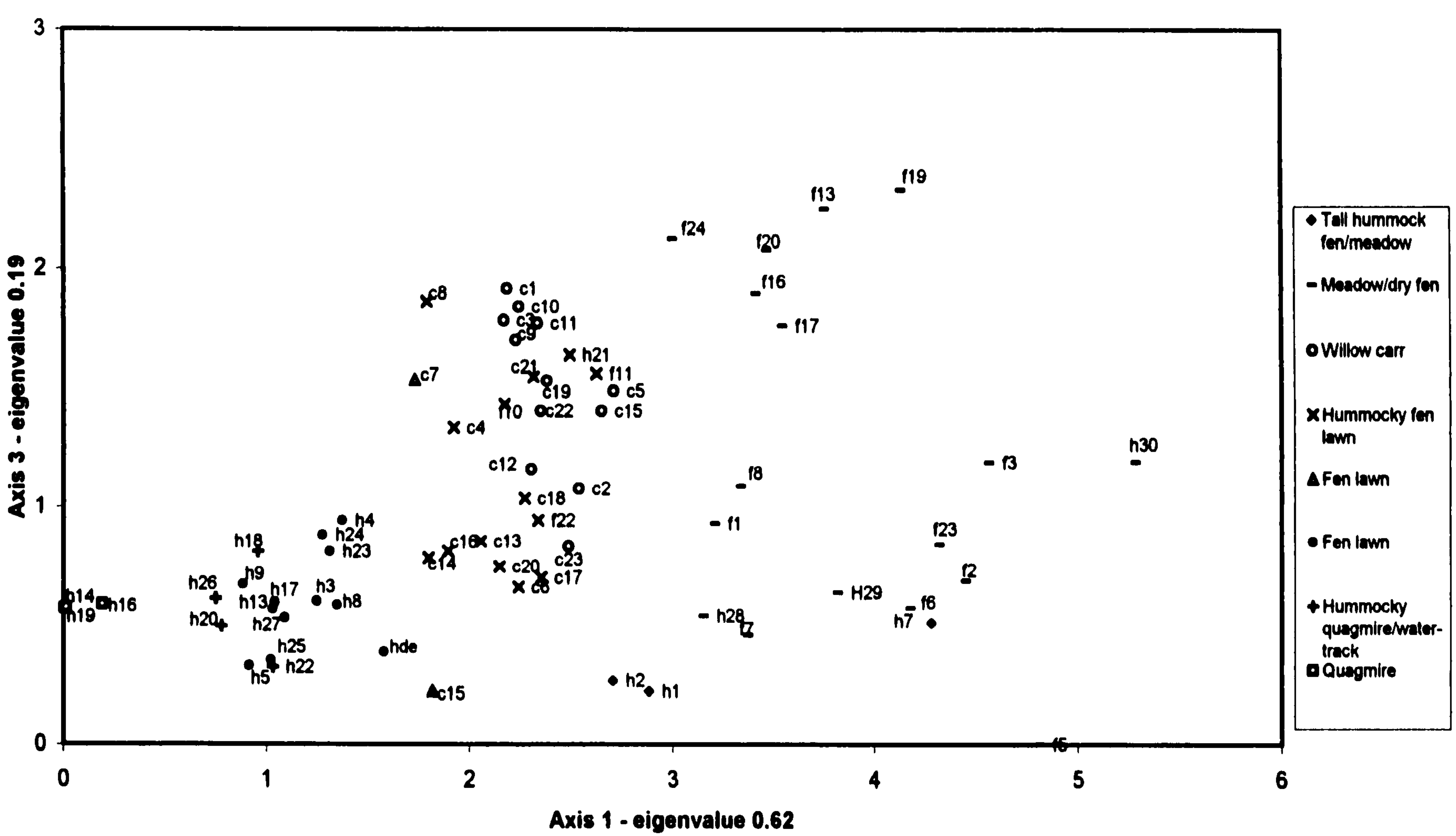

Figure 2.15. Axes 1 and 3 of a DCA ordination of releves. Symbols indicate the TWINSPAN subclasses to which the releves belong. See text for additional details.

Table 2.2. Ordination diagnostics for the DCA and CCA. See text for explanation.

	Axis 1	Axis 2	Axis 3	Axis 4	Total Inertia
DCA Gradient Length	5.29	3.37	2.33	2.48	
DCA Eigenvalues (unconstrained)	0.62	0.34	0.19	0.16	5.34
CCA Eigenvalues (constrained)	0.52	0.42	0.20	0.18	2.04
Cumulative Percentage of Species Variance accounted for by CCA	9.7	17.5	21.3	24.7	

Releves from each study site show a tendency to cluster near one another, with the array of study sites forming a gradient across axis 1. Such arrangement suggests the presence of site specific influences on vegetational composition. Also exhibited in the axis 1 gradient is a trend going from the most hydric, quagmire releves on the left, to drier, meadow releves on the right. Axis 2 is dominated for most of its length by a gradient occurring on Crooked Creek Fen with sites from High Creek Fen and Fremont's Fen becoming important at the lower end of the gradient. Axis 2 strongly corresponds to changes in vegetation from the mire margin to its expanse (See Figs. 2.2 - 2.4 for releve locations). Tall willow carr vegetation releves (association *0100) are located at the top of the axis 2 gradient. This vegetation grades into short, open-canopy carr and fen areas in which shrubs are common (cluster *0101). Between roughly 1.4 and 0.75 on axis 2 are the fen expanse communities and open, wet meadow sites. Low on axis 2, vegetation samples are once again from sites located on the fen margins, but these marginal sites have little or no shrub cover. Such sites tend to have well developed microtopography and they may or may not be situated on organic soils. Axis 3 (Fig. 2.15), is not readily interpretable from the DCA alone, although regional effects are somewhat apparent.

Species placement along axes 1 and 2 is shown in Figure 2.16. Species characterizing each of the vegetational classes defined by TWINSPAN are enclosed within polygons. The suite of species enclosed by each polygon provides an indication of the typical composition found within each community, because species placement represents the species' optimal habitat with respect to the underlying synthetic gradients. Exclusion from a polygon does not necessarily mean a species is never found within a given vegetational type since a species may

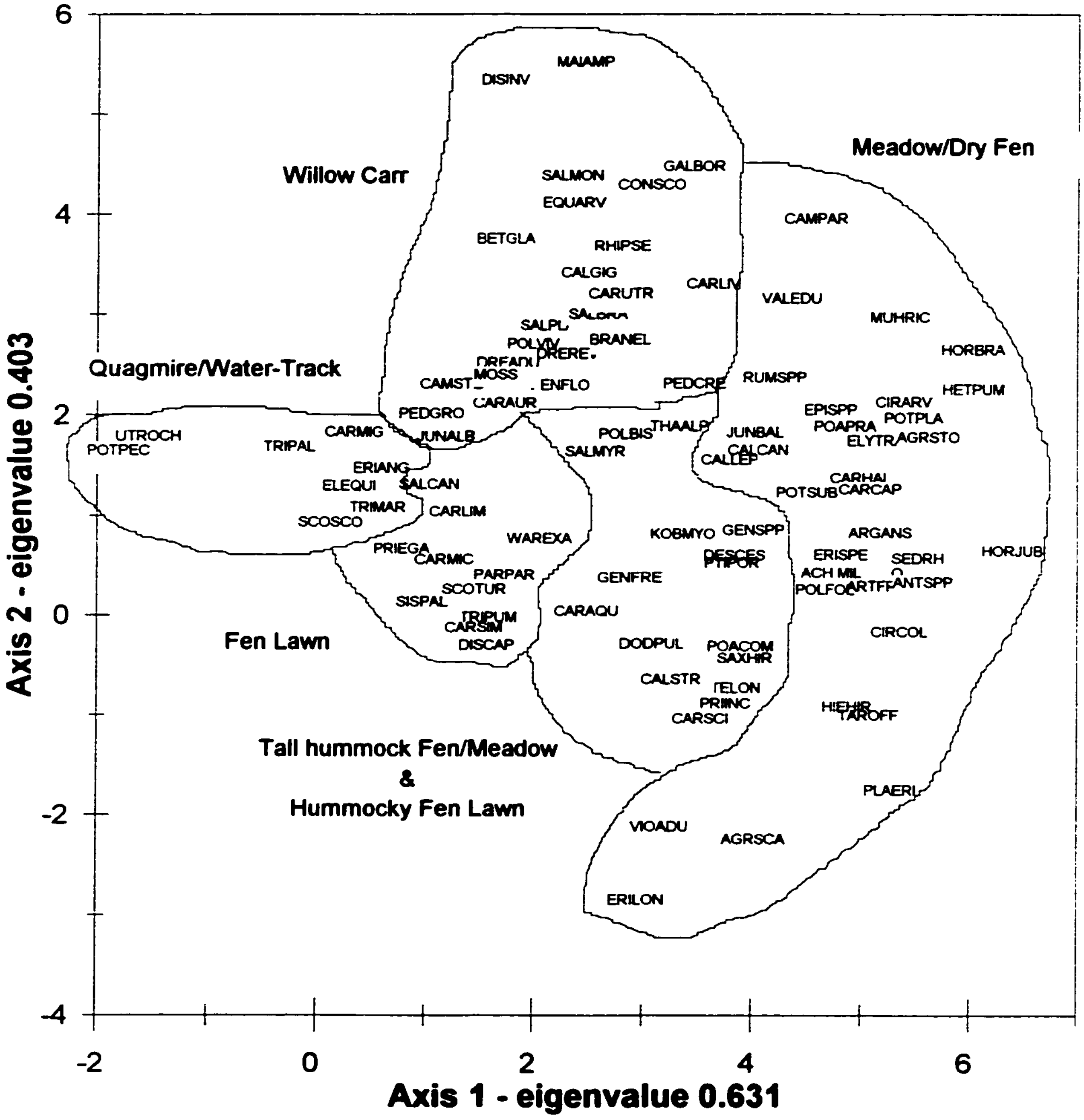

Figure 2.16. Axes 1 and 2 of a DCA ordination of species from intact wetland sites. See text for additional details.

have its environmental optimum in one habitat, but it is found in others at a lower abundance level. Such is the case with many generalist species like *C. aquatilis* and *C. simulata*.

FEN ENVIRONMENT

Hydrology

Releve environmental data were grouped according to the TWINSPAN group in which they were classified (see Fig. 2.5). Table 2.3 contains a summary of hydrologic characteristics measured at the mires. Mean values included within the table were calculated over the period of record. Additional hydrologic data including seasonal hydrographs can be found in Appendix 5. Mean water table depth ranged between -40.3 cm in the meadow/dry fen areas to 1.6 cm in the quagmires (Table 2.3). Parenthetical numbers next to the water table depth values are the standard deviations of the between-releve seasonal averages.

The meadow/dry fen areas had the most between-releve variability in average water table depth. During a season these sites were also subject to the largest fluctuations in water table, with an average standard deviation of 26.9 cm in the case of the meadow/dry fen areas. The quagmire areas had the highest average water table at 1.6 cm, and the least variability between-fens and within-fens during the sampling season. On the average, standard deviation of water tables measurements was only 2.8 cm. The water tables of the other fen vegetation types ranged between these values. Fen lawn sites have water tables approximately at the ground surface and show little fluctuation in water table throughout the year. The hummocky

Table 2.3. Summary of hydrological measurements performed from 1995 - 1998. Parenthetical numbers following values are within-vegetational class standard deviations.

	Tall hummock Fen/Meadow	Meadow/Dry Fen	Willow Carr	Hummocky Fen Lawn	Fen Lawn	Quagmire
Mean Water Table Depth (cm)	-27.9 (12.6)	-40.3 (21.6)	-9.2 (11.3)	-7.5 (10.1)	0.3 (2.1)	1.6 (0.9)
Mean Seasonal Water Table Deviation (cm)	19.2	26.9	11.3	12.8	3.9	2.8
Mean Potentiometric Surface Height (cm)	-38.0 (29.8)	-44.9 (30.7)	-7.4 (15.0)	-5.9 (9.6)	4.1 (7.8)	1.5 (3.3)
Mean Seasonal Potentiometric Deviation (cm)	25.5	31.0	10.4	11.8	5.0	8.2
Mean Seasonal Head (cm)	-12.4 (18.9)	-5.0 (14.3)	1.4 (9.4)	0.6 (4.1)	4.4 (7.3)	0.1 (4.6)
Mean Seasonal Maximum Water Table Height	-6.8 (15.0)	-10.6 (27.3)	1.4 (4.9)	6.5 (14.2)	3.8 (2.0)	4.1 (1.3)
Mean Seasonal Minimum Water Table Height	-54.8 (7.8)	-68.0 (22.6)	-19.6 (25.3)	-35.1 (63.5)	-4.8 (7.3)	-1.1 (1.0)

areas – the tall hummock meadow/fen and hummocky fen expanse – have water tables that are on average below the surface, however, they may have standing water for periods during the season.

Patterns in potentiometric surface were similar to those displayed by the water table (Table 2.3 and Appendix 5). The meadow/dry fen areas had the deepest potentiometric surface and showed the greatest seasonal variability. In contrast to the water table, poteniometric surface was highest in the fen expanse sites. These sites also had the lowest seasonal variability in surface height.

Average hydraulic head also varied between vegetation types. The tall hummock fen/meadow had negative head on the average, indicating that these areas are generally sites of ground water recharge, although there was variability between sites. The highest average head values were found in the fen lawn sites where ground water discharge zones are prevalent.

Water and Soil Characteristics

Chemical and physical characteristics of soil and water are presented in Table 2.4. There was little difference between the average water pH measured within the different vegetational types. An exception is that average pH of meadow/dry fen sites was slightly lower than that of other sites, although these sites also had high between site variance. Soil pH followed the same general pattern as water pH, however, soil pHs tended to be lower.

Water electrical conductivity (EC) was remarkably similar in the carr and fen lawn sites. The tall hummock fen/meadow releves had highest conductivities, with the

Table 2.4. Summary of soil and water data collected within each of the vegetational types. All units are parts per million unless otherwise noted. Parenthetical numbers are standard deviations of the means.

	Tall Hummock Meadow/Fen	Meadow/Dry Fen	Willow Carr	Hummocky Fen Lawn	Fen Lawn	Quagmire
Water EC (μS)	850 (300)	640 (480)	520 (130)	520 (130)	520 (100)	560 (80)
Water pH	7.36 (0.15)	6.71 (0.93)	7.79 (0.20)	7.79 (0.26)	7.46 (0.41)	7.44 (0.14)
Water Ca	219.0 (61.3)	125.6 (68.6)	98.4 (42.0)	115.8 (56.3)	103.1 (36.7)	128.2 (16.8)
Water Mg	65.6 (35.6)	27.1 (10.3)	16.1 (12.4)	17.8 (10.5)	30.1 (10.6)	41.4 (9.6)
Water Na	19.5 (4.4)	17.7 (10.0)	7.8 (12.0)	12.5 (10.9)	6.9 (2.0)	8.8 (2.3)
Water K	1.2 (0.3)	0.6 (0.5)	1.4 (2.6)	0.8 (0.8)	0.8 (0.9)	0.4 (0.4)
Water P	0.1 (0.0)	0.1 (0.1)	0.1 (0.3)	0.1 (0.1)	0.1 (0.0)	0.1 (0.0)
Water Fe	0.2 (0.1)	1.4 (1.3)	0.6 (0.6)	1.7 (3.0)	0.9 (2.2)	0.2 (0.1)
Water Mn	0.04 (0.03)	0.04 (0.04)	1.10 (1.90)	0.70 (1.40)	0.03 (0.03)	0.05 (0.05)
Water CaC03	774.2 (353.3)	403.7 (202.7)	311.9 (126.3)	359.5 (170.7)	381.3 (124.0)	490.1 (76.1)
Soil pH	7.6 (0.1)	6.8 (0.7)	7.6 (0.4)	7.4 (0.7)	7.2 (0.3)	7.4 (0.2)
Soil EC (μS)	1500 (300)	1700 (100)	700 (300)	900 (400)	1800 (700)	1900 (400)
Soil OM	36.5 (12.2)	57.0 (15.7)	41.6 (15.7)	51.5 (16.5)	59.7 (16.7)	61.3 (13)
Soil $CaCO_3$	487067.0 (118454.0)	82255.9 (101284)	314425.0 (223541.0)	8116.7 (8277.1)	172914.0 (189746.0)	166643 (127422.0)
Soil NO_3	19.0 (4.0)	27.3 (26.3)	16.0 (11.5)	8.8 (0.6)	11.7 (2.8)	14.1 (4.6)
Soil P	5.1 (1.8)	8.7 (5.7)	10.5 (12.1)	10.9 (8.6)	8.5 (4.9)	12.2 (5.3)
Soil K	135.6 (66.4)	135.6 (65.1)	121.5 (67.5)	165.0 (156.7)	129.5 (48.1)	117.7 (47)
Soil Zn	8.7 (4.5)	19.2 (16.7)	6.4 (4.5)	12.4 (8.4)	7.9 (3.3)	8.5 (4.9)
Soil Fe	642.4 (394)	940.1 (451.7)	612.5 (284.1)	1027.3 (253.6)	395.6 (224)	300.9 (195.8)
Soil Mn	22.5 (10.7)	28.7 (21.1)	89.9 (66.6)	149.7 (91.8)	18.5 (24.0)	16.2 (7.5)
Soil Cu	5.4 (1.9)	5.4 (2.4)	5.1 (1.2)	8.6 (8.0)	4.9 (1.6)	4.5 (1.6)
Soil Ca	8581.0 (1542.0)	10770.1 (2520.6)	10309.4 (1983.2)	7395.4 (1491.3)	9937.5 (2295.3)	12051.4 (1664.3)
Soil Mg	1292.0 (169.0)	1146.1 (684.9)	549.5 (283.8)	831.7 (241.8)	1308.9 (430.4)	1732.3 (254.3)
Soil Na	114.6 (48.9)	286.9 (222)	93.7 (34.7)	205.2 (57.1)	126.5 (46)	152 (39.5)
Hummock Height (cm)	41 (5)	38 (28)	27 (20)	27 (19)	15 (7)	3 (3)
Hummock Cover (%)	24 (2)	17 (11)	25 (12)	18 (8)	14 (3)	10 (4)
Peat Depth (cm)	47 (40)	21 (19)	105 (74)	129 (94)	50 (39)	50 (14)

meadow/dry fen following. Soil EC was more variable than water EC. Quagmire soils had the highest EC of all vegetation types, followed by the fen expanses. Marginal carrs had the lowest conductivity. There were large differences in ion content of the pore water of the different vegetational types. Calcium, the dominant cation in all of the samples obtained, ranged from 219.0 mg/l in the tall hummock fen/meadow sites, down to 98.4 mg/l in the marginal carrs. Average calcium content across all sites was 131.7 mg/l. The concentration of other cations roughly corresponds to the pattern displayed by calcium, and there was close correspondence between water EC and cation content. As suggested by the EC measurements, the two fen lawn vegetation types did not show systematic differences in total cation content.

The pattern of soil calcium differed from that of water calcium, with the hummocky fen lawns sites having the lowest average soil calcium and quagmires the highest. As with water, calcium was the dominant cation measured in the soils. Systematic relationships between soil cation content and EC between vegetational types are not evident.

Surficial and subsurface soil characteristics also varied between the vegetation types. The deepest peat was typically found in the hummocky fen lawns and the marginal carrs, while the shallowest organic layer is in the meadow/dry sites. Actually, many of the latter sites were not located on organic soils, but rather on mineral soils with a thick O horizon. In the remaining vegetational subclasses, average peat depth was rather constant at approximately 50 cm. Surficial microtopography as expressed by hummock-hollow formation was most developed in the tall hummock fen/meadow areas where the hummocks averaged 24 cm in height and covered 41% of the ground surface. Quagmires have the most poorly developed microtopography with average hummock height being only 3 cm, and hummocks covering approximately 10% of the ground surface. In general, the more mesic vegetational types examined have the greatest development in hummock-hollow topography. However, in the driest meadows, such as those examined at releve F5 and F6, microtopography does not develop due to the low level of soil organic matter which comprises the hummocks. The very hydric fen expanses tend to possess low, scattered hummocks which are hardly noticeable.

Average soil organic matter (OM) showed a somewhat inverse relationship to microtopography development. Quagmires and fen lawns have the highest organic matter contents, although at approximately 60 %, organic matter content is not particularly high for histolic soils. The organic matter content of other mire soils measured here ranged from 36 - 57 %.

DIRECT GRADIENT ANALYSIS

Canonical correspondence analysis (CCA) was used to directly relate the vegetational and environmental data sets. Figure 2.17 shows the results of the CCA. Point markers correspond to the TWINSPAN groups as in the DCAs above, and the vectors correspond to directions of change in the environmental variables. The interaction of hummock height and hummock cover was used as a variable in this analysis to synthesize the effects of both microtopographical attributes.

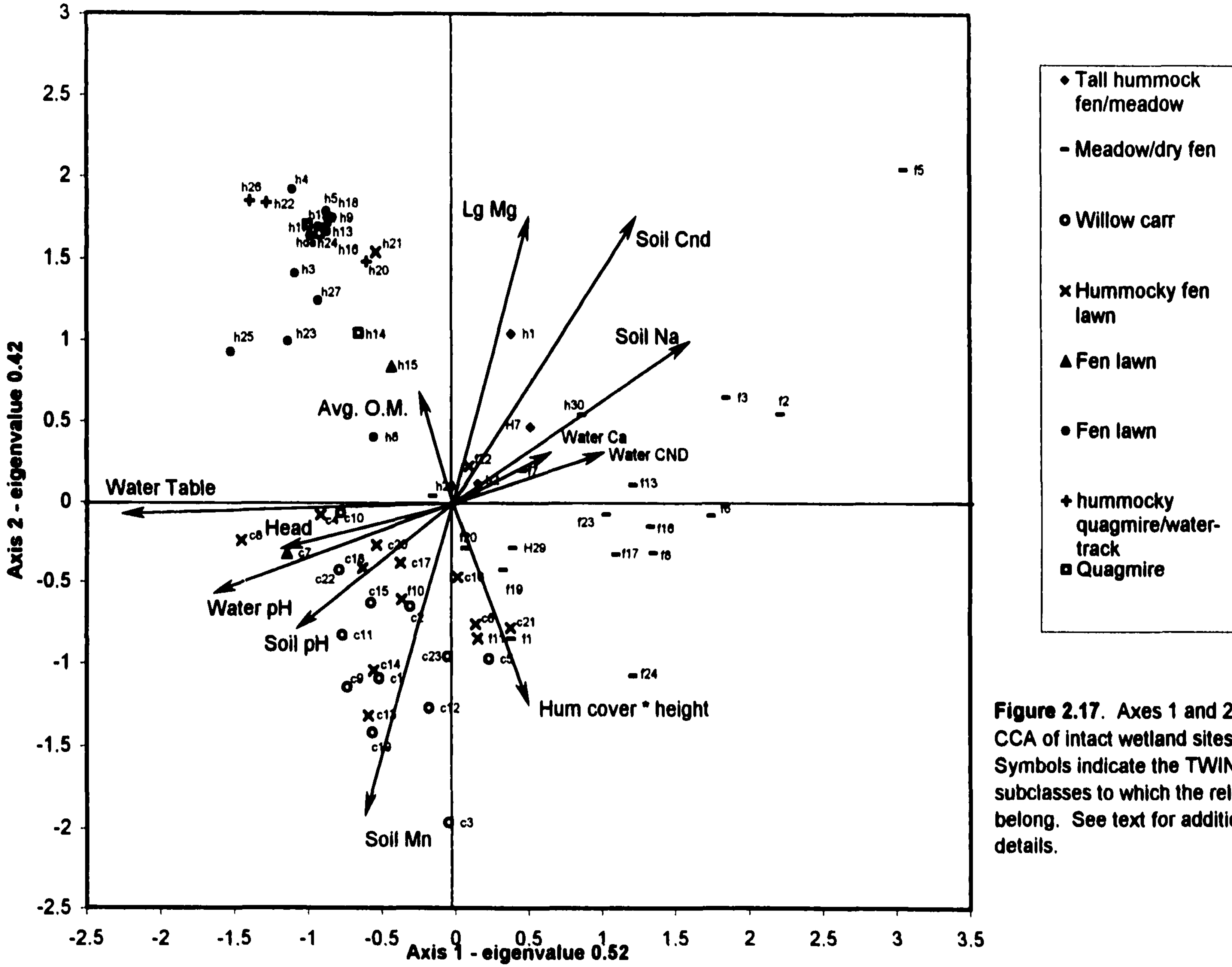

Figure 2.17. Axes 1 and 2 of a CCA of intact wetland sites. Symbols indicate the TWINSPAN subclasses to which the releves belong. See text for additional details.

Vector orientation indicates the direction in which an environmental factor is increasing in value, while its relative length denotes the strength of the factor's correlation with vegetational change. A vector's orientation relative to another vector also describes the correlation between the two environmental factors. That is, nearly parallel vectors pointing in the same direction are highly positively correlated, nearly parallel vectors in opposite directions are highly negatively correlated, while vectors orthogonal to each other are uncorrelated. Additional detail about releve environment and a species' environmental preference can be extracted from the diagram by drawing perpendicular lines from a vector to the species or releves of interest. The order in which these lines intersect the vectors relates the relative value of the factor at the site. An example of diagram interpretation is provided below.

Table 2.2 presents the CCA diagnostics for the first four ordination axes (only two shown in Fig. 2.17). Eigenvalues relate the importance of each axis. Dividing an axis's eigenvalue by the total inertia (the sum of all eigenvalues) gives the percent of variance accounted for by that axis. The cumulative percentage of variance accounted for by the CCA axes is given in the bottom row. Unconstrained eigenvalues are those that are calculated based only on species data and represent the total variance in the species data. Typically, constrained eigenvalues are lower than unconstrained ones since species data are adjusted to be linear combinations of the environmental variables, although this is not always the case. Dividing the sum of the constrained eigenvalues by the sum of the unconstrained eigenvalues provides a measure of how much of the change in species composition has been accounted for by the measured environmental factors and how much is due to unmeasured factors.

An example of diagram interpretation is as follows. In Fig. 2.17 the vector for water table depth points in the direction of increasing water table height. This factor is highly negatively correlated with water conductivity (nearly parallel but pointed in opposite directions) and is nearly uncorrelated with hummock cover*height (vectors at nearly 90 degrees to one another). Water table depth is strongly correlated with the axis 1 gradient since it is nearly parallel with axis 1, and based on its relative length, it has a strong correlation with vegetational changes that occur in the releves arrayed along axis 1. Extending the water table vector in both directions and drawing perpendicular lines from it to the releves, one can see that releve H25 has the highest water table, followed by releve C8, then H26, etc. Releve F5 has deepest water table measured.

Eigenvalue reductions between the DCA and CCA were not large, indicating that relatively little vegetational information was lost by the CCA (Table 2.2). The measured environmental factors account for 38% of the species variance, that is, 62% of species variance was due to unmeasured environmental factors. Axis 1 is most highly correlated with water table depth, soil sodium, and pore water pH (Table 2.5). Axis 2 is most highly correlated with soil Mn, soil Mg, soil EC and microtopography. The factors most highly correlated with the axes also receive high weights in the CCA as shown by the canonical coefficients (Table 2.5). From these results it may be inferred that differences in water table height most strongly affect species composition, with soil sodium and pore water pH also exerting a strong influence. The second most important direction of variation corresponds with a soil chemistry gradient, further influenced by the effects of microtopography. Other measured environmental factors also significantly influence the vegetation but to a lesser degree compared to those mentioned. A Monte Carlo permutation test determined that both axes are significant ($p=0.005$).

Table 2.5. Intra-set correlations and canonical coefficients for the CCA.

	Intra-set Correlations				Canonical Coefficients			
Parameter	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Soil pH	-0.42	-0.31	-0.40	-0.31	-0.05	-0.12	-0.17	-0.14
Soil EC	0.51	0.71	-0.02	0.05	-0.09	0.32	0.03	-0.09
Soil OM	-0.08	0.27	0.10	0.39	-0.17	0.06	0.15	0.17
Lg Soil Mn	-0.24	-0.76	-0.02	-0.05	0.00	-0.20	-0.14	-0.08
Lg Soil Mg	0.22	0.72	-0.42	-0.01	-0.03	0.21	-0.52	-0.20
Lg Soil Na	0.66	0.40	0.21	-0.01	0.31	-0.08	0.31	0.04
Water Ca	0.28	0.14	-0.35	0.46	-0.03	0.21	0.18	0.23
Water EC	0.42	0.13	-0.46	0.51	0.08	-0.09	-0.19	-0.01
Water pH	-0.65	-0.24	0.29	-0.55	-0.15	0.16	0.16	-0.21
Water Table Depth	-0.89	-0.02	0.00	0.19	-0.40	0.14	0.04	0.18
Hydraulic Head	-0.50	-0.10	-0.21	0.38	-0.04	-0.02	0.01	0.11
HumCover*Hum Height	0.22	-0.50	-0.15	0.27	0.13	-0.23	-0.12	0.06

As in the DCA, the releves grouped by TWINSPAN tended to cluster in the CCA, although more interspersion is evident. Between-site differences in vegetation and environmental factors are more evident in the CCA than in the DCA. Much of the difference in stand placement is due to the between-wetland differences in environmental conditions and this segregation by site is responsible for much of the interspersion of TWINSPAN groups.

The tall hummock fen/meadow and meadow/dry fen sites are associated with nutrient rich soils and waters that are circumneutral to slightly acidic. Vegetation in these areas is also associated with relatively deep water tables and well developed microtopography. The willow carr and hummocky fen lawn sites, particularly those found at Crooked Creek Fen, have the most alkaline pore water and soils of the vegetation types. Soils tend to be rich in manganese but low in other cations. These sites are also associated with high water tables and well developed microtopography. The fen lawn sites and quagmires of High Creek Fen are located in areas high in soil organic matter, with high pHs, high water tables, moderately high soil cation concentrations, but with poorly developed microtopography (Fig. 2.17, Table 2.4) .

Comparison of the DCA and CCA diagrams (Figs. 2.14, 2.15, and 2.17) shows that the arrangement of sites is noticeably different between the techniques, in particular along axis 2, indicating that this axis has been significantly altered by the CCA. To evaluate this observation, Spearman's rank correlation of site placement by DCA and CCA was performed using the Dunn-Sidak significance correction due to multiple comparisons (Table 2.6). This analysis corroborates visual comparisons. Axis 1 of the DCA and CCA are highly correlated, but the axis 2 scores are not significantly correlated. CCA axis 2 is highly correlated with DCA axis 3, however, indicating that CCA axis 2 mainly depicts the DCA axis 3 gradient.

Table 2.6. Correlation matrix between DCA and CCA axes.* indicates significance of $p<0.05$, ** is $p<0.001$

Axis	DCA 1	DCA 2	DCA 3	DCA 4
CCA 1	0.869**	-0.068	0.183	0.107
CCA 2	-0.388*	-0.207	-0.609**	0.359
CCA 3	0.016	-0.244	0.381	0.199
CCA 4	0.011	-0.145	-0.031	0.076

DISCUSSION

Classification and Indicator Species

According to the rich to poor fen classification which is based on minerotrophy, pH, and species composition (Du Rietz 1949, Sjörs 1950a, Gorham and Pearsall 1956, Sjörs 1961b, Sjörs 1963, Gorham 1967, Sjörs 1983, Malmer 1986), the calcareous fens examined in this study can be classified as extremely rich fens. This corroborates Cooper's (1996) classification of High Creek Fen which was based on species indicators and a small number of water samples.

The basis and criteria of this classification were discussed in detail in Chapter 1 (See pg. 17). The most commonly measured water parameters in mire studies are pH, electrical conductivity (EC), and the concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, although pH, EC, and Ca^{2+} are thought to be the most valuable in distinguishing between fen types. In extremely rich fens, water pH has been found to range between 6.5 and 8.2, Ca^{2+} between 18 and 120 mg/l, and EC from 16 to 456 μS (see also Table 1.1, pg. 19). The mean pH of pore water measured at the South Park fens is 7.4, ranging from 3.9 to 8.2. The value of 3.9 was obtained from Fremont Fen station 2. Three other Fremont's Fen sites in the vicinity of station 2 also have low pH values (< 5.75). This area of the fen also contains other extreme values that are highlighted below. The cause for the pocket of low pH values in a contiguous wetland having average values as high as 7.8 is uncertain but is probably related to local heterogeneities in the underlying parent material. Although Fremont's Fen sits entirely upon Quaternary alluvium, it is underlain by a number of different geological members (Fig. 1.4c, pg. 37). Investigation of the possible effects of these differing deposits is beyond the scope of this study, but their influence is likely significant.

Calcium concentrations in South Park fens ranged between 24 and 291 mg/l, with a mean of 115 mg/l. It is interesting that the mean level of this cation is near the highest values measured in other extremely rich fens, thereby showing the high degree of minerotrophy present in South Park's fens. Interestingly, Fremont's Fen station 2 has the highest calcium concentration of the sites examined. When the correlation between pH and Ca^{2+} in all samples was tested, a negative correlation was found ($r = -0.36$, $p = 0.001$). When the extreme values found at Fremont's Fen station 2 were removed the correlation became insignificant, although still negative ($r = -0.20$, $p = 0.07$). Malmer et al. (1992) likewise found a poor relationship between calcium and pH within rich fens.

Electrical conductivity (EC) is frequently used as a synthetic measure of the water's nutrient status. The EC of these fen waters ranged widely, from 90 to 2090 μS with a mean of 575 μS. All of the conductivity measurements obtained during this study were above the minimum ECs measured within extremely rich fens throughout the world, and the mean EC measured in this study was above the highest measured in other fens. Again, the highest average EC was found at Fremont's Fen station 2. Other nutrient concentrations were at or above the range of values measured in other extremely rich fens (see Table 1.1, pg. 19).

Plant species are frequently employed as synthetic indicators of fen minerotrophy and the approach has been used productively since it was first developed (Du Rietz 1949). Problems arise in the generic application of developed species indicators in new regions, however, since floras and species habitats can vary between regions. This problem has been addressed by previous authors and has frequently been treated as an additional ecological gradient or direction of variation (Sjörs 1950b, Malmer 1986, Chee and Vitt 1989, Bridgham et al. 1996). The regional floristic gradient is especially important when comparing fens located in the mixed southern Rocky Mountain flora with fens in the boreal floristic province.

South Park's calcareous fens have species indicators of rich and extremely rich fen conditions as found in European and Canadian fens. Species occurring within Colorado that have been considered to be rich fen indicators in prior studies are the herbs *Carex lanuginosa*, *C. livida*, and *Habenaria* (*Limnorchis*) *hyperborea* and the mosses *Scorpidium scorpioides*, *S. turgescens*, *Calliergon trifarium*, *C. giganteum*, *Campylium stellatum*, and *Tomenthypnum nitens* (Nordqvist 1950, Sjörs 1950a, Sjörs 1959, Sjörs 1961a, Slack et al. 1980, Karlin and Bliss 1984, Chee and Vitt 1989, Glaser et al. 1990, Malmer et al. 1992). These species may also be common in and characteristic of extremely rich fens, but they do not necessarily indicate extremely rich fen conditions. That is, the presence of such species is necessary, but not sufficient to indicate extremely rich fen conditions.

Few previously designated extremely rich fen indicator species occur in Colorado. In studies such as Sjörs (1961a), Sjörs (1963) and Glaser (1990), *Triglochin maritimum*, *T. palustris*, *Kobresia simpliciuscula*, *Juncus albescens*, *Carex microglochin*, *C. scirpoidea*, *Pentaphylloides floribunda* (*Potentilla fruticosa*), and *Utricularia intermedia* have been reported as generally indicative of extremely rich fen conditions. *Salix candida* also frequently occurs in extremely rich fens, but its value as an indicator species was not evaluated in those studies. Surprisingly, the common extremely rich fen indicator, *Muhlenbergia glomerata*, which has been found on one occasion in Colorado (Weber 1990), has not been identified in any of the South Park's fens. It seems that *M. richardsonis* may replace *M. glomerata* in southern Rocky Mountain calcareous fens.

The fens of South Park share a number of other species in common with the boreal and arctic fens such as *Carex aquatilis, C. rostrata, C. limosa, Salix planifolia,* and *Juncus arcticus*, but these species have wide ecological tolerances and thus have little value as indicators of minerotrophy.

Within Colorado, and probably the southern Rocky Mountains, there are problems in using a number of the above species indicators. For instance, *Triglochin maritimum* is commonly found growing in saline areas not associated with fens or mires. *Pentaphylloides floribunda* (*Potentilla fruticosa*) is a generalist species in this region and may be found growing in meadows, carrs, and virtually any fen habitat in Colorado. Likewise, *Carex lanuginosa* and *Habenaria hyperborea* can be found in variety of wetland conditions, and *Kobresia simpliciuscula* most commonly grows in the alpine zone in non-wetland conditions.

Because several of the species indicators used in other geographic regions are of less use in the Southern Rocky Mountains, additional region-specific indicators must be designated. Based on this study and on previous work done in these fens and in calcareous fens in Montana, Wyoming, and California (Lesica 1986, Major and Taylor 1988, Fertig and Jones 1992, Cooper 1996, Sanderson and March 1996), a suggested list of extremely rich fen indicators for the southern Rocky Mountains includes *Trichophorum pumilum, Salix candida, S. myrtillifolia, Carex microglochin, C. viridula, Eriophorum gracile, Scorpidium scorpioides, S. turgescens,* and *Calliergon trifarium.* In the Rocky Mountains north of Colorado, *Muhlenbergia glomerata* also seems a valuable indicator.

If fen conditions are known to exist at a site, additional species may be used to supplement the above list. As discussed above, these species may be found in other habitats, but when found in fens they are very strong indicators of high minerotrophy. These species are *Triglochin maritimum, T. palustris, Carex scirpoidea, Kobresia myosuroides, K. simpliciuscula,* and *Thalictrum alpinum.*

Gradient Analysis

While regional floristic gradients in part differentiate southern Rocky Mountain extremely rich fens from their boreal counterparts, the within-fen environmental and vegetational patterns are similar between the fens of these two regions. Within the calcareous mires of South Park, vegetational gradients related to differences in water table depth, location from the mire margin to its expanse, microtopography, and soil and water chemistry are evident.

Water Table Gradients

As in most wetland systems, hydrology exhibits the greatest control over plant species composition at these sites (Fig. 2.17). The most hydric of the terrestrial mire systems are the quagmires and water tracks, which are clustered at the extreme left side of the DCA (Fig. 2.14) and to the right in the TWINSPAN (Fig. 2.5). These sites are located on quaking soils comprised of an approximately 10 - 25 cm thick vegetation mat, underlain by an unconsolidated peat-water mixture. Similar soil compositions have been described in the water tracks of fens in boreal regions (e.g. Racine and Walters 1994). Aquatic and highly hydrophilic species such as *Eleocharis quinqueflora, Triglochin maritimum, T. palustris, Utricularia* spp., and *Potamogeton pectinatus* dominate these areas, although plant coverage is fairly sparse (Table 2.1). The mosses *Scorpidium scorpiodes,* and *S. turgescens* commonly carpet the shallow-water hollows. When hummocks are present, species such as *Juncus balticus, Kobresia simpliciuscula, Carex simulata, C. aquatilis, Salix candida, Trichophorum pumilum* and *Thalictrum alpinum* will also generally be found.

Water tracks and quagmires have similar species compositions and often intergrade with differentiation being based largely on surficial physiognomy. Water tracks tend to be linear fen features in which water is conveyed relatively quickly, they are often slightly steeper than the surrounding fen, and coverage by sedges may be high compared to quagmires. Quagmires on the other hand, have a more broad, amorphous shape, with a relatively low topographical gradient. They have lower plant coverage compared to water tracks (Table 2.1) and possess large patches of open water. Virtually all surfaces may be covered with marl and the bottoms are layered with algae and iron-flocculating bacteria. At a larger scale, quagmires can actually be part of the mire-wide water track system and generally serve as pathways of preferential water flow.

The quagmires and water tracks described in this study seem directly comparable to the mire "mud-bottoms" and "carpets", respectively, described by Sjörs (1950b) and Nordqvist (1950) in Swedish mires. Variance in species composition occurs between South Park and Swedish and Minnesotan water tracks and quagmires, but important indicator species such as *Scorpidium scorpioides, Triglochin palustris, T. maritima,* and *Utricularia intermedia* are present in most cases. Interestingly, unlike in the Minnesotan and Swedish fens (Nordqvist 1950, Sjörs 1950b, Glaser et al. 1990), *Carex limosa* and *Eriophorum angustifolium* did not occur in the these water tracks, although the species are present elsewhere in South Park fens.

At the other extreme of the water table gradient are the meadow/dry fen sites (Fig. 2.14). Such sites are located on either organic or mineral soils and are dominated by graminoids, such as *Deschampsia cespitosa*, *Juncus arcticus* and *Elymus trachycaulus*, and low forbs like *Argentina anserina*, *Antennaria microphylla* and *Polygonum bistorta* are common. Sedges are not as prevalent as in other vegetational types, their distribution being confined to the wetter areas within by the dry fen releves. Plant species growing in such areas must be able to withstand large fluctuations in the water table, with standing water often being present early and late in the growing season and water table depressions of a meter or more during July and August (Appendix 5). Such conditions create a mixed flora with presence of upland species able to survive temporary anoxic soil conditions due to flooding, and wetland species capable of surviving and competing during water table drawdowns.

High Creek Fen releve 30 is included within the meadow/dry fen group but is distinct from other releves in that it has a nearly closed canopy of blue spruce (*Picea pungens*). This was the only releve with any tree coverage and the tree canopy composition was not included in the TWINSPAN data. Placement of this small forested site within a meadow class is artificial, but while the canopy is different from other meadow releves, the understory composition is relatively similar which led to the reported grouping. At the next division of the TWINSPAN, this releve was separated from the others (not shown).

Mire Margin to Expanse

The margin-expanse gradient is best represented in the DCA (Fig. 2.14), where marginal releves are located towards either end of axis 2 and expanse sites are located near the center. Mire margin and expanse communities are also well represented in the TWINSPAN wherein the releves in the carr subclass are located toward the margins, while most lawn releves are within the expanses. Factors driving the margin-expanse gradient are not clear in the CCA, and this gradient is not readily apparent in Fig. 2.17. The shift from willow carr to open carr to fen expanse on Crooked Creek Fen is visually evident, however, and is clearly displayed by the DCA. There are two likely explanations for the absence of the margin-expanse gradient in the CCA. Either environmental factors relative to this gradient were not measured, or this within-site gradient was masked by stronger between-site gradients. The second option seems more likely in this case. Factors generally related to this gradient were measured (e.g. Jeglum and He 1995) and a CCA including only releves from Crooked Creek Fen (not shown) showed the mire margin-expanse gradient as axis 1. Based on the Crooked Creek Fen CCA, marginal sites are associated with nutrient-rich soils high in iron, calcium, manganese, and potassium, while expanse sites have higher pH pore waters. This suggests that, as has been noted in other studies, nutrient levels of soils and waters decrease from the margin to the expanse due to plant uptake and adsorption to the peat (Gorham 1957, Moore and Bellamy 1974).

The other pole of the margin-expanse gradient is located at the bottom of DCA axis 2 which includes marginal, meadow/dry fen and fen lawn releves not having a significant shrub component. Segregation of these sites from the fen expanse can be seen in the CCA

(Fig. 2.17). These marginal sites are associated with relatively low water tables, high soil and water EC, and high soil sodium and magnesium. Significant hummock-hollow development is also generally present. Physiognomically and vegetationally these sites are different from the mire margin communities described by other authors in that a shrub canopy is not present. While visual differentiation of this type of marginal vegetation is more difficult than when gross changes in physiognomy occur, these marginal communities are an important component of fens in this region.

The bulk of releves fall into one of the fen lawn subclasses or associations, the majority of which are located within the mire expanse. Most of these sites are located in the left half of the CCA, with a segregation of High Creek Fen releves in the upper quadrant and Crooked Creek and Fremont's Fen releves in the lower quadrant. Because of the overriding influence of intra-regional changes in vegetation, gradients within these fen expanses are largely obscured.

Two lawn subclasses possessing poorly developed microtopography (fen lawns; Fig. 2.5) were produced in the TWINSPAN, although, they were not differentiated by name. The first of these subclasses seems to not be a natural grouping, but rather a repository for two somewhat unique vegetation types, while the second is a logical grouping of related releves. Crooked Creek releve 7 was located on a upwelling apron and is dominated by extremely rich fen lawn species, but it also has a significant cover of bog birch (*Betula glandulosa*) which sets it apart from the other extremely rich fen communities. High Creek Fen releve 15 quite is similar to Crooked Creek releve 7, but it also posses a population of the sedge *Carex* *livida*. This was the only releve which contained this species, thereby making it distinct in the TWINSPAN.

The mire margin-expanse gradient is essentially a synthetic spatial representation of underlying environmental gradients. On these fens it can be related to within-site changes in water and soil chemistry, and hydrology. As described above, little of this gradient is shown in the CCA, which raises a question regarding axis comparison between the DCA and CCA. Axis correlations (Table 2.6) suggest that CCA axis 2 most closely represents DCA axis 3 (Fig. 2.15). Comparison of the ordination diagrams suggests the same, although the CCA axis 2 is a mirror image of DCA axis 3, since they are negatively correlated. The second axis of the CCA is mainly driven by changes in soil and water chemistry. Its significant correlation with all DCA axes highlights the pervading influence of these factors on mire species composition.

The presence of a mire margin-expanse gradient has been well documented in the peatland literature (e.g. Sjörs 1948, Du Rietz 1949, Sjörs 1950b, Moore and Bellamy 1974, Malmer 1986, Jeglum and He 1995, Pakarinen 1995, Johnson 1996b). The importance of this gradient at the mires examined during this study and its similarity to that described in a Montana calcareous fen (Lesica 1986) refutes the assertion of Cooper (1996) that this gradient is unimportant in Rocky Mountain calcareous fens.

Regional Patterns

The unique combination of site characteristics makes each fen somewhat distinct, and regional differences are evident in the analyses. A PCA based on soil chemistry entirely separated High Creek Fen sites from Crooked Creek Fen sites, with interspersion of Fremont's Fen sites into each group (Johnson 1998). The differences in soil chemistry likely result from the differing geological and geomorphological settings of each fen. High Creek Fen lies on the Maroon Formation overlain with Quaternary alluvium derived primarily from the Maroon, Belden and Coffman Formations (Stark et al. 1949, Singewald 1950, Tweto 1974). These formations are composed of limestones, sandstones, dolomites, and shales. Fifteen meter thick gypsiferous strata have also mapped in the vicinity of High Creek Fen (Appel 1995). Fremont's Fen also lies on Quaternary alluvium, but this fen spans several different formations which form north-south oriented beds (U.S.G.S., Milligan Lakes Geologic Map). The deposits on which Fremont's Fen sits include the South Park, Laramie, Foxhills, and Reinecker Ridge Formations, the Pierre Shale and Eshe Porphyry. Fewer limestone beds occur in these members, and they include range of deposits primarily sandstone, shale, volcanically derived, and coal. The variation in underlying geology likely gives rise to the wide range of ground water characteristics found on Fremont's Fen.

Unlike the other two sites, Crooked Creek Fen lies in a trough underlain by red, arkosic sandstone bedrock of the Maroon formation (Stark et al. 1949). Inter-bedded in this sandstone are limestone and dolomite strata. Another difference of Crooked Creek Fen is that beaver have had a strong influence on its formation and expansion. As evidenced by lacustrine strata in soil cores, many of the peat aprons and fen expanse sites were at one time beaver ponds. Abandoned beaver ponds that are undergoing this type of terrestrialization (*Verlandung*, *sensu* Weber 1908) are currently found at the head of the mire (Fig 1.15). Beaver activity has not occurred at either of the other fens.

While such regional differences exist between these calcareous fens, they are all floristically related, possessing a large number of calciphilous species indicative of extremely rich fen conditions. All sites also have water and soils considerably more nutrient rich and alkaline than other Rocky Mountain fens. The majority of southern Rocky Mountain subalpine fens are found in granitic basins and are typically classified as moderate or transitional fens, having pHs between 5.0 - 6.7, calcium concentrations between 1.4 and 15 mg/l, and ECs between 13 and 52 μS (Cooper and Andrus 1994, Cooper 1996, Johnson 1996b; see also Table 1.2, pg. 23). The typical subalpine transitional fens have many species in common with the extremely rich fens such as *Carex aquatilis, C. rostrata, Salix planifolia, Salix monticola, Eriophorum angustifolium* and *Pedicularis groenlandica* (Chee and Vitt 1989, Cooper 1990, Cooper and Andrus 1994, Johnson 1996a). However, these generalist species can be found in virtually all Rocky Mountain fen environments, and therefore, while such species may be common or even dominate areas within extremely rich fens, their presence is non-diagnostic of extremely rich fen conditions. Consequently, the pervading floristic composition of these fens may mislead investigators if classifications are based on dominant species alone. This fact highlights Gorham (1950)and Wheeler's (1980) assertions that it is not the presence of single species that is important to fen classification, but rather the suite of species present.

Conclusions

The three calcareous mires studied are classified as rich to extremely rich fen complexes based on water chemistry and indicator species criteria. Mean calcium concentration on these fens is 115 mg/l, EC averages 575 µS and mean pH is 7.4. Such characteristics illustrate the alkaline, nutrient-rich environment of South Park's calcareous mires. Because of the rarity of such conditions in the southern Rocky Mountains, a large number of rare or regionally endemic plant species grow in these mires. A list of species with a high fidelity for extremely rich fen conditions was developed, although single species were frequently found to be inconclusive indicators of such conditions. Instead, suites of species should be used to infer minerotrophy.

Mire vegetation was classified into five classes, eight subclasses, and twelve associations. Within sites, these vegetation types respond to four primary gradients: depth to the water table, microtopography, position relative to the mire margin or expanse, and soil and water chemistry. There is also a regional vegetation gradient present attributed to geologic and geomorphic differences between sites. Regional differences had a strong effect on mire vegetation and made the vegetational composition of each site distinct, even though many of the same extremely rich fen indicator species were present at each site.

CHAPTER III

THE ENVIRONMENTAL IMPACTS OF PEAT MINING AND DRAINAGE ON CALCAREOUS FENS IN SOUTH PARK, COLORADO

ABSTRACT

The environmental impacts of peat mining and drainage were examined in three calcareous fens in Park County, Colorado. Each fen had both intact and mined or drained areas. Large impacts due to peat mining are still present several years after the cessation of mining. In areas receiving no post-mine reclamation, vegetational coverage and species richness were markedly different from the intact fen. In areas regraded with stockpiled peat, species richness was not significantly different from intact areas, and vegetational cover was approaching that of the intact fen. Mined plots were segregated from intact plots on a detrended correspondence analysis illustrating the differences in species composition between the two areas. Impacts to the abiotic environment are apparent in mined areas. Surficial microtopography was greatly diminished or eliminated by mining. Soil porosity, bulk density and chemistry, and water quality were also affected by mining.

Drainage by ditching significantly altered most aspects of the fen ecosystem. Species richness was significantly reduced and few fen species are present in the drained area.

Microtopography, characteristic of fens, is absent in the drained area and physical soil attributes have been altered. Ground water uranium concentration is elevated at both a mined fen and in the drained fen. Release of uranium held in the soils results from the change in the soil environment caused by mining and ditching. This study shows the that Rocky Mountain fens are highly susceptible to anthropogenic impacts and that these impacts may not be mitigable in a meaningful time frame.

INTRODUCTION

The calcareous fens of South Park, Colorado are an important biological and environmental resource of the southern Rocky Mountains (Cooper 1996, Johnson 1996a, Sanderson and March 1996), yet approximately 20 % of these fens have been seriously impacted by peat mining, and an unknown percentage have been damaged by draining (Sanderson and March 1996). Although both of these practices cause an obvious disturbance to the area the actual biotic and environmental impacts caused by these activities have not been investigated.

This lack of information significantly impairs the ability of land managers to objectively evaluate permit applications for projects potentially impacting fens. An assessment and description of the changes associated with mining and drainage is also a logical first step towards the design of effective fen restoration strategies. The floristic value of the South Park's calcareous fens, coupled with the likelihood of future development pressures in the area, has created a need to initially focus on calcareous fens. But South Park's fens may also provide good models of the nature of impacts caused by mining, ditching, and related land uses in subalpine fens in general, since similar ecological processes are important on subalpine fens throughout the Rocky Mountains (Chapter 2, Cooper and Andrus 1994, Johnson 1996b).

This study comparatively examines three calcareous fens in South Park, Colorado, each of which has areas that are essentially intact and other areas that have been historically impacted by peat mining or drainage by ditching. The specific goals of this study are to: (1) contrast the vegetational composition of intact fens with that of impacted fens; and (2) describe the on-site environmental effects of peat mining and ditching including changes in the water, soil, and hydrologic factors that result from these practices.

METHODS

The sites and field methods used in this study are consistent with those described in the previous two chapters. Three fens were examined, each having areas that are either intact or impacted by a historical land use. Treatment after impact has also varied. Portions of High Creek Fen were mined for peat during the 1970's and 1980's. During the procedure, a portion of the mined peat was mishandled and devalued, and consequently abandoned as spoils near the mine pit. After The Nature Conservancy (TNC) acquired the fen in 1992, the mine was regraded using the spoiled peat, and returned to roughly the same grade as prior to mining (Allen Carpenter, TNC, 1995, pers. comm.).

Fremont's Fen was extensively peat mined, although intact portions of fen still remain. During the mining process, a series of drainage ditches and roads were constructed that crisscross the mined part of the fen. The exact age of the mine is not known, nor is the date that it was abandoned, but mining ceased at least 15 years ago based on residents' accounts.

The majority of Crooked Creek Fen is intact except that portion which is below a single ditch which bisects the fen perpendicular to its slope. The position and orientation of the ditch makes Crooked Creek Fen an ideal situation in which to compare intact fen to drained fen. The ditch bisecting the fen intercepts virtually all ground water to a depth of between one and one and a half meters and carries it off site. The locations and extents of these impacts can be seen in Figs. 2.2 - 2.4 (pgs. 69 - 71). Refer to Chapters One and Two for additional details of the study fens and the South Park region.

At each fen a matrix of environmental sampling points, consisting of a shallow ground water well and one or more piezometers, was installed in 1995 or 1996. Thirty-four stations were placed at High Creek Fen (Fig. 2.2), twenty-seven at Crooked Creek Fen (Fig. 2.3), and twenty-four at Fremont's Fen (Fig. 2.4). To facilitate comparison of impacted and non-impacted areas, several sampling points at each fen were located in areas that had been either mined for peat or drained. Impacted areas were sampled with approximately the same spatial intensity as intact areas. Because impacted fen areas were less extensive than the intact areas, fewer samples were taken in the impacted compared to the intact areas. At High Creek Fen, seven stations were located in mined areas, although at one station (HC 31) no water measurements were made. At Fremont's Fen five stations were located in mined areas, while at Crooked Creek Fen four stations were located in the drained area.

The vegetational and environmental characteristics present at each sampling point were assessed using the methods described in Chapter 2 (pg. 66). In addition to the environmental parameters described in Chapter 2, soil porosity and dry bulk density were measured. For measurement of porosity and bulk density, a sample was extracted from the upper 20 cm of the soil at each sampling station. Samples were obtained using a 5 cm diameter piston corer. This corer is designed to extract samples from saturated soils with minimum compression. Once extracted, the lower portion of the sample was cutoff flush with the bottom of the corer, the sample was removed from the corer and then the sample top was trimmed to remove vegetation and create a flat surface.

In a lab at CSU, soil samples were placed in filter paper baskets, saturated in deoxygenated water and weighed on an electronic balance. Samples were then dried to a constant weight at 105 °C. Bulk density was calculated by dividing the sample's dry weight by its volume. Porosity was measured as the volumetric water content of the soil at saturation using the formula:

$$\frac{(SaturatedSampleWeight - DrySampleWeight)}{SampleVolume}$$

Data Analysis

Detrended correspondence analysis (DCA) from the Canoco 4.0 program was used to reconstruct vegetation gradients and examine the effects of disturbance on vegetation composition (Ter Braak and Smilauer 1998). Ordination axes were detrended using twenty-six segments, and the biplot scaling option was in effect. Before the ordination was performed, species scores were log transformed using a log (x+1) transformation. Since only frequency data were available for moss species, these species were given zero weight in the analysis, although total moss coverage was active in the ordination.

The differences between the edaphic, surficial and vegetational characteristics of impacted and intact fen areas were tested using two-sample t-tests. Separate-variance p-values were used since variances tended to be unequal owing to the disparity in sample sizes. Non-parametric, Mann-Whitney U-tests were used to test for differences in water chemistry between mined and intact areas since the number of mined water chemistry sample sizes was small and non-normally distributed. A one-sample t-test was used to identify significant water chemistry differences between the drained and intact portion of the Crooked Creek Fen.

Sample stations located in the intact fen areas encompass a wide variety of habitats with a large variance in environmental conditions (Chapter 2). Because this large variance reduces the resolution of statistical tests, p-values less than 0.10 are here considered significant.

A microtopographical index was created to synthesize the effects of both hummock height and total coverage within a releve. The index was calculated by standardizing hummock height and percent coverage by dividing by each's respective standard deviation. The two standardized values were then averaged to produce the index score.

RESULTS

The Effects of Disturbance on Fen Water Tables

The water table in mined areas of High Creek Fen was on the average deeper than that in intact areas (Fig. 3.1), but at Fremont's Fen water table depth was equivalent in mined and un-mined areas. To contrast the relative stability of water table heights, water table standard deviations were compared using two-sample t-tests. On High Creek Fen, water tables in mined areas showed a higher degree of fluctuation compared to water tables within intact portions of the fen (Fig. 3.1). On Fremont's Fen water table fluctuations were not significantly different.

The drained section of Crooked Creek Fen possesses a significantly deeper water table than either the intact portions of Crooked Creek Fen or the other two sites (Fig. 3.1). Water table fluctuations were also larger in the drained portion of Crooked Creek Fen.

Ordination of Fen Vegetation

Alteration of fen vegetation is perhaps the most obvious effect of peat mining or drainage. In all areas, differences in vegetational composition and structure were still visually obvious fifteen or more years after the initial disturbances. Figure 3.2 shows a DCA diagram of releves based on species composition. Releves from intact portions each fen tend to cluster near one another due to inter-site vegetational differences. The inter-site vegetational differences were discussed in Chapter 2. Separated from the intact releves are those that were located in areas impacted by peat mining and ditching. To the right of the diagram are

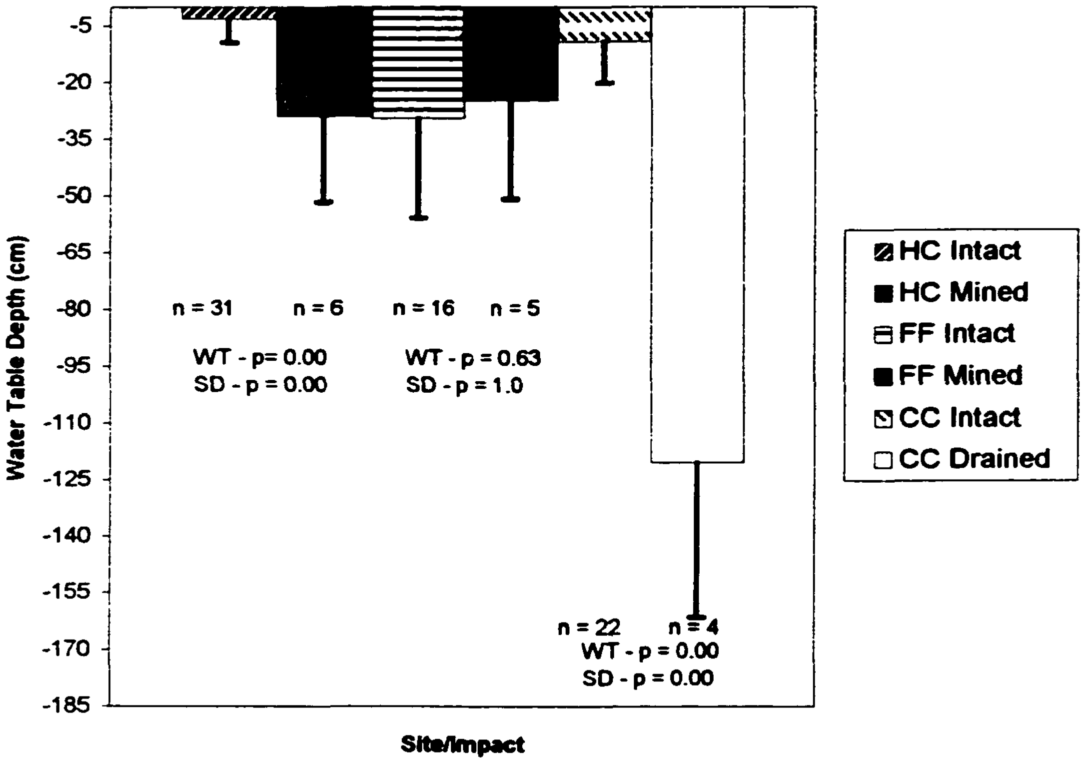

Figure 3.1. Mean water table depth in intact and impacted areas from 1995 to 1998 on High Creek Fen and 1996 to 1998 at the other sites. N is the number of wells in each category, WT is water table height and SD is standard deviation. Error bars are season standard deviations. P-values are for tests of differences between intact and impacted area water table depths and standard deviations.

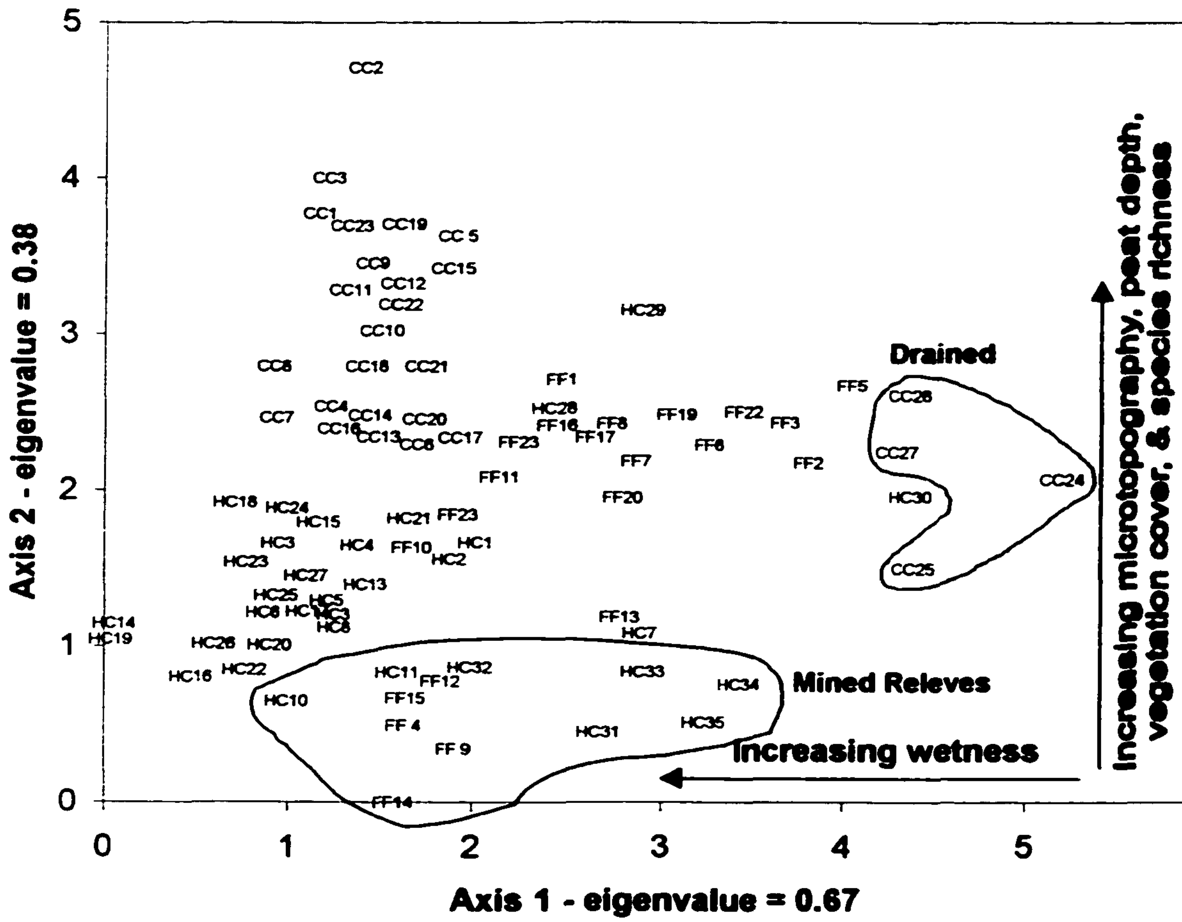

Figure 3.2. Detrended correspondence analysis of releves. Releves located in mined and drained areas have been enclosed in polygons. Labels have been placed over data points, but some labels have been shifted slightly for clarity.

clustered the drained releves, while mined releves are arrayed along axis 1 near the bottom of axis 2.

Axis 1 scores are highly significantly correlated with water table depth (p=0.00; Table 3.1), indicating that the axis primarily corresponds to a moisture gradient. The most hydric sites, including water-tracks and quagmires, are located to the left on axis 1 while the dry meadow and drained releves are plotted at the opposite end. Axis 2 (Fig. 3.2) contains the mire margin to expanse gradient evident in the ordinations from Chapter 2, but it also shows the vegetational effects of peat mining. Releve scores along axis 2 are significantly, positively correlated with total vegetation cover, microtopography, peat depth and species richness (Table 3.1), demonstrating that reduction of these factors is associated with peat mining.

The Effects of Mining on Vegetation

Vegetation cover is significantly lower in formerly mined as compared to unmined areas (Fig. 3.3). At Fremont's Fen very little vegetation grows within the mined expanses, while in the mined area of High Creek Fen reclaimed with spoiled peat, plant coverage is about two-thirds of that in intact areas. Species richness is significantly lower in the mined versus the intact portions of Fremont's Fen ($p = 0.00$), while in the mined and reclaimed areas of High Creek Fen, species richness is statistically similar to that of the intact fen ($p = 0.33$). The mined and reclaimed areas of High Creek Fen also have a higher species richness than that of mined areas on Fremont's Fen ($p = 0.01$; Table 3.2).

Table 3.1. Correlations of site factors with DCA axes. Correlation significance values are provided parenthetically and statistical significance is indicated by asterisks, where * is p<0.10 and ** is p<0.05 after Dunn-Sidak correction for multiple comparisons.

	Axis 1	Axis 2	Axis 3	Axis 4
Vegetation Coverage	0.18 (0.96)	0.66 (0.00**)	-0.48(0.00**)	-0.05 (1.00)
Species Richness	0.10 (1.00)	0.34 (0.05*)	-0.05 (1.00)	-0.08 (1.00)
Microtopography Index	-0.14 (1.00)	0.48 (0.00**)	0.03 (1.00)	-0.09 (1.00)
Peat Depth	-0.12 (1.00)	0.43 (0.00**)	-0.36 (0.02**)	0.20 (1.00)
Water Table Depth	-0.85 (0.00**)	-0.10 (0.99)	0.45 (0.00**)	-0.13 (0.94)

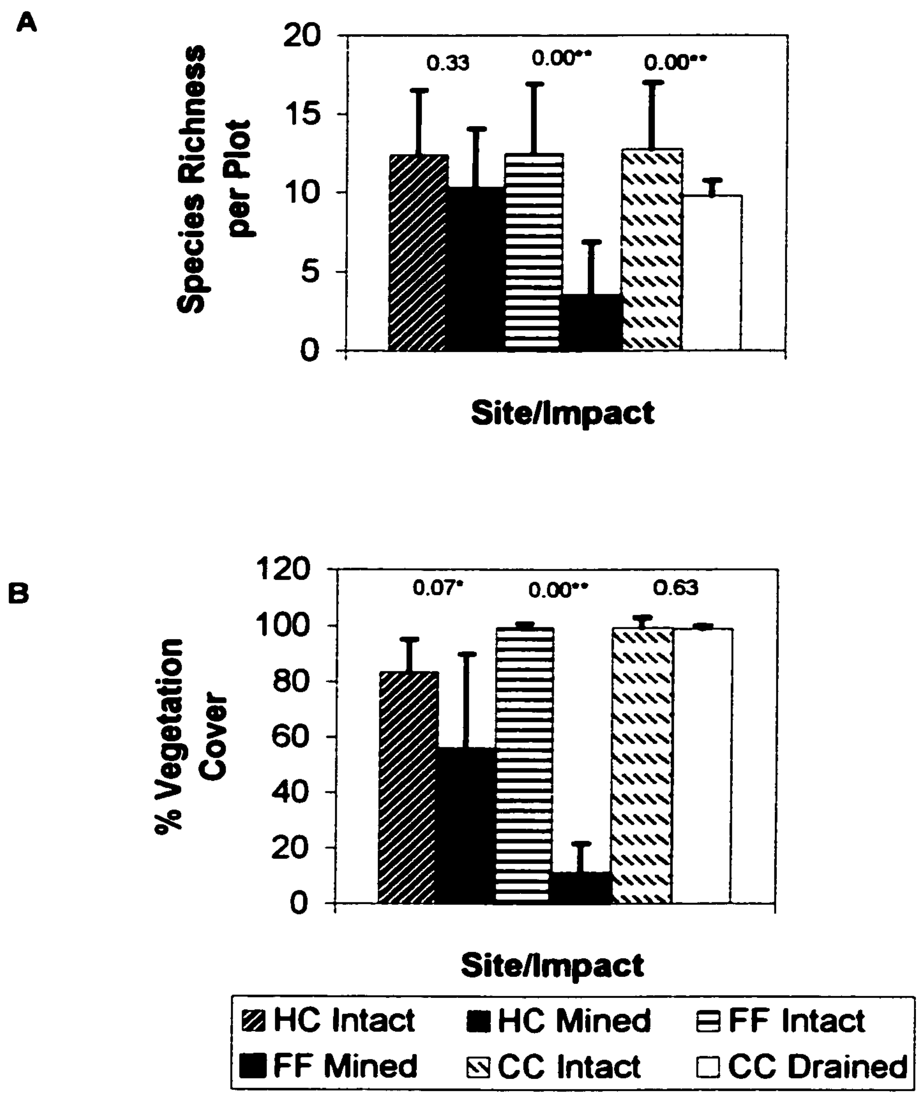

Figure 3.3. Summary bar graphs of site vegetational characteristics: (a) Mean species richness in releves grouped by site and impact; (b) Percent total vegetational coverage in releves grouped as above. Bars show the sample standard deviation. Numbers over bars are p-values from comparision of intact and impacted characteristics within sites. * indicates $p<0.10$, ** $p<0.05$. HC is High Creek Fen, FF is Fremont's Fen, and CC is Crooked Creek Fen.

Table 3.2. Significance values of Mann-Whitney U-tests comparing the environmental conditions present in mined and reclaimed areas of High Creek Fen and those of unreclaimed portions areas of Fremont's Fen. * is $p < 0.10$ and ** is $p<0.05$.

Parameter	HCM - FFM	HCI - FFI	HCI - CCI	FFI - CCI
W pH	0.36	0.23	0.00**	0.00**
W EC	0.06*	0.08*	0.00**	0.89
W Ca	0.06*	0.06*	0.80	0.19
W Mg	0.06*	0.00**	0.00**	0.23
W Na	0.64	0.00*	0.17	0.10*
W K	0.64	0.10*	0.17	0.41
W P	0.06*	0.00**	0.77	0.77
W Fe	0.36	0.01*	0.80	0.23
W Mn	0.36	0.33	0.16	0.69
W Sr	0.64	0.98	0.00**	0.00**
W U	0.06*	0.00**	1.00	0.00**
W V	0.14	0.06*	0.00**	0.55
W Ni	0.06*	0.00**	0.02**	0.08*
W Cr	0.14	0.00**	0.00**	0.07*
W B	0.06*	0.00**	0.00**	0.01**
W Ba	0.17	0.01*	0.00**	0.00**
W Si	0.06*	0.00**	0.04**	0.02**
S pH	0.01**	0.00**	0.00**	0.00**
S EC	0.17	0.51	0.00**	0.00**
S Ca	0.42	0.64	0.41	0.86
S Mg	0.03**	0.00**	0.00**	0.00**
S Na	0.03**	0.01**	0.39	0.00**
S K	0.57	0.34	0.50	0.96
S P	0.63	0.39	0.80	0.74
S Fe	0.11	0.00**	0.18	0.00**
S Mn	0.10*	0.03**	0.00**	0.20
S Sr	0.55	0.71	0.98	0.65
S U	0.07*	0.01**	0.03**	0.29
S Cu	0.92	0.11	0.09*	0.58
S Zn	0.24	0.02**	0.01**	0.00**
S NO_3	0.28	0.07*	0.18	0.17
S Pb	0.30	0.10*	0.09*	0.92
S $CaCO_3$	0.22	0.00**	0.02**	0.00**
Microtopography Index	0.21	0.08*	0.12	0.62
Peat Depth	0.68	0.00**	0.00**	0.00**
Dry Bulk Density	0.53	0.00**	0.08*	0.08*
Porosity	0.03*	0.31	0.52	0.66
Species Richness	0.01**	0.42	0.00**	0.03**
Vegetation Cover	0.01*	0.00**	0.00**	0.95
Organic Matter	0.14	0.14	0.06*	0.45

The mined areas at Fremont's and High Creek Fen share several species in common (Table 3.3), but overall their vegetation differs due to the post-mining reclamation activities employed (Figs. 3.4 & 3.5). The reclaimed peat mine at High Creek Fen is vegetated by a mix of perennial graminoid and forb species, such as *Deschampsia cespitosa, Juncus balticus, J. alpino-articulatus, Triglochin* spp., and *Argentina anserina*. Sedges are notably scarce within the reclaimed expanses and are generally only present near the mine margins where vegetative expansion has facilitated colonization. The species primarily responsible for revegetating the mined expanse of Fremont's Fen are *Agrostis scabra, Carex aquatilis, Deschampsia cespitosa,* and *Triglochin palustris.* Personal observations indicate that most of the revegetation at this fen has arisen from vegetative spread either from the intact vegetation on the mine margin, or from a small number of establishment events within the mine expanse (Fig. 3.5). The patterns and processes of revegetation were experimentally evaluated and will be discussed in the following chapter.

The Effects of Draining on Fen Vegetation

At Crooked Creek Fen, vegetation has been strongly affected by drainage. Areas which were presumably fen lawns have had their vegetation converted to that found in the mesic meadow releves (Fig. 3.2). The drained releves are dominated by perennial grasses and forbs such as *Poa pratensis, Hordeum jubatum, H. brachyantherum, Elymus trachycaulus, Juncus balticus, Argentina anserina* and *Artemisia frigida* (Table 3.3). The shrub *Pentaphylloides floribunda* is also quite common. This mesic grassland species composition contrasts strongly with the highly hydrophilic fen vegetation located only a few meters away

Table 3.3. Average species coverage at the three fens. Releve species abundance data have been grouped according to the site and impact type in which they were located. Raw cover values have been placed in Braun-Blanquet cover classes where: +<1%; 1 = 1-5%; 2= 6-25%; 3=26-50%, 4=51-75%; and 5= 76-100%. "P" indicates species presence when percent cover values were not obtained. HC is High Creek Fen, CC is Crooked Creek Fen, and FF is Fremont's Fen.

Species	Abbreviation	HC Intact	HC Mined	FF Intact	FF Mined	CC Intact	CC Drained
Achillea millefolium	ACHMIL			+	+		
Agrostis scabra	AGRSCA		1	+	1		
Agrostis stolonifera	AGRSTO			+			
Antennaria sp.	ANTSPP	+		+			
Alopecurus borealis	ALOBOR			1			
Argentina anserina	ARGANS	1	3	1	+	+	2
Artemisia frigida	ARTFRI			+			2
Astragalus agrestis	ASTAGR			1			
Aster lanceolatus	ASTLAN						
Aster occidentalis	ASTOCC		+	1			+
Betula glandulosa	BETGLA					+	
Calamagrostis canadensis	CALCAN	1		1	+	+	
Calamagrostis stricta	CALSTR			1	+		
Caltha leptosepala	CALLEP			+			
Campanula parryi	CAMPAR	+					
Carex aquatilis	CARAQU	2	1	2/3	1	3	
Carex aurea	CARAUR	+				+	
Carex capillaris	CARCAP			+			
Carex hallii	CARHAL	+		+		+	
Carex limosa	CARLIM					+	
Carex livida	CARLIV	+					
Carex microptera	CARMIC	+				+	
Carex microglochin	CARMIG	+					
Carex scirpoidea	CARSCI	1	+	+		+	
Carex simulata	CARSIM	2		2		2	
Carex utriculata	CARUTR	1	+	1		2/3	
Chenopodium redowskii	CHERED						
Cirsium arvense	CIRARV	+	+	+			+
Cirsium coloradense	CIRCOL	+	+	+			+
Conioselinum scopulorum	CONSCO	+				+	
Crepis runcinata	CRERUN	+	+	1	+		+
Danthonia sp.	DANSPP		+				
Deschampsia cespitosa	DESCES	1	2	3	1	1	1
Distegia involucrata	DISINV					+	
Dodecatheon pulchellum	DODPUL	+	+	+		+	
Eleocharis quinqueflora	ELEQUI	2	1	+		1	
Elymus trachycaulus	ELYTRA	1	1	1			2
Epilobium lactiflorum	EPILAC	+					
Epilobium spp.	EPISPP			+	+	+	
Equisetum arvense	EQUARV		+				
Equisetum spp	EQUSPP					+	

Species	Abbreviation	HC Intact	HC Mined	FF Intact	FF Mined	CC Intact	CC Drained
Erigeron lonchophyllus	ERILON	+					
Erigeron speciosus	ERISPE			+			
Eriophorum angustifolium	ERIANG	+					
Eriophorum gracile	ERIGRA					+	
Galium boreale	GALBOR	+				+	
Gentiana fremontii	GENFRE	+	+	+		+	
Gentian spp.	GENSPP			1		+	
Hierochloë hirta	HIEHIR	+	+	+			
Hordeum brachyantherum	HORBRA	1		1			1
Hordeum jubatum	HORJUB	1	+	+			1
Heterotheca pumila	HETPUM			+			
Juncus albescens	JUNALB					+	
Juncus alpinoarticulatus	JUNALP					+	
Juncus arcticus ssp. ater	JUNBAL	1	1	2		+	2
Juncus longistylis	JONLON		+			+	
Kobresia myosuroides	KOBMYO	1		2		1	
Kobresia simpliciuscula	KOBSIM	1	+	1		1	
Koeleria macrantha	KOLMAC		+	1		+	
Lappula redowskii	LAPRED						1
Lepidium ramosissimum	LEPRAM						+
Limnorchis hyperborea	LIMHYP	+				+	
Maianthemum amplexicaule	MAIAMP					+	
Moss sp.	MOSSPP	1		1		3	
Muhlenbergia richardsonis	MUHRIC	+		1			
Parnassia parviflora	PARPAR					+	
Pascopyrum smithii	PASSMI						1
Pedicularis crenulata	PEDCRE	+					
Pedicularis groenlandica	PEDGRO	+	+	+		+	
Potentilla fruticosa	PENFLO	+	+	+	+	1	1
Plantago eriopoda	PLAERI	+					
Poa compressus	POACOM		+	+			1
Poa glauciflorus	POAGLA		+				
Poa pratensis	POAPRA	+		1		+	3
Polygonum bistortioides	POLBIS	+		+		+	
Polygonum viviparum	POLVIV	+					
Polygonum arvense	POLARV						
Polemonium foliosissimum	POLFOL			+			
Potamogeton pectinatus	POTPEC	+					
Potentilla plattensis	POTPLA			+			
Potentilla subjuga	POTSUB	+	+	+			1
Primula egaliksensis	PRIEGA	+	+			+	
Primula incana	PRIINC	+	+	+			
Ptilagrostis porteri	PTIPOR			+			
Ranunculus cymbalaria	RANCYM		+			+	
Rumex spp.	RUMSPP	+		+			
Salix brachycarpa	SALBRA	+		1		2	
Salix candida	SALCAN	+				1	
Salix monticola	SALMON					1	+

Species	Abbreviation	HC Intact	HC Mined	FF Intact	FF Mined	CC Intact	CC Drained
Salix myrtillifolia	SALMYR	+		+		+	
Salix planifolia	SALPLA	+				2	
Saxifraga hirculus	SAXHIR						
Sedum rhodanthum	SEDRHO			+			
Stellaria longipes	STELON			+			
Swertia perennis	SWEPRE					+	
Sisyrinchium pallidum	SISPAL					+	
Taraxacum officinale	TAROFF	+	+	+			
Thalictrum alpinum	THAALP	1	+	1		1	
Trichophorum pumilum	TRIPUM	+				1	
Triglochin maritima	TRIMAR	1	1		+	+	
Triglochin palustris	TRIPAL	1	1		1		
Utricularia ochroleuca	UTROCH	+					
Valeriana edulis	VALEDU	+		+			
Viola adunca	VIOADU	+					
Zigadenus elegans	ZIGELA	+					
Brachythecium nelsonii	BRANEL			P		P	
Calliergon giganteum	CALGIG			P		P	
Calliergon stramineum	CALSTR					P	
Calliergon trifarium	CALTRI					P	
Campylium stellatum	CAMSTE					P	
Distichum capillare	DISCAP					P	
Drepanocladus aduncus	DREADU					P	
Drepanocladus revolvens	DREREV			P		P	
Philonotis fontana	PHIFON					P	
Mniobryum albicans	MNIABL					P	
Rhizomnium pseudopunctatum	RHIPSE			P		P	
Scorpidium turgescens	SCOTUR					P	
Scorpidium scorpiodes	SCOSCO	P				P	
Warnstorfia exannulata	WAREXA			P		P	

Figure 3.4. Revegetation on the mined portion of High Creek Fen that has been regraded with peat spoils. This photograph shows the extent of approximately four years of recovery.

Figure 3.5. View east across Fremont's Fen from the margin of the peat mine. Much of this area still lacks vegetation, although scattered clumps can be seen that have resulted from isolated establishment events.

in the intact portion of the fen (Fig. 3.6). The intact fen vegetation by comparison is dominated by hydrophilic fen species such mosses, sedges and willows (Chapter 2). These species are absent from the ditch impacted portion of the wetland.

Species richness in the drained area is 10 spp/plot which is significantly lower than the 13 spp/plot found in the intact areas (Fig. 3.3). Draining has had no detectable effect on total vegetational cover at Crooked Creek Fen, though ($p = 0.63$; Fig. 3.3).

Water Chemistry

Table 3.4 contains mean water chemistry values from releves grouped by site and impact type, the standard deviation of these samples, and p-values testing for differences between intact and impacted water chemistry values. Aluminum, titanium, lead, zinc, molybdenum, and cadmium concentrations were also measured but were below ICP detection levels in all or most of releves, so these parameters were not included in statistical analyses (see Appendix 3 for water chemistry values).

A number of water chemistry parameters differed between the three study sites (Table 3.2) indicating that each fen was influenced by ground emanating from different of geologic deposits. Therefore, within-fen comparisons of intact and impacted areas is more appropriate than grouping data according to impact type alone.

In general, systematic differences were not detected in the water chemistry of impacted versus intact areas (Table 3.4). Electrical conductivity and uranium concentration were found to be higher in the mined compared to intact portions of High Creek Fen, while manganese and chromium concentrations were lower. No significant differences between mined or intact fen

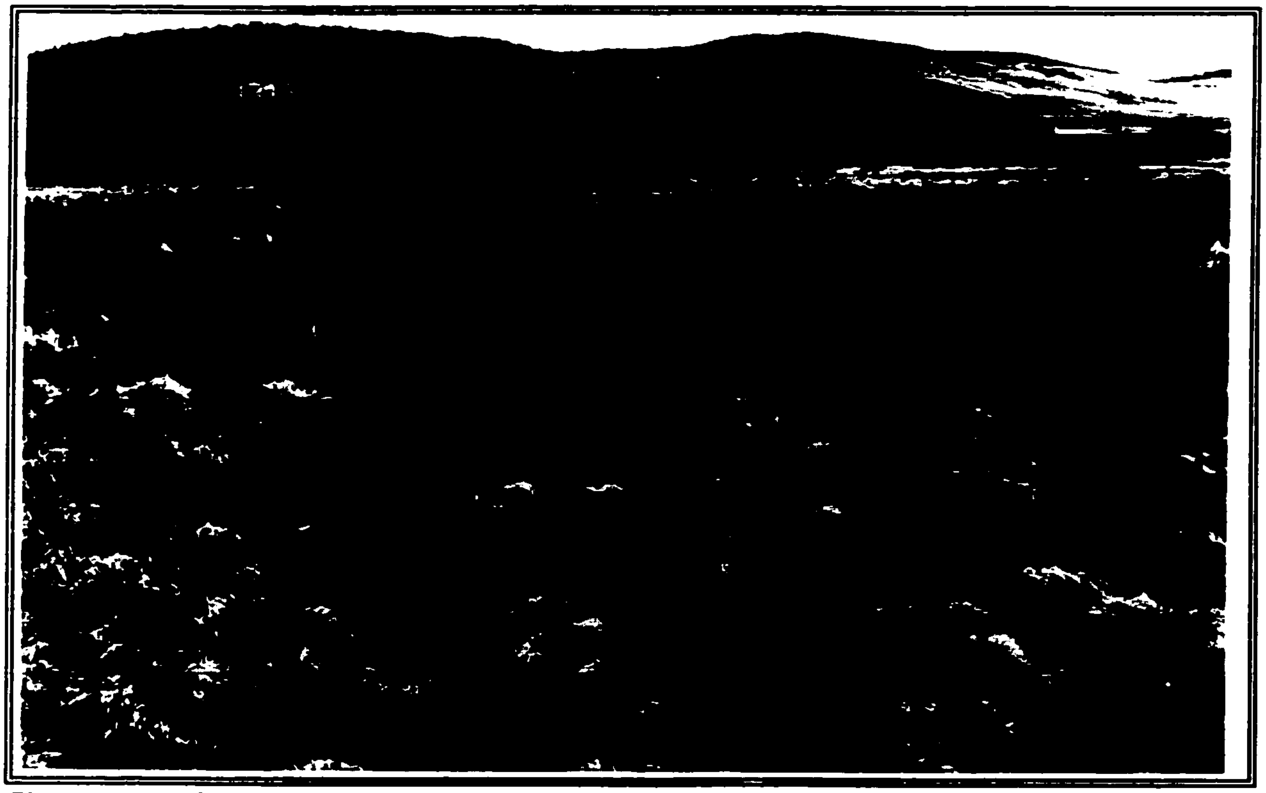

Figure 3.6. View southeast from near Crooked Creek Fen station 17. The path of the ditch can be seen near the middle of the photograph separating the hummocky, extremely rich fen vegetation from the mesic meadow vegetation that has resulted from draining.

Table 3.4. Mean water chemistry values for sites after releves had been grouped by site and impact. Units are mg/l except EC which is in micro siemens/cm^2. Mann-Whitney U-tests were used to compare intact versus impacted areas within fens, except in the case of Crooked Creek Fen where a one-sample t-test was used. Significance values of comparisons are given in the columns labeled "p". * indicates significance of $p < 0.10$, ** is significance of $p < 0.05$.

Site	pH	p	EC	p	Ca	p	Mg	p	Na	p	K	p
HC Intact, n=25	7.33 (0.24)	0.49	580 (150)	0.01**	114.74 (49.31)	0.66	39.05 (15.64)	0.95	7.54 (4.23)	0.23	0.95 (0.48)	0.53
HC Mined, n=4	7.37 (0.48)		730 (110)		120.89 (81.89)		48.29 (36.17)		10.80 (6.31)		1.63 (1.47)	
FF Intact, n=7	7.09 (0.47)	0.38	470 (220)	0.38	75.79 (71.20)	0.77	13.32 (10.42)	0.38	20.99 (15.16)	0.38	0.53 (0.55)	0.37
FF Mined, n=2	7.12 (0.04)		310 (20)		33.81 (2.53)		6.49 (1.40)		12.09 (5.13)		0.81 (0.51)	
CC Intact, n=21	7.75 (0.16)	0.23	460 (100)	0.08*	116.72 (43.98)	0.00**	17.14 (10.99)	0.00**	9.53 (12.17)	0.99	1.20 (2.04)	0.05*
CC Drained, n=1	7.36 (0.04)		370 (40)		190.52 (0.00)		25.28 (0.00)		9.58 (0.00)		0.26 (0.00)	

Site	P	p	Mn	p	V	p	Ni	p	Cr	p
HC Intact, n=25	0.10 (0.03)	0.90	0.05 (0.05)	0.06*	0.01 (0.00)	0.12	0.01 (0.00)	0.90	2.98 (1.48)	0.10*
HC Mined, n=4	0.12 (0.09)		0.02 (0.03)		0.01 (0.01)		0.01 (0.01)		1.50 (1.89)	
FF Intact, n=7	0.05 (0.02)	0.73	0.43 (1.00)	0.56	0.01 (0.00)	0.59	0.01 (0.00)	1.00	0.01 (0.01)	0.42
FF Mined, n=2	0.05 (0.00)		0.04 (0.04)		0.01 (0.00)		0.01 (0.00)		0.01 (0.00)	
CC Intact, n=21	0.11 (0.20)	0.00**	0.97 (1.76)	0.21	0.05 (0.20)	0.38	0.05 (0.20)	0.36	0.06 (0.20)	0.31
CC Drained, n=1	0.32 (0.00)		0.47 (0.00)		0.01 (0.00)		0.01 (0.00)		0.01 (0.00)	

Site	Sr	p	B	p	Ba	p	Si	p	U	p
HC Intact, n=25	0.33 (0.14)	0.41	0.17 (0.11)	0.80	0.17 (0.06)	0.23	6.85 (3.65)	0.15	0.0073 (0.0064)	0.06*
HC Mined, n=4	0.34 (0.22)		0.25 (0.34)		0.13 (0.05)		3.99 (2.70)		0.2430 (0.2829)	
FF Intact, n=7	0.50 (0.39)	0.38	0.05 (0.09)	0.64	0.08 (0.08)	0.77	14.82 (7.35)	0.38	0.0005 (0.0002)	0.08*
FF Mined, n=2	0.23 (0.03)		0.01 (0.00)		0.06 (0.05)		10.55 (1.05)		0.0008 (0.0003)	
CC Intact, n=21	0.14 (0.21)	0.00**	0.05 (0.19)	0.38	0.35 (0.18)	0.01**	8.87 (3.96)	0.01**	0.0062 (0.0060)	0.01**
CC Drained, n=1	0.35 (0.00)		0.01 (0.00)		0.23 (0.00)		6.15 (0.00)		0.0168 (0.0000)	

water chemistry were found on Fremont's Fen, except that uranium levels were marginally elevated in the mined areas. The water sample obtained in the drained portion of Crooked Creek Fen was found to have statistically higher concentrations of calcium, magnesium, phosphorous, strontium and uranium, and lower EC and concentrations of potassium, barium and silica than to the intact portions of that fen.

The most striking difference in water chemistry between the intact and impacted areas was in uranium concentration, particularly at High Creek Fen. Background ground water uranium levels measured in the intact portions of High Creek Fen averaged 0.0079 mg/l. Ground water uranium concentration within the peat mined areas was significantly higher ($p=0.06$) averaging 0.2430 mg/l, or approximately thirty times background levels (Table 3.5). In the 1995 samples, differences were even more extreme, with mined areas averaging more than 150 times the background uranium concentration (Table 3.5). Uranium concentrations were similarly elevated in surface water samples where background concentration was 0.0086 mg/l compared to 0.4151 mg/l in mined areas.

There is some evidence that elevated uranium levels are also associated with disturbance at the other two fens. At Fremont's Fen the difference in uranium concentration of ground water in the intact versus mined areas was marginally significant ($p = 0.08$; Table 3.4), but the average difference between the intact and mined areas was only 0.0003 mg/l. Therefore, if uranium levels at this fen are in fact elevated, the difference seems negligible. At Crooked Creek Fen, ground water uranium concentration in the drained area was nearly triple the fen's background level, which was significantly higher than the mean of intact samples based on a one-sample t-test ($p=0.01$; Table 3.4). Although this result was highly significant, it is based on only one sample from the drained area.

Table 3.5. Mean uranium concentration in ground water, surface water and soils at intact and mined portions of High Creek Fen. Parenthetical numbers are standard deviation; n = sample size. * indicates significance of $p < 0.10$, ** is significance of $p < 0.05$.

Sample Year	**1995**			**1996**			**1997**			$\bar{x}$		
Source/Site Condition	**Intact**	**Mined**	**p-value**	**Intact**	**Mined**	**p-value**	**Intact**	**Mined**	**p-value**	**Intact**	**Mined**	**p-value**
Ground Water (mg/l)	0.0028 (0.0043) , n=22	0.4430 (0.4624) , n=2	0.02**	n.a.	n.a.	n.a.	0.0118 (0.0196) , n=13	0.0430 (0.0470) , n=4	0.17	0.0079 (0.0064)	0.2430 (0.2829)	0.06*
Surface Water (mg/l)	0.0139 (0.0234) , n=7	0.652 (6901), n=2	0.04**	n.a.	n.a.	n.a.	0.0056 (0.0070) , n=7	0.0212 (0.2037) , n=2	0.14	0.0086 (0.0128)	0.4151 (0.6296)	0.07*
Soil (mg/kg)	16.12 (15.80), n=24	90.75 (57.16), n=4	0.00**	11.85 (9.35), n=10	39.93 (34.17), n=6	0.05*	12.38 (9.63), n=10	46.40 (55.33), n=6	0.06*	15.9 (14.3)	47.3 (45.7)	0.00**

Soil and Surface Characteristics

Table 3.6 contains mean soil chemistry values from releves grouped by site and impact type, the standard deviation of these samples, and the results of two-sample t-tests comparing intact and impacted soil chemistry values. As with water chemistry data, differences exist in soil characteristics between sites (Chapter 2) making discussion of effects of disturbance on individual sites more informative. Potassium, manganese, and calcium carbonate were significantly lower in the soils of mined as compared to unmined areas at both Fremont's Fen and High Creek Fen (Table 3.6). Electrical conductivity, phosphorous, calcium and lead were also found in significantly lower concentrations in the mined soils of one or the other fen, although the significance was not consistent between fens. Soil uranium concentration in mined portions of High Creek Fen was significantly higher ($p = 0.01$; Table 3.6) than the background level, on the average approximately four times it (Table 3.5).

Surficial and physical soil characteristics were strongly affected by peat mining (Fig. 3.7). Loss of microtopographic complexity was the most consistent effect of peat mining. Little hummock-hollow microtopography remains within the mined areas of both fens. At High Creek Fen, limited microtopography exists as a result of the regrading process and subsequent colonization by cespitose grasses such as *Deschampsia cespitosa* and *Agrostis* spp. Not surprisingly, peat depth was also affected by mining, although losses on an absolute scale were generally modest. At High Creek Fen, average peat depth was significantly reduced ($p = 0.01$) and the depth in mined areas was only about half of that in intact areas, but this resulted from only about a 20 cm loss of peat. At Fremont's Fen average peat

Table 3.6. Mean soil chemistry values for sites after releves had been grouped by site and condition. Units are mg/k unless otherwise noted.

Site	pH	p	EC (µ/S)	p	OM (%)	p	NO_3	p	P	p	K	p
HC Intact, n=28	7.19 (0.34)	0.13	1810 (540)	0.00**	50.1 (13.8)	0.02**	12.5 (4.3)	0.63	9.9 (5.3)	0.00**	116.27 (41.2)	0.05*
HC Mined, n=7	7.50 (0.45)		1220 (280)		35.2 (17.1)		13.5 (4.2)		4.9 (1.7)		76.92 (41.0)	
FF Intact, n=17	6.53 (0.57)	0.08*	1630 (1040)	0.45	57.3 (16.6)	0.20	25.5 (27.2)	0.40	8.5 (5.2)	0.23	137.49 (83.5)	0.00**
FF Mined, n=5	5.52 (0.96)		2100 (1170)		48.4 (11.2)		18.7 (9.1)		5.8 (3.6)		66.79 (15.0)	
CC Intact, n=23	7.67 (0.31)	0.42	630 (240)	0.00**	45.4 (19.1)	0.40	13.7 (5.1)	0.00**	9.2 (9.6)	0.41	141.21 (149.4)	0.06*
CC Drained, n=4	7.80 (0.23)		1510 (940)		54.3 (18.8)		300.2 (361.5)		13.4 (4.0)		78.28 (16.1)	

Site	Zn	p	Fe	p	Mn	p	Cu	p	Ca	p	Mg	p
HC Intact, n=28	8.8 (4.0)	0.82	414.0 (230.2)	0.23	15.8 (8.5)	0.09*	4.5 (1.4)	0.24	10586.5 (2291.7)	0.07*	1447.4 (498.1)	0.85
HC Mined, n=7	8.5 (3.1)		655.6 (469.4)		10.0 (4.0)		5.6 (2.3)		8534.1 (2373.2)		1475.6 (309.0)	
FF Intact, n=17	19.9 (16.5)	0.37	1045.4 (374.8)	0.51	50.4 (61.1)	0.09*	6.1 (3.9)	0.64	10200.5 (2841.7)	0.71	957.5 (411.8)	0.74
FF mined, n=5	14.4 (9.5)		1249.5 (613.2)		22.2 (13.0)		5.5 (1.9)		11531.7 (7328.0)		887.0 (407.4)	
CC Intact, n=23	6.4 (3.7)	0.00**	500.3 (261.7)	0.40	75.2 (53.3)	0.55	5.6 (2.4)	0.20	10004.3 (2172.3)	0.01**	571.5 (246.9)	0.00**
CC Drained, n=4	21.0 (13.7)		384.8 (111.2)		65.0 (24.9)		3.9 (1.1)		13478.7 (2584.6)		1021.1 (326.6)	

Site	Na	p	Sr	p	Pb	p	$CaCO_3$	p	U	p
HC Intact, n=28	119.0 (45.0)	0.83	166.8 (126.1)	0.27	31.9 (16.8)	0.14	19.2 (11.4)	0.00*	15.9 (14.3)	0.00
HC Mined, n=7	114.6 (48.0)		122.5 (80.1)		19.7 (8.6)		6.3 (5.9)		47.3 (45.7)	
FF Intact, n=17	292.7 (216.2)	0.67	155.6 (76.6)	0.83	24.2 (13.4)	0.08*	6.5 (5.3)	0.07*	8.3 (4.8)	0.76
FF mined, n=5	332.0 (154.5)		148.0 (63.5)		14.0 (8.9)		2.9 (3.0)		9.4 (6.9)	
CC Intact, n=23	105.5 (48.9)	0.41	163.8 (88.5)	0.47	24.4 (12.6)	0.16	27.7 (14.9)	0.54	9.7 (2.9)	
CC Drained, n=4	125.9 (40.2)		130.8 (16.2)		15.0 (7.8)		22.7 (16.9)		12.1 (9.0)	0.30

depth in mined areas was only four centimeters less than that in intact areas, and this difference was not statistically significant. This comparison is misleading, though, because the extensive mining which occurred at the site took place within the deep-peat areas of the fen. The remaining (intact) peat areas are essentially only those with peat that was too shallow to mine profitably. The actual reduction of peat depth by mining was probably much higher but undeterminable. This situation may be present to a lesser degree on High Creek Fen as well.

Soil bulk density was higher in mined fen areas, although the difference was only statistically significant on High Creek Fen (Fig. 3.7). As explained above in regards to peat depth, this lack of significant difference on Fremont's Fen is probably due to the removal of the highest quality, organic-rich peat during the mining process. Increases in the bulk density of mined soils results from the removal of the less decomposed, fibric upper peat layers and exposure of well decomposed, compact basal peat. As expected from the bulk density data, on High Creek Fen mined soils also showed a significant reduction in soil porosity.

Soils in the drained portion of Crooked Creek Fen were found to have significantly higher ECs and concentrations of nitrate, zinc, calcium and magnesium and lower concentrations of potassium compared to intact fen soils (Table 3.6). As in mined areas, loss of microtopography was the greatest surficial effect of draining (Fig. 3.7). Peat depths were not significantly different between the drained and undrained portion of Crooked Creek Fen. Because peat only accumulates in areas with perennially saturated soils, this corroborates the assertion that the drained portion of the fen once experienced hydrologic conditions similar

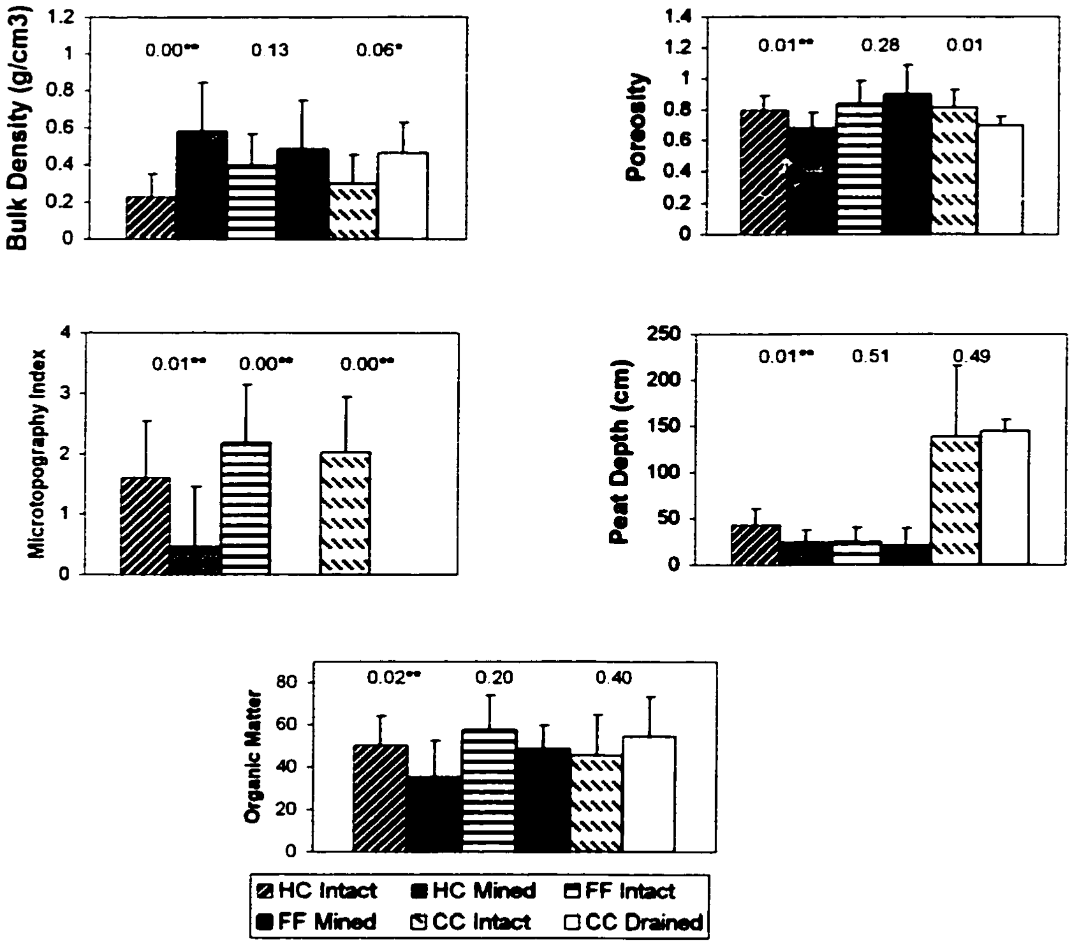

Figure 3.7. Mean physical soil and microtopographical characteristics for releves grouped by site and impact. Error bars show the sample standard deviation. Numbers over bars are p-values from comparision of intact and impacted characteristics within sites. * indicates $p<0.10$, ** $p<0.05$. HC is High Creek Fen, FF is Fremont's Fen, and CC is Crooked Creek Fen.

to the intact portions of the fen. The mean bulk density of drained soils was higher and the porosity lower than that of intact soils, indicating that collapse of soil structure is occurring in the drained organic soils (Fig. 3.7).

DISCUSSION

The Effects of Peat Mining on the Fen Environment

Peat mining imposes considerable deleterious effects on most aspects of the fen ecosystem by reducing vegetation cover and species richness (Fig. 3.3), altering species composition (Fig. 3.2), eliminating microtopography and altering edaphic properties (Figs. 3.7). Mining can also alter aspects of the soil and ground water chemical environment (Tables 3.4 to 3.6) These disturbances seriously impair the fen's ability to perform many of its natural environmental functions such as provision of plant species habitat, short-term water storage and water quality improvement. Most of the effects of mining noted in this study are consistent with those described in studies of boreal peatlands (Brooks and Predmore 1978, Paine et al. 1987, Salonen 1991, Salonen et al. 1991, LaRose et al. 1997).

The loss of vegetative cover is perhaps the most apparent impact of mining. Since peat mining is a surface, or strip-mining method, virtually all plant life along with the soil propagule bank is removed from the utilized area. Revegetation of mine sites, at best, takes several years with extensive post-mining reclamation, while the time for natural revegetation to occur is on the order of decades. On Fremont's Fen, where no restoration has been attempted, much of the mined area is still barren even after at least 15 years (Fig. 3.3). Revegetation on this site has been predominantly through vegetative expansion of a few species from the intact mine perimeter, augmented by isolated establishment events in the mined expanse (Pers. obs.). This type of protracted natural revegetation appears to be the norm in abandoned mines based on a comparison of this study's findings with those of other investigators (e.g. Salonen et al. 1991). Additionally, as Salonen et al. (1991) observed, the vegetation that does invade tends to be species-poor and highly patchy in its distribution which well fits the observations of the current study.

At High Creek Fen where peat spoils were regraded over much of the mined area, revegetation has been much more rapid. Plant cover is much higher than at Fremont's Fen, cover is more uniform, and species richness is of the level found in the intact fen (Figs. 3.3 -3.5). These improvements have come about in approximately five years. Species composition still differs between the impacted and intact portions of High Creek Fen, with the impacted area having a higher cover of grasses and forb species (Table 3.3); fortunately, the majority of pioneering species are native to intact fens. Based on these results, reintroduction of native fen topsoil to peat mines greatly improves the revegetation of mined sites. Further consideration of revegetation after disturbance is provided in the following chapter.

Peat mining also has significant effects on abiotic aspects of the fen environment. The most universal effects are on those processes regulated by the fen surface and peat body. In the course of mining all natural microtopography is removed. Microtopography, in the case of South Park fens, is mainly comprised of hummocks and hollows. These features create surficial roughness which strongly influences short-term water storage and reduction of surface water flow velocity (Brooks and Predmore 1978). Thus, elimination of this topography reduces the fen's ability to buffer spikes in the flow volume of outlet streams and diminishes the water storage properties of the fen.

Loss of the peat body through extraction causes the greatest reductions in water storage since the peat is the primary organ of water storage on the fens. Porosity, a measure of the water holding capacity of soils, was found to average between 0.79 and 0.89, indicating that 79 to 89 % of the soil profile consists of water at saturation. Consequently, removal of a given volume of peat removes an amount of water storage capacity from the wetland equivalent to the excavated volume times the soil porosity.

Investigators have observed that removal of a substantial portion of the peat body and its inherent storage capacity can also lead to more erratic water table behavior or increased surface water depth (LaRose et al. 1997 and references therein). At High Creek Fen, the water table fluctuates more in mined than in intact areas (Fig. 3.1), but these mined areas were located on the fen margin which normally has a deeper more variable water table than the fen expanse. On Fremont's Fen no disparity in water table fluctuations between mined and unmined areas was evident (Fig. 3.1). These results seem at odds with LaRose et al. (1997), however, the sampling interval of this study was too coarse to pick up short-term water table changes resulting from storms and instead focused on seasonal changes in water levels. Also, the previous studies of mined peatland hydrology (LaRose et al. 1997 and references therein) primarily considered ombrotrophic systems, and highly minerotrophic peatlands such as South Park's have different hydrologic regimes since the comparatively consistent ground water inputs buffer the effect of irregular atmospheric inputs. Thus, it is inconclusive whether mining generally increases water table fluctuation on these subalpine fens. Examination of the short-term hydrologic effects of mining would be valuable in developing a more complete picture of the effects of peat mining.

While changes in water table variability are uncertain, alteration of surface water patterns were evident. At stations 10 and 11 in the mined portion of High Creek Fen, troughs formed by peat extraction still exist. In these troughs, surface water tended to pond early and late in the growing season, flooding that area and inhibiting plant growth. In mined areas of Fremont's Fen, alterations of surface water behavior were also noted. In most subalpine fens when surface water is present, it blankets the fen and flows across its surface as diffuse sheet flow, although some distinct channels can be present as well. This diffuse surface flow, caused by the shallow slope and dense vegetation, distributes water across the wetland and helps maintain an equable water content in the peat body. On Fremont's Fen, surface water has become channelized into numerous rivulets which have incised into the soft, denuded peat. This water is not available to the expanses between these channels, and these expanses are often prone to surface desiccation. This pattern of surface water distribution may inhibit the establishment of fen species which are sensitive to soil moisture depletions.

While impacts to fen vegetation and hydrology brought on by mining are the most pronounced, aspects of water quality can also be affected. Wetlands have generally been noted to enhance the quality of water flowing through them. One way this improvement is effected is by the reduction of surface water velocity which causes suspended particles to settle out of the water column and eventually be incorporated into the soil profile. This mode of water quality enhancement occurs on calcareous fens, as well as other fens in the Rocky Mountains, as evidenced by the high mineral content of the peat and occasional mineral strata present in peat profiles (Wilson 1969, Cooper 1990). The loss of microtopography and vegetation, as well as channelization, all hinder the ability of impacted wetlands to improve water quality in this fashion because of the resultant higher surface water velocities. Quantification of this attribute was beyond the scope of this study, however.

Various ground water parameters were altered by peat mining, but the particular effects varied between sites (Table 3.4). This is seemingly due to natural differences in the ground water chemistry between each fen resulting from their distinct geologic settings (Chapter 2). As a result of these site specific effects, generalized patterns in water chemistry alteration cannot be formulated. Disturbance mediated elevation of uranium will be considered in a separate section.

Differences in soil characteristics of mined sites versus unmined areas were more common than differences in water chemistry (Table 3.6). Typically, metal content in mined peat was lower than in intact peat suggesting that metals are being leached from the newly exposed soils. Such leaching could result when formerly anoxic peat is exhumed and becomes oxidized, which changes in the redox potential of the soil. If such leaching is occurring, changes in water quality may have been more pronounced nearer to the time of initial impact.

The Effects of Drainage on the Fen Environment

The presence of the ditch on Crooked Creek Fen causes an abrupt increase in the depth to the water table (Fig. 3.1). This altered hydrologic regime also has more extreme fluctuations in the water table compared to the intact portions of the fen. The increased fluctuations likely result from the larger role that irregular atmospheric inputs play in the drained fen hydrology.

Vegetation in the ditch-impacted part of the fen consists of those species common to mesic grasslands in the Rocky Mountains, such as *Elymus trachycaulus*, *Poa pratensis*, *Hordeum brachyantherum*, and *Pentaphylloides floribunda*. All of the characteristic calcareous fen species, most notably the sedges and willows, are absent from the drained fen. Also missing are the brown mosses, which are abundant in the intact portion of Crooked Creek Fen. The exact vegetational composition before draining cannot be known, but it was presumably similar to that which currently exists in the fen above the ditch, since there is no environmental feature other than the ditch that would cause an abrupt ecological change, and the drained soils are composed of fibric peat of approximately the same depth as in the intact portions of the fen.

Although some differences exist between intact and drained soil and water chemistry, consistent patterns are not currently evident. Some parameters are elevated and some reduced in the drained as compared to the intact fen. Brooks and Predmore (1978) point out that upon initiation of drainage a large initial flux of chemicals, colloids and particles may be exported from the affected wetland. If such was the case at Crooked Creek Fen, these effects have already been attenuated.

The elevated nitrate and uranium concentrations found in the drained area do seem directly attributable to the effects of drainage. At pHs between 3 and 7, under reduced conditions of 0 - 400 mV, ammonium is the dominant form of nitrogen (Waughman 1980).

Under more alkaline and oxidized conditions nitrate becomes the dominate nitrogen form. Because of these characteristics ammonium is predicted to be the most common form of nitrogen in fens, with nitrate being comparatively diffuse (Waughman 1980, Sikora and Keeney 1983). At Crooked Creek Fen, mean nitrate concentration in the oxidized, drained peat was 300.2 mg/l, compared to 13.7 mg/l in the hydric, intact fen peat. This again suggests that nitrate is the dominate nitrogen form in anaerobic fen soils, whereas ammonium is prevalent in the oxidized soils. This relationship has also been suggested in studies of other subalpine fens (Cottrell 1993, Johnson 1994). Differences in the form of nitrogen may influence the local flora since the two nitrogen forms are metabolized in different physiological processes and plant organs (Marshner 1995). The patterns of uranium enrichment will be considered below.

Subsidence of peat bodies following drainage has been commonly noted in the literature (Egglesmann 1975, van der Molen 1975, Schothorst 1977, Groothjans et al. 1988). Subsidence occurs through three processes: oxidation of organic matter, compression due to loss of buoyancy, and shrinkage resulting from the collapse of soil structure (van der Molen 1975, Schothorst 1977, Brooks and Predmore 1978). Evidence for subsidence at Crooked Creek Fen is provided by the condition of the drained peat which is extremely dry and granular at the surface. Such characteristics are indicative of organic matter oxidation, which is the major cause of subsidence (Schothorst 1977, van Diggelen et al. 1991). Additionally, soil bulk density is higher and porosity lower in the drained compared to the intact portion of the fen (Fig. 3.7), even though the percent organic matter in each area is comparable. This too indicates subsidence, in this case, via the collapse of soil structure (Egglesmann 1975).

The actual amount of subsidence cannot accurately be determined at this site because surface elevations before drainage are not available.

The current vegetational, edaphic, and hydrologic conditions present in the drained portion of Crooked Creek Fen underscore the predominant role of ground water in fen hydrology in the semi-arid western United States. The impacted and unimpacted portions of this fen are each located in identical landscape positions and receive the same amount of atmospheric water input. The single factor that has been altered is the amount ground water allowed to reach the drained area. This clearly shows that without an intact ground water system the fen ecosystem cannot be maintained. These results demonstrates that catastrophic impacts to fens occur with a one meter or greater increase in water table depth. Smaller increases in water table depth would also prompt environmental changes, but the magnitude of these impacts cannot be directly determined from available data. Based on the experience of European and boreal peatland scientists, it is doubtful that many edaphic characteristics of drained fens can be fully restored to their pre-impact conditions (Clymo 1983, Ingram 1983, van Diggelen et al. 1991). It is unclear the extent to which other hydrologic or vegetational attributes can be restored.

The Effect of Disturbance on Ground Water Uranium Concentration

The most striking difference in water quality between mined and intact sites is in the concentration of uranium at High Creek Fen, where it was found to be many times higher in mined areas than in intact areas. Uranium has been found to be readily sequestered in peat (Kochenov 1965, Lopatkina 1967, Borovec et al. 1979), and high concentrations have been found in the peat of Colorado fens (Owen et al. 1992, Owen and Breit 1995, Owen and Otton 1995). Under the anoxic conditions found within an intact peat body, sequestered uranium is essentially immobile (Kochenov 1965, Lopatkina 1967). It can be re-mobilized, however, if soils become aerobic, such as when peat is extracted and stockpiled for processing or drained. It is highly probable that the elevated uranium levels measured in the mined portions of High Creek Fen are the direct result of the environmental changes caused by mining. This cannot be experimentally demonstrated, though, since pre-impact uranium measurements do not exist. The seriousness of High Creek Fen's elevated uranium concentration is difficult to quantify since there are no promulgated water quality standards for the metal. This enrichment is of concern though since High Creek is a significant tributary of the South Platte River which supplies a large percentage of the Denver metro area's drinking water.

Uranium concentrations vary across the three fens studied as the result of the discrete distribution of uranium-bearing deposits in South Park and the Mosquito Range. Wilmarth (1959) found significant deposits of uranium in the Maroon Formation in the Garo mining district of South Park. This area is only about 7 km to the east of High Creek Fen, and aquifers located in this formation are one of the base-rich water sources for the fen. Significant uranium deposits are also located in the Alma mining district which is just a few kilometers west of Crooked Creek Fen in the Mosquito Range (Pierson and Singewald 1953). As predicted by the presence of uraniferous deposits in the vicinity, the ground water sample obtained from the oxidized, drained peat of Crooked Creek Fen has nearly triple the uranium level of ground water in the intact fen. No uranium-bearing deposits have been mapped in the vicinity of Fremont's Fen, consequently, this fen does not show elevated ground water uranium concentrations in the mined areas.

Conclusion

The sites examined in this study have different impact histories, and have been subject to differing post-impact restorations. This situation has the advantage of encompassing the variation of land use situations which can occur in subalpine fens, but it has the disadvantage of not providing true replication of observations. At all of the impacted areas examined, large changes in the biota and environment of the fens still exist even many years after the initial disturbance. The specific effects of these impacts varied between sites due to differences in regional setting and the post-impact restoration. Peat mining alters site vegetation, edaphic and surficial characteristics, and aspects of water and soil chemistry. Particular changes in water and soil chemistry resulting from mining vary between sites due to differences in ground water characteristics. For instance, uranium concentration in water and soil can be elevated in mined areas but only if the uraniferous deposits are found in the vicinity of the fen. Drainage also has far reaching and severe effects on the fen ecosystem, altering the vegetational, hydrologic and chemical environment.

It is unclear the extent to which impacted fens can be restored, and success is dependent upon the nature and extent of the disturbance. As shown on High Creek Fen, reintroduction of native fen topsoil can speed revegetation, although the process still takes a number of years. Without such an approach to restoration, revegetation occurs extremely slowly and may not be complete within any meaningful time frame. As is clear from Crooked

Creek Fen, maintenance of the natural ground water system is of critical importance to fen survival, and so must be highly protected if these systems are to continue to exist and function on the landscape.

CHAPTER IV

REVEGETATION AT CALCAREOUS SUBALPINE FENS FOLLOWING DISTURBANCE: PATTERNS IN THE PROPAGULE BANK AND EXTANT VEGETATION

ABSTRACT

Revegetation of mechanically disturbed treatment plots was studied. Treatments simulated peat mining and restoration using either natural revegetation or reintroduction of surficial peat. Treatment plots were located in either intact fen or in areas historically impacted by peat mining or draining. Treatments reduced species richness in intact fen blocks and richness generally increased during the experiment. In previously impacted areas, species richness reattained control levels by the end of the first growing season. Total vegetational coverage increased during the experiment, although in hydric sites increases were minimal. Species composition in intact fen treatment plots did not recover to control condition. In previously impacted areas, treatment plot species composition became indistinguishable from controls. There was no change in propagule bank species richness or composition during the experiment, indicating a rapid initial recovery. Similarities between the propagule bank and extant vegetation were generally low and did not vary during revegetation. Similarity between the propagule bank and extant vegetation was greatest in control plots, followed by

tilled and NPB plots, respectively. This study has shown that intact fens are highly susceptible and slow to recover from disturbance, but under most conditions reintroduction of native topsoil can significantly speed revegetation of disturbed areas.

INTRODUCTION

Many fens in South Park have been historically altered by peat mining and drainage. In mined sites, the restoration methods employed have ranged from allowing natural revegetation to regrading the site with side-cast peat from the mine. Most restoration strategies employed are closer to the former than the latter, though. Logic dictates that reintroduction of topsoil should aid in site reclamation since that layer contains the majority of the soil seed bank and vegetative propagules (collectively called the propagule bank). Such an approach has been used in wetland restoration with positive results (van der Valk and Pederson 1989, van der Valk et al. 1992, McDonald 1993, Vivian-Smith and Handel 1996, Brown and Bedford 1997), although, the role that the propagule bank plays in wetland ecology and restoration is far from consistent across wetland types. In some wetland systems, a strong positive relationship between extant vegetation and the seed or propagule bank has been observed (van der Valk and Davis 1978, Leck and Graveline 1979, Ungar and Riehl 1980, Parker and Leck 1985, Badger and Ungar 1994). At others, little or no relationship between the two floras has been found (Jerling 1983, McGraw 1987, Ungar and Woodell 1993, Raffaele 1996). Ungar and Woodell (1993) suggested that there is a positive association between vegetation and propagule bank compositions in annual dominated wetlands, whereas little or no correlation is present in wetlands dominated by perennial species. Many of the aforementioned studies support this general relationship.

In systems in which there is little correlation between extant vegetation and propagule bank composition, it could be expected that reintroduction of topsoil would not aid in revegetation after disturbance. Since subalpine fens are dominated by perennial species reproducing mainly through vegetative propagation, the seed bank may have little effect on vegetation dynamics and restoration success. On the other hand, reproductive parts besides seeds, most commonly rhizomes, abound in fen soils and these propagules could have a strong positive influence on restoration success. Therefore, the effectiveness of topsoil reintroduction for restoration of subalpine fens is unclear. Because of this uncertainty it has been difficult for regulatory agencies and managers to promulgate and defend restoration requirements in subalpine fens.

Many fens in South Park had been impacted before their ecological importance was known and most of these sites were poorly reclaimed following the destructive use. Because of the acknowledged importance of these sites (e.g. US Fish & Wildlife Service Peatland Policy Statement, 1998) there has been increased interest in restoring the historically impacted fens, as well as those which have been impacted by contemporary projects. Historically impacted wetlands may not respond in the same way to a given restoration approach as recently damaged wetlands, though. For example, Wisheu and Keddy (1991) found that the propagule bank of a shoreline wetland was seriously damaged by soil disruption, and Brown and Bedford (1997) showed that wetland seed banks lose wetland species after drainage. To evaluate how historical impacts influence the effectiveness of restoration approaches, this study examines fens that had been previously impacted by peat mining or draining, as well as those which are essentially pristine.

The goals of this project are to further our understanding of vegetational recovery on fens after disturbance, how the propagule bank influences extant vegetation composition and dynamics, and examine the propagule bank's potential role in fen restoration. This study has four specific objectives: (1) to examine the effect of simulated surface mining on vegetation and investigate subsequent patterns of revegetation; (2) to assess the composition of the propagule banks of intact calcareous fens and compare them to fens subjected to either peat mining or ditching; (3) to compare the species composition of extant vegetation and the propagule bank; and (4) to determine whether reintroduction of the native propagule bank is an effective way to improve fen restoration.

METHODS

Study Area

A detailed description of South Park and the three study areas is provided in Chapters One through Three. In brief, three fens were examined, each having areas that are either intact or that have been impacted by some historical land use. Treatment after impact has also varied. Portions of High Creek Fen were mined for peat during the 1970's and 1980's. During the procedure, a portion of the mined peat was mishandled and devalued, consequently, the miners abandoned it as spoils near the mine pit. After the acquisition of the fen by TNC in 1992, the mine was regraded using the spoiled peat, and returned to roughly the same grade as prior to mining (Allen Carpenter, TNC, 1995, pers. comm.).

Fremont's Fen was extensively peat mined, although intact portions of fen still remain. During the mining process, a series of drainage ditches and roads were constructed that crisscross the fen. The exact age of the mine is not known, nor is the date that it was abandoned, but mining ceased at least 15 years ago based on residents' accounts.

The majority of Crooked Creek Fen is intact except that portion which is below a single ditch bisecting the fen perpendicular to its slope. This ditch intercepts virtually all surface and ground water to a depth of approximately1.5 m. The locations and extents of these impacts can be seen in Figs. 2.2 - 2.4 (pgs. 69 - 71).

Experimental Design

Experimental plots were arranged in block configurations. Blocks were initially laid out as 2 m x 2 m squares. The squares were then divided into 1 m x 1 m quarters and two quarters treated. Plot treatments were designed to simulate many of the effects of peat mining and two different restoration approaches. One quarter of each block had the upper 20 cm of peat extracted using a shovel to remove the seed bank (e.g. Leck et al. 1989 and references therein). This treatment, referred to as "no propagule bank" (NPB), was applied to imitate the effects of peat mining without any post-mining reclamation – a common occurrence, at least historically, in Park County mines.

A second quarter of each block was tilled. The tilling consisted of cutting the peat to a depth of approximately 20 cm and then thoroughly chopping and mixing it. As much living vegetation as possible was removed from the soil during the tilling. This second treatment, called the tilled treatment, was intended to simulate a peat mine restoration in which a layer of native topsoil is reintroduced to the site upon the cessation of mining. The third quarter was left intact as a control and the fourth quarter was unused except that a monitoring well was installed in it using the methods described in Chapter Two. Well water depths were measured approximately bi-monthly from 1996 to 1998.

The blocks containing the treatment plots were installed in June 1996 and arrayed in a complete block design. Since mining can take place in both intact fens and fens which have been drained, blocks were located in both situations. To evaluate vegetational recovery in actual peat mines, blocks were placed in areas which historically have been mined. Because of its status as a preserve, no experimental blocks could be placed within the intact portions of High Creek Fen. Nine blocks were placed in essentially pristine fens, six blocks were placed in fens impacted by mining, and four blocks were placed in fens impacted by draining. Together, this resulted in nine possible experimental configurations. For brevity, treatments will generally be referred to using a compound designation. For instance, intact-tilled will indicate a tilled treatment plot of a block located within an intact fen, while mined-control indicates a block's control plot located in an area that had been previously mined. Table 4.1 shows the impact type and mean water table depth present at each block.

To monitor the vegetational recovery and the role played by the propagule bank in this recovery, the percent cover of species was estimated and propagule bank samples obtained on July 11 - 12 and September 15 - 16, 1996, and July 20 - 21 and September 25, 1997. Vegetational composition was measured a fifth time on August 5 - 6, 1998, but no propagule

Table 4.1. The impact type and mean water table depth from 1996 to 1998 at each study block. Parenthetical numbers are sample standard deviations.

Block Number	Mean Water Table Depth (cm)	Impact Type
HC 1	-39.8 (35.8)	Mined/Reclaimed
HC 2	-50.5 (39.4)	Mined/Reclaimed
HC 3	-42.5 (13.9)	Mined/Reclaimed
HC 4	-60.4 (19.0)	Mined/Reclaimed
CC 1	-5.1 (9.0)	Intact
CC 2	-27.2 (21.7)	Intact
CC 3	-0.1 (2.0)	Intact
CC 4	-6.9 (5.5)	Intact
CC 5	-129.8 (36.2)	Drained
CC 6	-100.7 (27.6)	Drained
CC 7	-76.9 (28.5)	Drained
CC 8	-83.6 (42.2)	Drained
FF 1	-14.9 (32.5)	Mined
FF 2	-40.0 (39.1)	Intact
FF 3	-2.6 (28.1)	Mined
FF 4	-31.7 (11.8)	Intact
FF 5	-22.4 (20.5)	Intact
FF 6	-59.9 (39.8)	Intact
FF 7	-53 (23.4)	Intact

bank samples were obtained. The July vegetational evaluations and propagule bank samplings occurred after seed germination had occurred, while the September sampling characterized vegetation and propagule bank after plants had set and released their seeds.

Propagule bank samples were collected by extracting eight randomly placed, 10 cm deep by 5 cm diameter soil samples from each plot. Each sample contained approximately 200 cm^3 of soil. The emergence, or germination method with stratification was used to evaluate the composition of the propagule bank (Thompson and Grime 1979, Roberts 1981, Gross 1990). After samples were obtained, they were placed in a cold room at 0 - 1°C at Colorado State University. After at least a 3 month stratification, replicate samples from each plot were homogenized and 1000 cm^3 of the soil placed in perforated plastic trays over a bed of fine, washed sand. Perforated trays were placed in shallow tubs so that a low water table could be maintained.

Evaluating the influence of both seeds and vegetative propagules on extant vegetation was the primary goal of this portion of the study; therefore, no attempt was made to systematically differentiate between plants arising from either means. To remain consistent with the nature of these data, the term "propagule bank" will be applied to the collection of plants emerging from the transplanted soils. For convenience the term "seedling" will be applied to young vegetative sprouts as well as true seedlings. Trays were checked frequently to monitor the emergence of seedlings. Seedlings were removed as soon as they could be identified, which often was not until flowering. The prolific vegetative spread of sedges and grasses precluded the counting of seedlings for calculation of seedling densities.

Data Analysis

Using this experimental design I sought to address the following hypotheses: (1) treatments have negative effects on extant species richness, vegetation coverage or composition; (2) treatment effects, if any, are attenuated over time; (3) most revegetation in fens arises from vegetative propagules; (4) the propagule bank undergoes succession following disturbance; (5) after disturbance, extant vegetation and the seed bank follow similar successional paths; and (6) site impact history alters vegetational recovery and the relationships between extant vegetation and the propagule bank. Each of these six hypotheses was applied to the differently impacted areas, as well.

For hypothesis testing, data were grouped to differentiate the effect of treatments within each of the three impact types examined. Data were first grouped by sample year, then impact type in which blocks were located (intact, mined, or drained), and finally by treatment (control, tilled, or NPB). Data were grouped in this manner to evaluate general patterns of vegetational recovery, based on the broad range of site conditions found within South Park's fens. Between-fen differences in environment were noted in Chapters 2 and 3, and Fremont's Fen and High Creek have been subjected to different types of restoration following peat mining. Grouped analysis explicitly incorporates inter-site variance which makes conclusions about revegetation more widely applicable. While allowing the elucidation of the general effects of impacts on vegetation recovery, this data structuring does obscure the particular patterns of revegetation present at individual sites. Therefore, site specific data are also presented for comparative purposes.

Most of the data collected did not meet assumptions of normality; therefore, more conservative, univariate, non-parametric tests were used to assess many of the treatment effects. All statistical tests were carried out using Systat version 7.0, unless otherwise indicated. Treatments were considered significantly different from controls when p-values were less than 0.05. Differences in single factors between experimental plots, such as species richness, were tested using a Kruskal-Wallace one-way analysis of variance (ANOVA), while temporal changes in single parameters within blocks were examined using two-way Friedman ANOVAs (Sokal and Rohlf 1981).

Similarity between extant vegetation and the propagule bank was examined by calculating a Sørensen similarity index for each plot (van Tongeren 1996). The index equation is 2w/(a+b), where w is the number of species shared between extant vegetation and the propagule bank, a is the number of species in the extant vegetation, and b is the number of species in the propagule bank. This index has probably been the one most commonly used for such comparisons, and has favorable properties such as a relatively low sensitivity to species richness (van Tongeren 1996). Paired t-tests were used to compare similarities between treatments and sample dates.

Multivariate comparisons of treatment plot species composition were carried out using the Multi-Response Permutation Procedure (MRPP) (1981a, Mielke et al. 1981b) as included within the PC-ORD version 3.04 statistical program (McCune and Mefford 1997). This recently developed test is one based on generating multiple data configurations and testing for a difference between the randomly generated configurations and the *a priori* configuration which is being tested. Biondini et al. (1985) and Zimmerman (1985) provide clear and detailed explanations of the theory and ecological applications of the test, but a brief explanation will be provided here. MRPP first calculates a matrix of dissimilarities between replicates within a given treatment. This provides a measure of average within-treatment distance measure. There are several distance measures which can be employed; Euclidian distance was used in this study. The procedure then calculates the distance between all replicates between treatments. From this distribution, an average distance is generated. The test statistic and p-value are calculated based on a comparison of the distance within *a priori* groups and average distance between randomly configured groups. The p-value represents the proportion of randomly configured groups which have a smaller "within-treatment" distance. For instance, if less than five percent of random configurations possess a smaller dissimilarity than the *a priori* grouping being tested, then differences due to treatment would be significant at the ninety-five percent confidence level. That is, replicate plots would be significantly more similar to one another than they are to different treatments.

RESULTS

PATTERNS IN EXTANT VEGETATION

Species Richness

Figure 4.1 shows the patterns in extant species richness within each wetland by year and by treatment. In 1996, control plots generally had higher richness than their associated treatment plots. The exception to this was at blocks located in heavily mined sections of

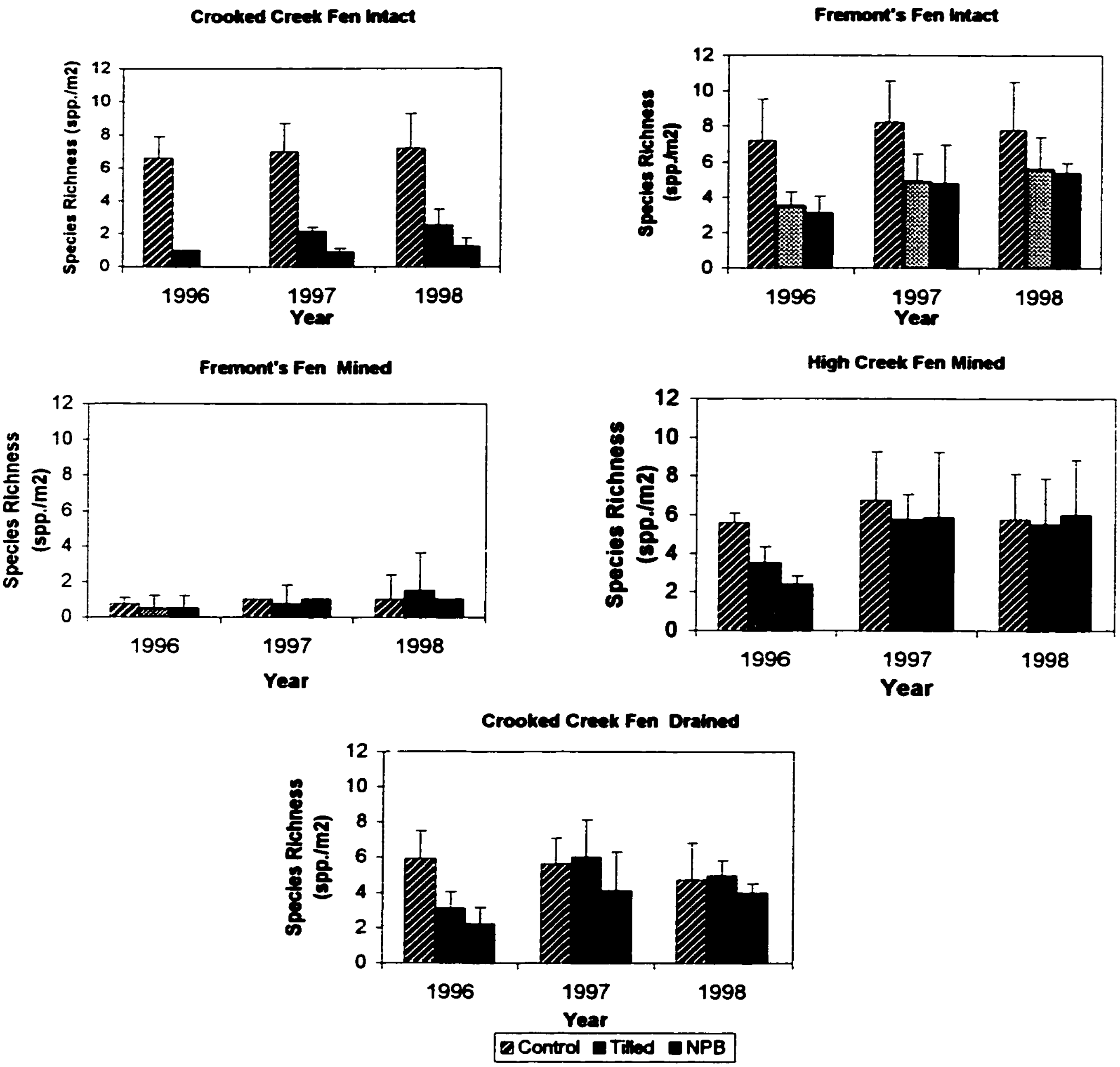

Figure 4.1. Species richness in treatment plots during the three years of the experiment. Plots have been grouped according to the site and type of impact in which they were located. Bars indicate the standard deviation from the mean. NPB is "no propagule bank".

Fremont's Fen where little vegetation was present. Overall, intact-controls had the highest species richness with an average of 7.3 spp/m^2 (Table 4.2). In treatment plots within intact fens, species richness increased throughout the experiment, although these plots never attained the level of richness found within the controls.

Species richness of the drained treatment plots recovered rapidly, and by the second year richness had essentially reattained control levels. Treatment plots located in mined areas showed two distinct patterns in species richness recovery depending on the site at which they were located. At Fremont's Fen, where large expanses of barren, mined peat exist, the species richness in treatment plots was always similar to that of controls and was quite low, between 0.5 and 1.5 spp/m^2. No apparent changes in species richness occurred in these sites during the experiment and there was no significant effect of treatment at these blocks ($p<0.05$).

In previously mined areas of High Creek Fen, initial species responses were similar to those found at intact sites with reductions in species richness closely following the intensity of treatment. By the second year in the experiment, richness had recovered in these plots and no difference between treatments and controls was evident.

Considering all three years of the experiment, there were significant differences in species richness between the control and treatment plots located within intact fens and amongst treatment plots in formerly impacted areas (Table 4.3). There were, however, no significant differences between controls and treatments in formerly impacted areas.

Table 4.2. Comparison of extant vegetation and propagule bank richness of treatments within the variously impacted areas. Parenthetical numbers are standard deviations. To facilitate comparability, some species in the extant vegetation have been grouped to correspond to the taxa used for seed bank analysis. Treatments are: C = control, T = tilled, NPB = no propagule bank. See Table 4.4 for a listing of taxa.

Impact Type	**Intact**						**Drained**			**Mined**					
Site	**Crooked Cr. Fen**			**Fremont's Fen**			**Crooked Cr. Fen**			**Fremont's Fen**			**High Creek Fen**		
Treatment	**C**	**T**	**NPB**	**C**	**T**	**NPB**	**C**	**T**	**NPB**	**C**	**T**	**NPB**	**C**	**T**	**NPB**
Seed Bank Richness	3.5 (1.7)	2.6 (1.2)	2.0 (1.2)	5.1 (2.5)	3.7 (1.5)	2.1 (1.8)	6.5 (2.0)	7.4 (2.6)	2.8 (1.5)	0.3 (0.8)	0.5 (0.8)	1.7 (0.4)	4.2 (1.9)	3.3 (2.8)	3.5 (2.2)
Extant Richness	7.1 (1.8)	1.6 (1.0)	0.3 (0.5)	7.9 (2.5)	4.1 (1.7)	3.6 (2.0)	5.7 (1.7)	4.0 (2.0)	2.7 (1.3)	0.8 (0.4)	0.5 (0.5)	3.6 (1.2)	5.8 (1.7)	4.1 (1.6)	3.5 (2.8)

Table 4.3. Significance values for the effect of treatment on species richness. NPB is the "no propagule bank" treatment.

Impact	**Intact**		**Drained**		**Mined**	
Treatment	**Control**	**Tilled**	**Control**	**Tilled**	**Control**	**Tilled**
Tilled	0.009*	1.0	0.203	1.0	0.150	1.0
NPB	0.023*	0.000*	0.325	0.002*	0.150	0.002*

* = significance at $p<0.05$

Vegetational Composition

Changes in Total Plant Coverage

Figure 4.2 shows changes in total vegetation coverage at each site within the three impact types. Tilled treatment plots generally had consistently higher vegetation coverages than NPB plots and plant cover tended to increase throughout the experiment. The primary exception to this was in the mined areas of Fremont's Fen where little vegetation exists. Vegetational coverage also increased in the NPB plots and at rates comparable to the tilled plots, but total coverage was generally less than in tilled plots.

When sites were grouped by year and impact type, Friedman ANOVAs and regression analysis indicated that no change occurred in control plots within any of the differently impacted areas ($0.28 < p < 1.0$), but total vegetation coverage significantly increased in all treatment plots except mined-tilled plots ($p<0.05$). In the mined-tilled treatments, plots either remained nearly bare if that was their condition before the treatment was applied, or were covered by *Potentilla anserina* and scattered grasses by the end of the first growing season if they were located in areas where prior restoration had occurred.

Development of Vegetational Structure

MRPP was used to detect differences in plot vegetational composition due to treatment. In 1996, an effect of treatment was found in all blocks ($p< 0.05$; Fig. 4.3), although significance was only marginal in the previously mined blocks ($p=0.04$). In 1997, an effect of treatment was still present in intact and drained blocks, but treatment plots in

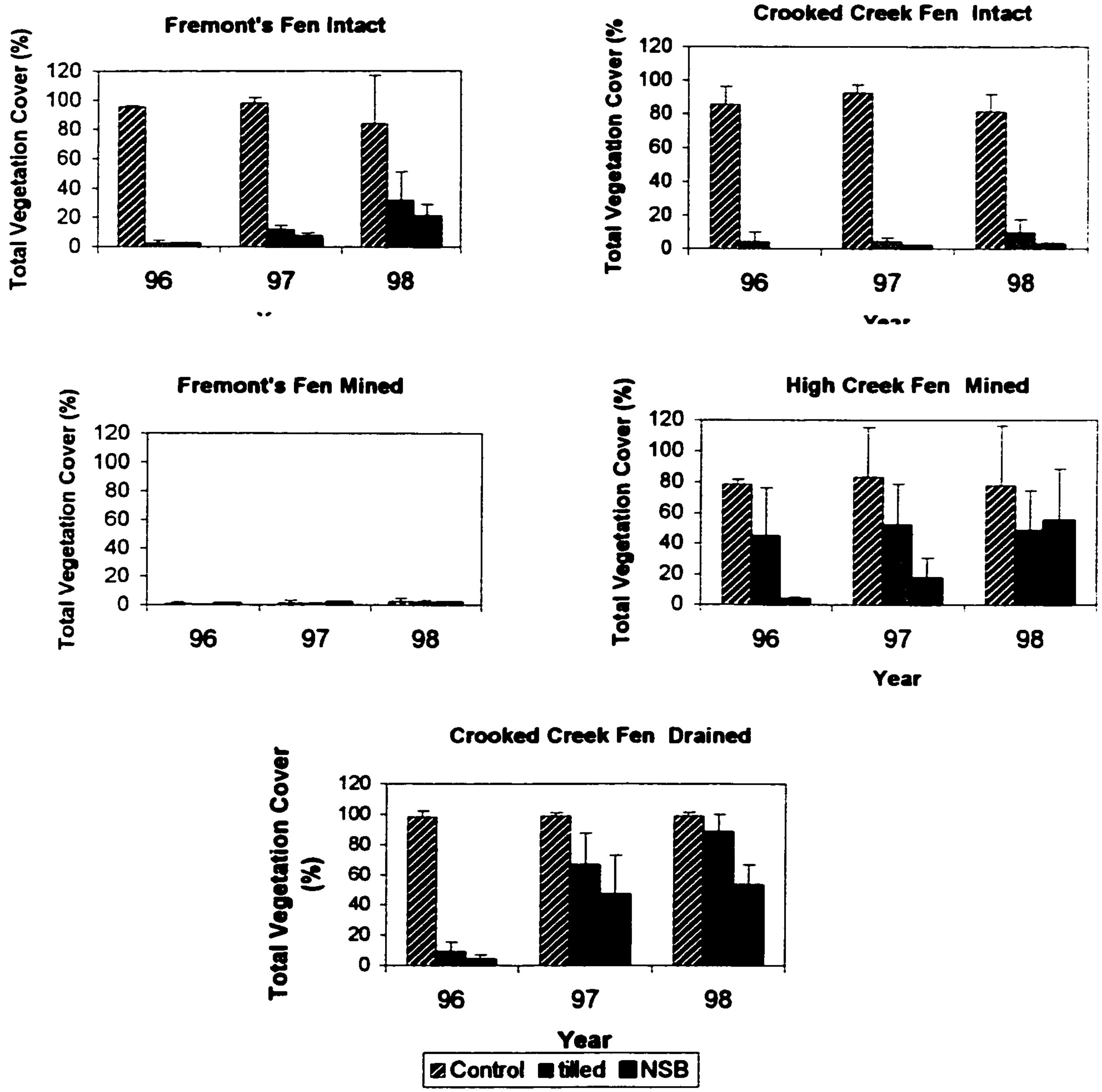

Figure 4.2. Total vegetational cover in treatment plots during the three years of the experiment. Plots have been grouped according to the site and type of impact in which they were located. Bars indicate the standard deviation from the mean.

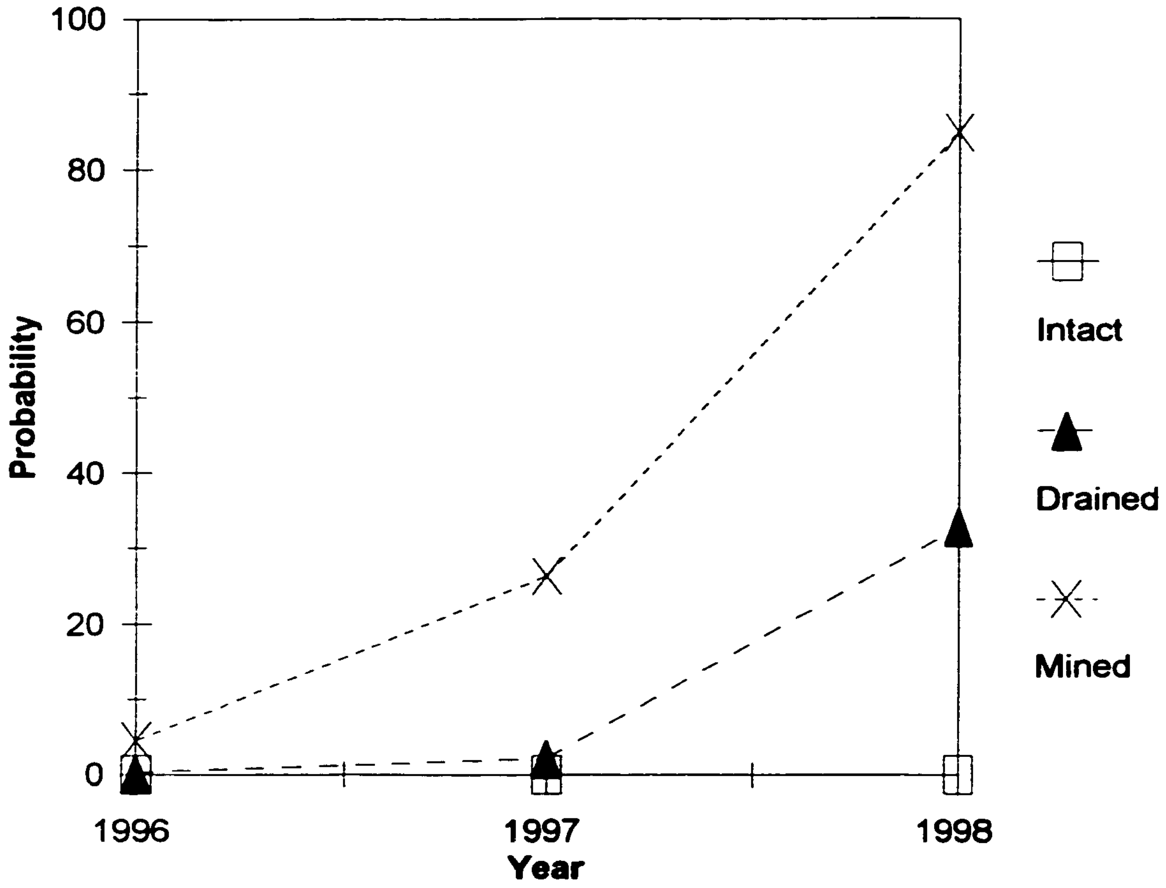

Figure 4.3. Probability values for MRPP testing for an effect of treatment. Tests were performed separately for each impact level and each year. Note that probabilities for intact sites were nearly zero, so the trend line is not evident in the graph.

mined areas could not be distinguished from their controls. By the final season of the experiment, vegetation in treated plots in both mined and drained areas were not statistically different from controls. Only in blocks from intact areas was there a pronounced treatment effect throughout the entire experiment.

Because within-treatment distance is a measurement of heterogeneity within a particular plant community, I have used this distance as a measure of α-diversity (within-habitat). Similarly, the distance between the various treatments is used here as a measure of β-diversity (between habitat). Control plot α-diversity remained similar throughout the experiment, indicating that little vegetational change or inter-seasonal measurement error occurred at these plots (Fig. 4.4). Treatment plot α-diversity was initially low resulting from the primary effects of the treatments, namely, removal of species and plant coverage (Fig. 4.4). Similarly, β-diversity was also low between the two treatments, but high between treatments and controls. As vegetational development occurred heterogeneity between replicate plots increased from their initially homogenous condition. The result of the developing heterogeneity was to increase the α-diversity within treatments and reduce β-diversity between treatments.

Replicates having comparable within-treatment distances as measured by MRPP may have similar species compositions, although this is not necessarily so. Comparable within-treatment differences could also indicate that plots simply have similar α-diversity, regardless of species composition. Examination of species data indicated that this was not the case, since within the variously impacted areas, treatments with comparable α-diversities also tended to have similar species compositions (Table 4.4).

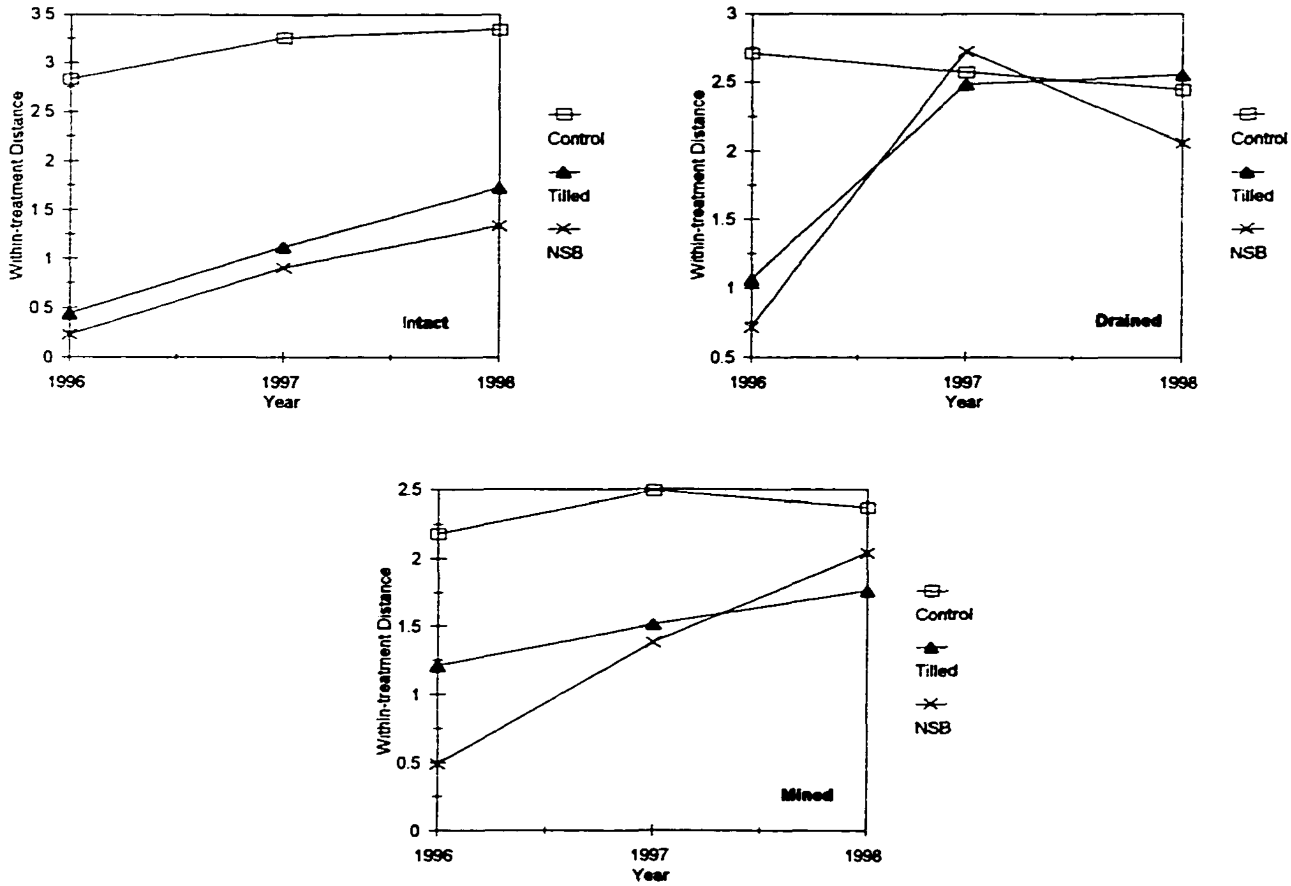

Figure 4.4. Within-treatment distances derived from MRPP, across years. Each graph shows the behavior of treatments within a given impact type. Refer to text for further details.

Table 4.4. Extant species composition of control and experimental treatments during the 1996 and 1998 sampling. Species abundances have been grouped into Braun-Blanquet abundance classes: +=<1%; 1=1-5%; 2=6-25%; 3=26-50%; 4=51-75; 5=76-100%. Treatment codes are: C = control, T = Tilled, and NPB = no propagule bank.

Impact Type	Intact						Drained						Mined					
Treatment Code	C		T		NPB		C		T		NPB		C		T		NPB	
Year	96	98	96	98	96	98	96	98	96	98	96	98	96	98	96	98	96	98
Litter	2	1					2	2		2		2						
Achillea millefolium	1	+						1				1						
Agrostis gigantea		2		2		2												
Agrostis scabra			+	1									+				+	
Antennaria microphylla	+	1																
Artemisia frigida							1	2	+			2						
Aster occidentalis	1		+		+	1							1	1		+		1
Aster spp.	+												+				+	
Calamagrostis canadensis		1																
Calamagrostis stricta				1		2	1						+		1		+	2
Carex aquatilis	3	2	+	1	1	1							+			1		
Carex aurea		1				2												
Carex hallii	+	1																
Carex lanuginosa														2		2		1
Carex scirpoidea	+																	
Carex simulata	2	3	+	1	+	1		+				+						
Carex spp.							1								+		+	
Carex utriculata						+												
Chenopodium rubrum											1							
Cirsium arvense	+	1					1				1	1	1	+	+	1	+	+
Cirsium coloradense	1	1			+		1	1			1	1						
Crepis runcinata	1				+													
Deschampsia cespitosa	2	2	+	2	+	2							2	2	1	2	+	1
Descurainia ramosissima									+	1								
Eleocharis quinqueflora	1	1												2		+		1
Elymus trachycaulus	2	2	+	1	+	+							1	1		1	+	1
Epilobium hornemannii				+														
Eqisetum variegatum	+																	
Erigeron spp.		+																
Festuca idahoensis	2	2	+										1				+	
Galium boreale	+																	
Hordeum brachyantherum		1		1			2			+		1				1		
Hordeum jubatum	1						2						+					
Juncus alpino-articulatus													1	2		1	+	2
Juncus balticus	3	2		1		1	3	3					1	+		2	+	
Juncus longistylis														1		1		1
Kobresia myosuroides	2	2																
Kobresia simpliciuscula	2	2				1												
Koeleria macrantha					1													
Lappula Redowskii							1	1	1	1	1	1						
Lepidium ramosissimum					+			1	+	2		5						
moss	2	2		+	+	1												

Impact Type	Intact						Drained						Mined					
Treatment Code	C		T		NPB		C		T		NPB		C		T		NPB	
Year	96	98	96	98	96	98	96	98	96	98	96	98	96	98	96	98	96	98
Muhlenbergia richardsonis	+																	
Parnassia parviflora		+																
Pascopyrum smithii							2	2		1	+	2				1		
Pentaphylloides floribunda	1	1																
Poa compressa						1											+	
Poa pratensis	1	2					3	2	+	1	1	2						+
Polygonum aviculare			+		+													
Polygonum bistorta	+	+																
Polemonium foliosissimum	1	+	+	+	+													
Potentilla anserina	2	2	+	2	1	2	2	2	1	3	2	4	4	3	1	2	3	3
Potentilla plattensis	1																	
Potentilla subjuga							1	1	+	2		1						
Puccinellia airoides													2					
Puccinellia distans													+					
Ranunculus cymbalaria				1		2							+		+	1		
Ranunculus hyperborea			1	1	1													
Rorippa sphaerocarpa	+						2											
Salix brachycarpa	1	1																
Salix candida	1	1																
Salix myrtillifolia	1	1																
Salix planifolia	1	1																
Sedum Rhodanthum	+	1				+												
Stellaria longipes	1		+		1	1												
Taraxacum officinale	1	1	+	+	+	+	+	+			1							
Thalictrum alpinum	1	1	+															
Triglochin maritimum	1		+		+	1								1	+	1	1	1
Triglochin palustre		1											1	1	+	+	1	1
Trichophorum pumilum	1	1																

Treatment Plot Species Composition in the Different Impact Areas

Many of the colonizing species found in the undrained blocks (i.e., intact and mined), such as *Carex aquatilis, C. simulata, Deschampsia cespitosa, Juncus balticus, Potentilla anserina* and *Triglochin maritimum* are common fen taxa that were also found within the intact-controls. In blocks of the mined areas, additional species such as *Calamagrostis stricta, Carex lanuginosa, Juncus alpino-articulatus, J. longistylis* and *Triglochin palustris* were also important pioneers. Although many of the species found in the treatment plots are common in fens, invasive species such as *Lepidium ramosissimum, Polygonum aviculare, Ranunculus cymbalaria,* and *Ranunculus hyperborea* were also noted.

The early succession species composition in the drained blocks was very different from that in the undrained blocks and drained treatment plots quickly revegetated. Drained-control plots were dominated by a mix of annual and perennial grasses, primarily *Hordeum jubatum, H. brachyantherum, Elymus trachycaulus, Pascopyrum smithii,* and *Poa pratensis*. Weedy and upland species including *Potentilla anserina, P. subjuga, Lappula redowskii, Artemisia frigida* were also generally present and often important in the drained controls. These same species became prevalent in the treatment plots, as well.

PATTERNS IN THE PROPAGULE BANK

The propagule bank investigation proved difficult owing to problems in identifying immature grass and sedge species, which were often the dominant taxa. Consequently, significant taxonomic detail was lost. Many of the grass species flowered during the greenhouse experiment and could be identified to species. Those which did not flower could frequently be identified to species or genus based on vegetative characteristics. When no identification was possible, grasses were classified as Poaceae. No sedges flowered in the greenhouse, and while *Carex aquatilis* could be recognized vegetatively, no other sedge species could. Therefore, all sedges except *C. aquatilis* were recorded as *Carex* spp. This taxon very likely also included species of elk sedge, either *Kobresia simpliciuscula* or *K. myosuroides*.

Table 4.2 presents mean, site-specific propagule bank species richness in treatment and control plots grouped by impact type. There were no statistically significant changes in propagule bank species richness throughout the experiment as the regression line slopes of richness versus year were not significantly different from zero.

Likewise, MRPP based on presence/absence data detected no effect of treatment on propagule bank species composition throughout the three years of monitoring ($p < 0.05$). This indicates that either treatments had no effect, or propagule bank composition recovered during a single season. The latter seems a more likely explanation since the removal of the upper 10 cm has been well documented to have an effect on seed bank composition (e.g. Leck et al. 1989).

Table 4.5 presents propagule bank species composition data. Plot data from each of the sampling events were additively combined to give the total number of plots in which species were found. Visual examination of these data shows clear differences between the frequency of species in the propagule banks of drained versus undrained plots (i.e. intact and mined). The dominant propagule bank species in drained areas are mostly upland grass

Table 4.5. The number of occurrences of species in the propagule bank. Data from all samplings have been combined into a total number of occurrences within plots. Treatment codes are: C = control, T = Tilled, and NPB = no propagule bank.

Status	Intact			Drained			Mined		
Treatment Code	C	T	NPB	C	T	NPB	C	T	NPB
Achillea millefolium	1	0	0	1	0	0	0	0	0
Agrostis gigantea	1	1	0	0	0	0	0	0	0
Agrostis scabra	0	2	0	0	1	0	0	0	0
Alopecurus alpinus	1	0	0	0	0	0	0	0	0
Antennaria microphylla	1	1	1	0	0	0	1	2	2
Artemisia frigida	0	0	0	7	9	0	0	0	0
Aster spp.	6	0	1	0	0	0	3	2	0
Calamagrostis canadensis	1	3	1	0	0	0	0	0	0
Calamagrostis stricta	0	0	0	0	0	0	1	1	0
Carex aquatilis	11	11	5	1	0	0	1	2	3
Carex spp	14	18	14	0	1	1	1	4	2
Chenopodium rubrum	2	2	0	0	1	1	2	1	0
Cirsium arvense	1	1	1	1	1	0	0	0	0
Cryptantha spp.	0	0	0	0	1	0	0	0	0
Deschampsia cespitosa	13	9	7	1	0	0	7	5	6
Descurainia ramosissima	3	0	1	9	9	5	0	0	0
Eleocharis quinqueflora	2	0	1	0	0	0	1	1	0
Elymus trachycaulus	3	1	0	4	8	5	4	2	0
Epilobium clavatum	1	0	0	0	0	0	0	0	0
Epilobium hornemannii	1	0	1	0	0	0	0	0	0
Eqisetum variegatum	0	0	1	0	0	0	0	0	0
Hordeum brachyantherum	0	0	1	5	1	3	1	0	0
Hordeum jubatum	0	0	0	7	5	2	0	0	1
Juncus alpino-articulatus	0	3	1	0	0	0	1	1	1
Juncus balticus	6	3	2	2	1	1	5	3	5
Jun longistylis	2	0	0	0	0	0	0	2	2
Lactuca spp.	0	0	0	0	0	0	0	0	1
Lappula redowskii	0	0	0	5	5	1	1	0	0
Lepidium ramosissimum	0	1	0	8	6	4	3	1	2
Muhlenbergia richardsonis	0	0	0	0	1	0	0	0	0
Muhlenbergia richardsonis	5	6	3	0	0	0	0	0	0
Parnassia parviflora	0	0	0	1	1	0	0	0	0
Poa spp.	0	1	0	7	9	1	1	0	2
Poaceae	4	4	0	3	3	3	1	1	1
Polygonum aviculare	2	1	1	0	0	0	0	0	0
Polygonum bistorta	2	0	0	0	1	0	1	0	0
Polemonium foliosissimum	4	1	0	0	1	0	0	0	0
Potentilla anserina	5	3	3	5	4	1	9	9	5
Potentilla plattensis	1	0	0	4	6	0	0	0	0
Potentilla subjuga	4	1	2	6	6	3	2	4	2
Puccinellia airoides	0	0	0	0	1	0	0	0	0
Puccinellia distans	1	0	1	1	4	1	0	1	0
Ranunculus cymbalaria	6	8	5	0	2	1	5	3	3
Ranunculus scleratus	0	0	1	0	0	0	0	0	0
Sisyrinchium pallidum	1	0	1	0	0	0	0	0	0
Stellaria longipes	6	0	0	0	0	0	1	0	0
Sedum Rhodanthum	1	3	0	0	1	1	0	0	0
Senecio spp.	4	2	0	0	0	0	1	0	2
Triglochin palustre	1	0	1	0	0	0	0	0	1
Thalictrum alpinum	1	0	0	0	0	0	0	0	0

species with many weedy annuals, such as *Artemisia frigida, Hordeum brachyantherum, H. jubatum, Lappula redowskii, Poa* spp. and *Puccinellia airoides.* These species were found almost exclusively in the drained plots. The roadside weed, *Descurainia ramosissima,* occurred occasionally in intact blocks, but was much more prevalent in the blocks of the drained fen. Common fen species such as *Carex aquatilis* and other sedges, *Deschampsia cespitosa, Eleocharis quinqueflora, Juncus alpino-arcticulatus, J. longistylus, Antennaria microphylla,* and *Aster spp.* were found almost exclusively in the undrained plots, while *Agrostis gigantea, Calamagrostis canadensis, Epilobium* spp., *Muhlenbergia filiformis* and *Sisyrinchium pallidum* were restricted to the propagule bank of such sites. Several generalist species such as *Elymus trachycaulus, Lepidium ramosissimum, Juncus balticus, Ranunculus cymbalaria, Potentilla anserina* and *P. subjuga* were found throughout treatments and impacts; although the first two species were more frequent in the drained blocks, the middle two preferred undrained plots, and the *Potentilla* spp. were common in all plots.

COMPARISON OF EXTANT VEGETATION AND PROPAGULE BANK

There was variability in comparisons of the species richness of extant vegetation and propagule bank, and no consistent patterns were evident (Tables 4.2 & 4.6). There were few differences the richness of extant vegetation compared to that of the propagule bank in both treatment and control plots. In the July 1996 sampling, no significant differences were found between the two floras using Friedman ANOVA ($p \geq 0.05$), while during the July 1997 sampling, significant differences in richness were found in the intact-control, intact-tilled plots, and mined NPB plots ($p < 0.05$).

Table 4.6. Significance values of Friedman ANOVAs comparing extant vegetation and propagule bank richness. Treatment codes are: C = control, T= Tilled, and NPB = no propagule bank.

Impact Type	Intact			Drained			Mined		
Treatment	C	T	NPB	C	T	NPB	C	T	NPB
July 1996	0.10	0.05	1.00	1.00	0.05	0.05	0.41	0.68	0.68
July 1997	0.03*	0.02*	0.74	0.62	0.62	0.05	0.22	0.10	0.01*

* significant at p <0.05 or smaller

Similarities between the species composition of the propagule bank and extant vegetation within plots did not vary from the beginning to the end of the experimental period, based on a pair-wise t-test of 1996 and 1997 data ($p>0.05$). Because compositional similarities did not differ, seasonal values at each plot were averaged to give a mean seed bank–extant vegetation similarity (Table 4.7). In all cases, the similarity between the propagule bank and extant vegetation was highest in intact plots, followed respectively by tilled plots and NPB plots. Observed similarities were rather low (0.11 - 0.45; Table 4.7) and the actual species similarity may be even lower than that reported due to the grouping of species and genera into higher level taxa.

DISCUSSION

There were marked differences in the treatment effects and patterns of revegetation in the plots located within differently impacted areas. Treatment effects were most pronounced in the intact fens, and vegetational recovery at these sites was quite incomplete by the end of the experiment (Figs. 4.1 - 4.4). Salonen et al. (1991) reported a similar type of protracted colonization in Finnish peatlands impacted by peat mining. Plots located in areas that had received previous impacts recovered much more quickly to pre-treatment status, and in most cases, treatment plots could not be distinguished from the controls at the end of the experiment.

Table 4.7. Sørensen similarity indices of propagule bank vs. extant vegetation composition, averaged across all sample periods. Parenthetical numbers are standard errors of the means. Treatment codes are: C = control, T = Tilled, and NPB = no propagule bank.

Impact Type	**Intact**			**Drained**			**Mined**		
Treatment	C	T	NPB	C	T	NPB	C	T	NPB
Sorensen Index	0.30 (0.04)	0.23 (0.04)	0.12 (0.04)	0.45 (0.06)	0.33 (0.06)	0.19 (0.07)	0.24 (0.05)	0.18 (0.05)	0.11 (0.04)

Disturbance in Intact Fens

Within the intact blocks, preservation of the propagule bank had small but noticeable effects on revegetation, and total vegetational coverage was generally higher in the plots possessing intact propagule banks (Fig. 4.2). In such cases, most of the increase in plant coverage can be attributed to lateral vegetative expansion arising from remnant vegetative structures such as rhizomes rather than to seedling establishment. The importance of vegetative propagation in wetlands dominated by perennial species, normally grasses and sedges, has been reported by several authors (e.g. Salonen et al. 1991, Wisheu and Keddy 1991, Raffaele 1996), and the dominant role of asexual propagation in recovery from disturbance has been documented in a wide variety of ecosystems such as forests (Ingersol and Wilson 1990, Rico-Gray and Garcia 1992), grasslands (Coffin and Lauenroth 1989, Milberg 1995), and Mediterranean shrub lands (Jimenez and Armesto 1992). As in these studies, asexual propagation was found dominate revegetation at the calcareous fens in this study (pers. obs.). Vegetative growth was especially important at Cooked Creek Fen treatment plots in hydrologically intact areas, where standing water in the plots was present throughout much of the growing season (Table 4.1). Here, no recruitment from the seed bank was ever observed, even though germinable seeds were found in the propagule bank. In such plots, species coverage and richness were quite low throughout the experiment and the vast majority of species coverage could be attributed to vegetative growth of *Carex aquatilis*, *C. simulata*, and/or *Triglochin* spp. In the more mesic plots at Fremont's Fen, recruitment occurred through a mix of reproductive modes. Vegetative expansion by sedges and *Triglochin* spp. played an important role in revegetation, but species such as *Agrostis* *gigantea, Calamagrostis stricta, Elymus trachycaulus, Stellaria longipes,* and *Ranunculus cymbalaria* were recruited from the seed bank. Other species, namely, *Juncus balticus, Potentilla anserina* and *Deschampsia cespitosa* increased coverage through both seeding and vegetative spread.

When asexual reproduction dominates wetland vegetational dynamics, there is generally a concomitantly low compositional correspondence between extant vegetation and seed bank (e.g. Wisheu and Keddy 1991, Ungar and Woodell 1993, Raffaele 1996). This relationship was also found in this study as evidenced by the low Sørensen index values (Table 4.7). This result is somewhat surprising since asexual sprouts were included in the propagule bank of this study. A possible explanation for this relationship is that the disparities between the species richness of the propagule bank and extant vegetation produced the low similarities. Also, the number of vegetatively regenerating species was low compared to the total number of species present in untreated or impacted areas.

Disturbance in Impacted Fens

Treatment plots in mined areas recovered to control levels by the second season of the experiment, although treatments affected the two mined fens differently. At Fremont's Fen where mining has been extensive and active restoration non-existent, treatments had virtually no effect on the measured parameters, because these plots had little or no vegetation upon the initiation of the experiment and this condition was maintained through the experiment (Figs. 4.2). These plots also possessed virtually no propagule bank. At Fremont's

Fen, site revegetation has been almost exclusively through marginal vegetative expansion and has proceeded quite slowly due to the small perimeter to area ratio.

At High Creek Fen, where mined areas were re-graded with peat spoils in 1992, the vegetation and propagule bank were much richer, and plant coverage more complete compared to the mined sections of Fremont's Fen. Preservation of the propagule bank at the High Creek Fen aided restoration of plant cover during the first two years of the experiment but not in the third year (Fig. 4.2). Maintenance of the propagule bank also had a positive effect on species richness at High Creek Fen during the first year of the study, but had no effect on the richness of plots in the mined portions of Fremont's Fen (Fig. 4.1). The dominant species present in these previously mined areas are those frequently associated with disturbed wetland areas such as *Triglochin maritimum, T. palustre, Deschampsia cespitosa, Agrostis stolonifera, A. gigantea, Potentilla anserina, Ranunculus cymbalaria, Juncus balticus,* and *J. alpino-articulatus*. All of these species actively recruit from seed banks, although each spreads vegetatively once established.

Treated plots recovered rapidly at drained sites and by the end of the experiment little difference between control and treatment plots was evident. At these blocks preserving the propagule bank speeded revegetation, but it did not have a lasting effect on species richness or plot α-diversity (Figs. 4.1 & 4.3). The rapid revegetation came about through seedling recruitment and the sprouting of intact grass and *Potentilla anserina* rhizomes. Although statistical tests showed that treatments could not be distinguished from controls by the end of the experiment, the plot flora, especially in the NPB plots, included a larger coverage of the weedy ruderal species *Lepidium ramossisimum, Descurania ramossisium, Potentilla anserina, Hordeum jubatum* and *Poa pratensis* as compared to controls (Table 4.4).

The Role of the Propagule Bank in Revegetation of Differently Impacted Areas

As discussed above, areas with disparate land use histories reacted differently to the experimental treatments. At the sites with intact hydrology, similarities between the propagule bank and extant vegetation were low with the propagule bank being less species rich and containing more ruderal species than the extant vegetation. The more hydric sites primarily relied on vegetative propagation for revegetation following disturbance even when a viable seed bank was present, perhaps because of germination inhibition or seedling mortality caused by standing water.

When disturbance is widespread and catastrophic, natural revegetation occurs quite slowly as is evidenced by the current site conditions found at Fremont's Fen. This is probably due to several factors working in conjunction. First, wetlands normally dominated by rhizomatous sedges and perennial grasses have often been found to support only a rudimentary seed bank (e.g. Raffaele 1996) and this was found at the intact fen sites where most recruitment originated from vegetative sprouting. Second, the lack of viable seed production in perennial graminoid dominated wetlands is further exacerbated by the low dispersability of the common fen species. Evidence for low disperability is provided by this study where, for instance, very few fen species were found in the seed bank of the drained portion of Crooked Creek Fen even though it was adjacent to the intact fen. Conversely, seedlings from many upland grass and forb species were identified in the intact portions of this site. Finally, after peat removal, an inhospitable environment detrimental to seedling survival is created. Salonen (1991) and LaRose et al. (1997), for instance, have shown that the peat surface exposed after mining experiences large fluctuations in the water table leading to periods of alternating inundation and desiccation.

Vegetation plots in the drained fen recovered quickly from treatments, much more so than treatments in the other areas. These results are similar to those of Salonen and Setälä (1992), who found that dry peat areas in an abandoned peat mine possessed much higher biomass than areas possessing hydric peat. Revegetation of drained plots primarily resulted from propagule bank recruitment and subsequent vegetative propagation. These plots had on the average the largest and most diverse propagule bank and the highest similarity between the propagule bank and extant vegetation. Based on personal observation most of the initial recruitment at these plots actually came from seeds, rather than vegetative sprouting, as was seen in the hydric sites. After initial establishment, vegetative propagation was an important means of revegetation.

There were no changes in the richness of the propagule bank during the experiment, indicating that the propagule bank is rapidly reconstructed after removal, but the characteristics of recovery varied in the different areas. At mined sites, only a few species needed to be added to the propagule bank for replenishment to occur, since it was so species-impoverished to begin with. To a lesser degree this was the same situation at the intact blocks, wherein the native propagule bank is small and the few species that are present can be replaced quickly. At the drained sites, the propagule bank was rapidly rebuilt due to the prolific seeding of the upland species surrounding the experimental plots.

Evaluation of Experimental Treatments

For the most part, the treatments seem to have achieved the goal of reproducing the community level impacts of mining and restorative strategies, although one m^2 treatment plots could never capture the full scope of impacts generated by a many hectare peat mine. Perhaps the main fault with the small scale plots is the large influence that surrounding vegetation had upon the plots. Plots had a small area to perimeter ratio which allowed relatively rapid colonization of the plot by vegetatively spreading species. Similarly, the presence of a concentrated seed source in the immediate vicinity also speeded revegetation of plots through seedling recruitment. Inclusion of test plots in previously mined areas helped mitigate this artificiality and facilitated the evaluation of the large-scale impacts of mining by reducing the edge effects otherwise present in the small experimental plots.

Management Considerations

Intact fens are most sensitive to disturbance and long-term vegetational changes resulting from land use practices such as mining or draining. At least fifteen years after mining, Fremont's Fen still has large expanses of barren peat. Areas that have seen some regrowth are species impoverished and usually have low plant coverage, because revegetation has almost exclusively resulted from vegetative spread from outside of the mine and little recruitment has occurred within the expanse of the mine. Recruitment events within the mined expanse are easy to identify, since they invariably consist of a mono- or bi-typic patch of either *Carex aquatilis, C. simulata, Triglochin* spp., or *Deschampsia cespitosa* resulting from vegetative spread or local seed-rain from the original individual. Revegetation through this mode is necessarily slow due to the large area to perimeter ratio of the mined area and the uncommonness of successful seed establishment.

Even though propagule recruitment is not the primary agent of revegetation, reintroduction of the upper layer of the soil to mined sites can significantly aid in revegetation, demonstrably increasing both species richness and vegetation cover. Probably the largest positive effect of this restoration technique is that it disperses potential recruits throughout the impacted area. In this case, even if initial propagule bank recruitment and establishment are low, the diffuse vegetation patches significantly increase the expansive perimeter and clones will more rapidly coalesce to form a vegetative mat. The localized seed rain resulting from the limited seed dispersal of these clones also helps to increase revegetation. Reintroduction of the upper soil layer also helps to ameliorate the harsh environmental conditions of the barren peat expanse by supplying a layer of more fibrous peat. While the above recommendations prescribe methods to speed revegetation on mined fens, it is imperative to recognize that even using aggressive restoration methods such as topsoil soil replacement, revegetation takes many years, especially in the more hydric fen areas. Further, revegetation does not necessarily imply restoration, since edaphic and other attributes may not respond well to restoration (Chapter 3). Still, the restoration methods need to be developed and employed to help mitigate some effects of mining even if the systems cannot be return to a completely pristine condition.

Conclusions

This study has evaluated revegetation in plots which received artificial disturbances reproducing some of the major effects of peat mining. Treatments were applied to these plots to simulate restoration approaches using either natural revegetation or the reintroduction of surficial peat after mining. The patterns of revegetation under these conditions were also evaluated.

Treatments had significant effects on vegetational characteristics, some of which were attenuated over the course of the experiment. Site history affected the rate and characteristics of revegetation. Treatments reduced species richness in blocks located in intact fens and richness generally increased throughout the experiment. In previously impacted areas, species richness reattained control levels by the end of the first growing season, so treatment effects were insignificant. Total vegetational coverage also generally increased during the experiment, although coverage gains in hydric, undrained sites were minimal. Maintenance of the propagule bank significantly speeded this revegetation, but in the wettest sites the presence of the propagule bank had only a marginal effect. Vegetational composition recovered most slowly in treatments located in intact fens and these treatments did not develop vegetation similar to their controls. In treatments located in previously impacted areas (i.e. mined and drained), treatment plot species composition became statistically indistinguishable from controls by the end of the experiment.

There was no change in either the species richness or composition of the propagule bank detected between the beginning and end of the experiment. This is attributed to the propagule bank recovering by the end of the first season of the experiment. There was a generally low correlation between the propagule bank and extant vegetation and similarity indices measuring this correlation did not vary throughout the experiment. Similarity between the propagule bank and extant vegetation was greatest in control plots, followed by tilled and NPB plots, respectively.

Many wetlands have been negatively impacted by land use practices. In South Park, Colorado fens and wet meadows have received the brunt of these impacts. As knowledge of the many important functions performed by these wetlands has come to light, a new emphasis on devising effective restoration strategies for damaged wetlands has arisen. Commonly employed restoration strategies range from the allowance of natural revegetation to reintroduction of native wetland topsoil. This study has shown that intact fens are highly susceptible and slow to recover from disturbance, but under most conditions reintroduction of native topsoil can significantly speed revegetation of disturbed areas.

CHAPTER V

SUMMARY AND SYNTHESIS

This dissertation has detailed the findings of a four-year study of the ecology of the calcareous fens found in South Park, Park County, Colorado. These fens contain some fifteen state rare or regionally endemic species, several uncommon plant assemblages or community types, and perform important environmental functions (Johnson 1996a). Such attributes make these fens one of the most important wetland resources in the state, and perhaps the Rocky Mountains. My aim has been to describe the vegetational assemblages and environmental conditions found on these fens, elucidate those environmental factors which influence patterns in species composition, investigate the ecological effects caused by peat mining and draining, and finally, evaluate patterns of vegetational recovery at experimentally disturbed sites. This chapter will summarize the major findings of this study and synthesize the major concepts of fen ecology in South Park.

Calcareous Fens – Origins and Attributes

South Park's fens are found in depressions and basins which have formed in the substrate. The substrate is most commonly alluvium and/or colluvium deposited during the

Bull Lake glaciation, but it can also be bedrock (as at Crooked Creek Fen, which lies on a bed of Maroon Formation sandstone). Most of these fens are located in shallow river valleys, which are either relict or still have active channels. The river valleys provide a depression which facilitates peat accumulation. Peat accumulation likely starts with a damming of the valley channel, but once the peat body has formed, the peat itself acts to impede water flow and helps maintain an elevated water table. In this way the fens are autogenous systems, however, in this region they need some type of catalytic event to initiate the formative process.

South Park's calcareous fens are only located in areas that receive large amounts of ground water discharge. Most commonly, such areas lie near the base of mountain and hill-slopes where changes in hydrologic gradient produce positive hydraulic head which discharges through porous or fractured strata. Fens may also be found more than a mile from any appreciable topographical gradient and in situations that are nearly flat, though. In such cases, ground water travels laterally under positive pressure below an occluding stratum until it can emerge through a disconformity such as a bedrock fracture.

Areas of ground water discharge within the fens can be either discrete or diffuse. In the former case discharge points are generally associated with particular surficial features such as raised peat aprons, springs, or rings of cobbles, and are fairly easy to identify with experience. In the latter case, discharge occurs across expanses with many small springs and may be more difficult to identify with certainty. Diffuse discharge is most commonly associated with expanses of quaking soil which appear abruptly and are often adjacent to much more mesic or upland areas.

Calcareous fens may have an inlet stream, outlet stream, both, or neither. In some cases, such as High Creek Fen, a surface inlet was historically present but is no longer active due to either anthropogenic or natural changes. Most fens have some type of surficial outlet, but Crooked Creek Fen is an example where no natural surface outlet is present. Currently, a ditch perpendicular to the hydrologic gradient dissects Crooked Creek Fen into two unequal portions and diverts essentially all surface and ground water to a depth of between 1 and 1.5 m. Beyond this ditch, no relict outlets have been noted in the drained portion. Consequently, surface and ground water must have originally continued traveling down gradient, past where the ditch now exists, eventually seeping back into the aquifer and evapotranspiring to the atmosphere.

The three fens studied have many species in common, including rich and extremely-rich fen indicator species, such as *Kobresia simpliciuscula, K. myosuroides, Triglochin maritimum* and *T. palustre*, and have pHs ranging between 6.8 and 7.9. Pore waters are also nutrient rich, with electrical conductivites between 516 and 608 μS, and calcium concentrations typically more than 100 mg/l, and often over 200 mg/l. Based on such attributes these fens are significantly different from the typical intermediate- or moderate-rich subalpine fen, and each fen is classified as an extremely-rich fen.

While these fens are clearly different from typical moderate-rich subalpine fens, large variances in species composition and environment occur both within and between fens. Landscape level factors such as geology, geomorphology, and geohydrology dictate the occurrence of calcareous fens, but differences in these attributes also influence the individual character of each fen. The vegetational differences between the fens studied illustrated in the ordinations of Chapter 2. Crooked Creek Fen for instance, possesses a richer and more extensive moss flora than the other sites studied. It also has a higher percentage of shrub cover and its water tracks are dominated by *Carex utriculata* and *C. aquatilis*. Fremont's Fen on the other hand is nearly devoid of shrubs, has a poorly developed moss flora, and possesses large expanses of relatively dry fen with highly developed microtopography. High Creek Fen is comprised of a series of sedge-dominated fen expanses connected by a network of water tracks and quagmires. Throughout High Creek Fen are scattered raised islands of buried alluvium whose canopies are dominated by blue spruce or willows.

Within each of these fens vegetation gradients are also present. The gradients are primarily due to differences in water table depth and position relative to the mire margin or expanse, but variation in water and soil chemistry also have an effect on local species composition.

The inherent heterogeneity exhibited by these wetlands raises questions about what exactly is encompassed by the term extremely-rich fen. As it is most commonly used in this region, this term refers to a wetland complex containing a mosaic of small scale habitats which may include fen expanses with organic soils, meadows located on mineral soil, willow carrs, marly flats, and isolated upland islands. Extremely-rich fen is technically a misnomer in this case, since the term fen implies pervasive organic soils. According to definitions in the peatlands literature these systems, rather, would fall under the definition of mire. Mire is a broad term that has not been subject to refinement based on chemical or species criteria, though. Therefore, I recommend that when the term fen is used to denote the entire peat and mineral soil expanse of these subalpine wetlands that is be modified to "fen complex" to explicitly recognize the mosaic of habitats to which one is referring. This makes the term consistent with traditional and regional usages and avoids the undesirable necessity of dividing an interconnected wetland complex into units having indistinct or arbitrary boundaries. When specifically referring to areas with organic soils the term fen alone can be used.

Using the above terminology, extremely-rich fen complexes should contain within some part of the contiguous wetland: (1) areas with organic soils; (2) pore water pH greater than 7.0; (3) pore water electrical conductivity of more than 200 µS; and (4) pore water calcium concentration greater than 30 mg/l. The wetland should also include plant species and associations indicative of extremely-rich fens as detailed in Chapter 2. Again, the entire wetland complex need not consistently possess all of these traits, but rather they must be found within the integrated and inter-dependent complex of wetland habitats.

Generalized Patterns and Processes in Calcareous Fens

Using the framework developed above, a general model of fen structure and ecology can be developed. Figure 5.1 shows an idealized calcareous fen complex which will be used to illustrate many of the points discussed in this section. Not all fens have all of the features shown in the figure, nor does the figure represent all possible fen configurations.

Figure 48a shows the landscape setting of the idealized fen. The fen is located at the base of mountain slopes and receives discharge of ground water that has been traveling below an occluding layer under positive pressure. As diagramed, the fen substrate is alluvium, although it could also be bedrock with the ground water moving between strata. The ground water discharges at a disconformity and emerges into the peat body causing the formation of

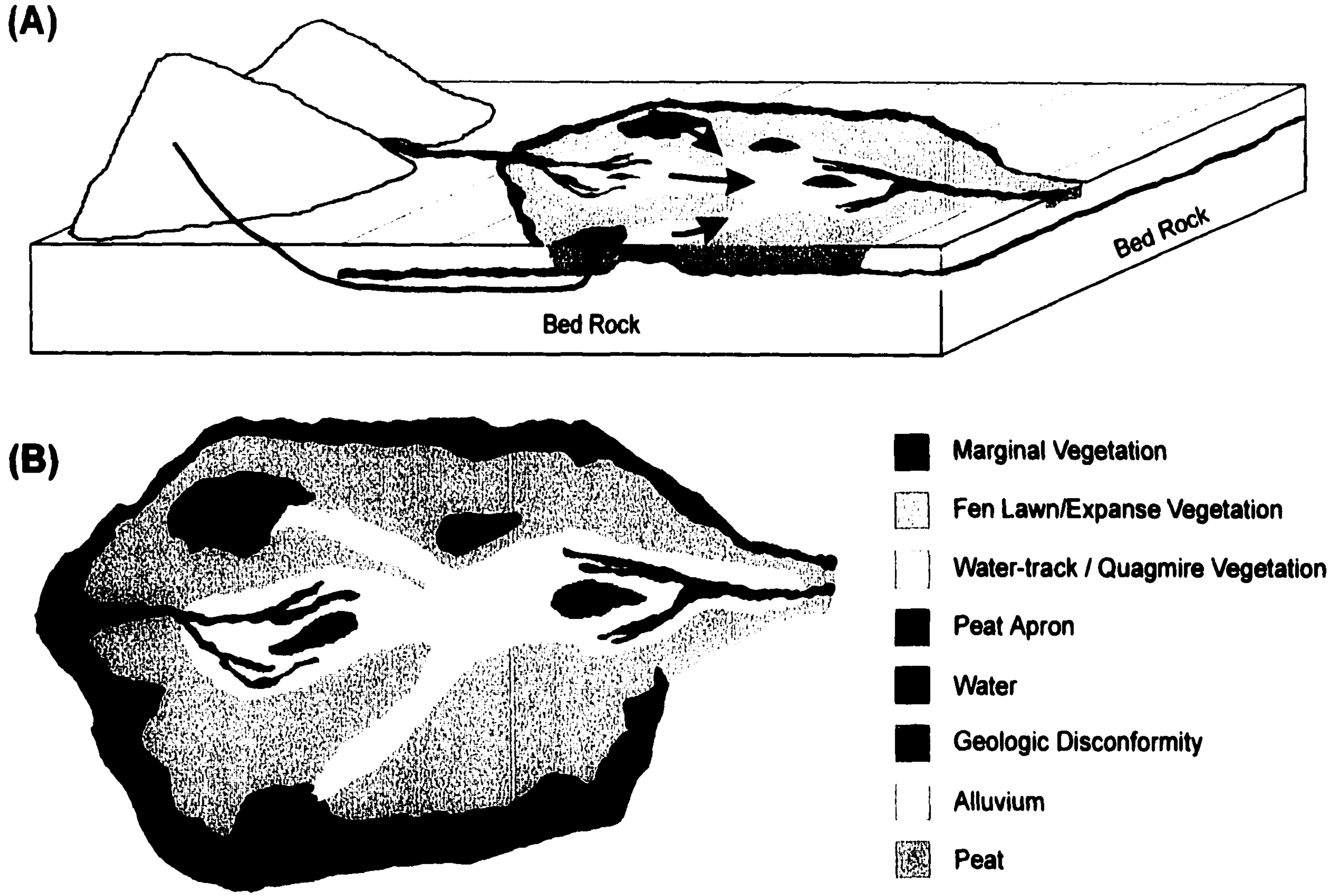

Figure 5.1. The upper figure (a) shows a landscape view of an idealized calcareous fen. The lower figure (b) shows the distribution of vegetational assemblages in plan view.

two peat aprons. A surface inlet is also present in this diagram. As the stream enters the fen, the low gradient and thick vegetation reduce the stream's energy causing a gradual reduction in channel depth until finally the channel is lost and the surface flow is dissipated across the fen surface. In some cases, a small channel or braided channel network runs the length of the fen. Whether or not this is the case depends to a large degree on the fen's topographical gradient. Water from the surface and ground water sources is preferentially conveyed along water tracks, which are typically linear floating mats of vegetation atop unconsolidated aqueous peat. The water tracks often become divided or braided by raised mounds of alluvium or knobs of bedrock. Near the toe of the fen, water-tracks coalesce and frequently surface channels will form owing to the increase in flow volume. Once formed, channels eventually join to form a single outlet stream.

Although flow rate and volume may be higher in the water-tracks, significant ground water also moves through the peat body. Such flow maintains water table elevations in the fen expanses and along the fen margin. Because ground water sources tend to be concentrated to inward of the fen margin, when the fen experiences high evapotranspiration loads and/or reductions in water input during the middle of the summer, marginal areas are more subject to water table drawdowns and often do not support organic soil accumulation.

The hydrologic patterns and chemical gradients present on these fens control gradients of species composition and the occurrence of vegetational assemblages. Figure 48b shows a hypothetical distribution of fen vegetational types. Fen margins, subject to water table fluctuations, have a drier hydrologic regime than that of the fen interior. They also tend to be more nutrient rich since ionic levels of the incoming water have not been attenuated by root uptake or adsorption to organics. This is especially true when water sources are located near to the fen margin. Fen margin soils and ground water may also have a higher salt content due to the evaporative deposition caused by soil drying. Marginal areas tend to be dominated by either of two plant community types. In fens with relatively steep topographical gradients and where surface flow is present during some portion of the season, willow carr vegetation develops. *Salix brachycarpa, S. monticola, S. planifolia,* along with various sedges and forbs characterize the flora of these sites. At fens with a low topographical gradient, generally those towards the interior of South Park, meadow vegetation develops. In the driest situations, this vegetation contains a number of salt-tolerant or halophilic species such as *Hordeum jubatum* and *Argentina anserina* and has little microtopography due to the lack of soil organic matter. In wetter marginal meadows, microtopography can be the most highly developed of any community type examined. Such sites are characterized by an abundance of *Deschampsia cespitosa, Kobresia myosuroides, Carex scirpoidea,* and *Thalictrum alpinum*. It is also in these areas that the globally rare plant *Ptilagrostis porteri* grows.

Fen margin communities may also be found within the fen expanses on the small rises which frequently occur. Although at first the term "margin" may in this case seem a misnomer, in fact these rises possess environmental conditions and species compositions very much like those found on the exterior of the fen. Such rises may possess either meadow or carr vegetation, but at least some shrub cover is usually present. These communities add greatly to the vegetational complexity of the fen and their presence adds significant floral and faunal habitat heterogeneity.

To the interior of the marginal vegetation are the fen expanse communities. These communities are typically dominated by sedges and have various degrees of coverage by willows and shrubby cinquefoil. Fen expanses may have significant microtopographical development, or it may be nearly non-existent. As a general rule, areas with higher shrub cover have more highly developed microtopography, whereas fen lawns possess little microtopographic complexity.

Within the fen expanses are also found the water-tracks and quagmires. These are the most hydric sites examined and, in some cases, seem only barely terrestrial. Water-tracks are relatively linear features with shallow, visibly flowing surface water throughout the year. Two types of water tracks were observed during this study – those dominated by *Eleocharis quinqueflora* and those dominated by *Carex utriculata* and *C. aquatilis*. The former are the most common and typical of water-tracks both within this region and globally. On the *Eleocharis*-dominated water tracks, plant coverage is sparse but evenly distributed, and the soils are coated with algae and sediment that has settled out of the water column. The water-tracks dominated by sedges do not fit the typical description of water-tracks described in the literature, yet they clearly play the same role in the fen system. Such water-tracks are found in higher gradient situations or where surface water is deeper than in the *Eleocharis*-dominated water-tracks. Water depths are typically 10cm or greater. There may also be narrow channels associated with these water-tracks cut by the relatively high energy surface water. The sedge dominated water-tracks likely occur because the large stature of the sedges allows them to withstand the high flow velocity and remain emergent in the relatively deep water.

Amorphous quagmires are found intermixed within the linear water-tracks, in broad, low-gradient areas. The low hummocks, which are the only features that breach the shallow surface water, are rich with accumulated marl, while deposits of algae coat the bottoms of the hollows. Very little emergent vegetation grows in the hollows, but aquatic species such as *Utricularia* spp. and *Scorpidium scorpioides* can be common. On the rises, small-statured plants such as *Trichophorum pumilum, Eleocharis quinqueflora, Triglochin* spp. and *Thalictrum alpinum* grow, along with occasional individuals of *Salix candida*.

Detailed comparison of calcareous fens may reveal particular differences between sites, such as in floristic composition or water chemistry. What is perhaps more enlightening though, is how such examinations reveal the similarity of calcareous fens to one another and to other types of subalpine fens. The calcareous fens described in this study exhibit the four gradients of vegetational change found in fens throughout the world including, gradients due to water and soil chemistry, position within the fen (mire margin to expanse), microtopography, and regionality. Such a finding in sites which superficially appear so distinct from other fens in the region lends encouragement to hopes of producing generalized models of subalpine fen ecology.

Disturbance to Fens and Their Revegetation

Subalpine fens are extremely fragile systems. The environment present in these fens has been quite stable since their inception several thousand years ago as evidenced by the significant accumulation of peat. In fact, these are likely some of the most stable ecosystems in the Rocky Mountain region. Perturbation of the natural conditions or mechanical disturbance have far reaching impacts, many of which are irreversible.

Peat mining strips away the organic soils which have taken thousands of years to form. This creates a barren surface, unconducive to revegetation. The entire propagule bank is removed in this process and with the limited seed dispersal and viability of the native species, little establishment through sexual means occurs. Instead, vegetative expansion from intact plants along the perimeter of mined areas is the primary mode of revegetation, although this process occurs quite slowly due to the large area to perimeter ratio. Also, the vegetation that does colonize such areas is species poor, which is a marked contrast to the native plant associations.

Peat mining removes much of the water storage capacity of the fen, altering the hydrologic properties of both the fen and, presumably, its receiving streams. Additionally, the surface water flowing across the denuded, exposed peat tends to incise small channels instead of moving as diffuse surficial flow. This, too, affects the fen hydrologic regime by inequitably distributing water across the fen and causing desiccation of the surfaces between the channels. Finally, peat mining decreases the ability of the fens to improve water quality by sedimentation and adsorption, and can lower the quality of water flowing through the fen. Reduction of water quality was most strongly seen at High Creek Fen, where significant amounts of uranium were released from the disturbed soils in the mined areas.

Removal of ground water inputs through ditching has profound effects on fen ecology. As shown at Crooked Creek Fen, ground water interception to a depth of one meter completely altered the wetland system. Significant impacts from lesser water table depressions would also occur, but such impacts cannot be described based on the information gathered in this study. Ground water interception on Crooked Creek Fen led to a nearly complete change in the species composition from that of a willow and sedge dominated system, to one of annual and perennial grasses and forbs. Draining has also caused a change in edaphic characters due to oxidation, shrinkage and compression of the peat body. These changes were seen in this study as increases in the soil bulk density in drained versus intact organic soils, and changes in the peat structure. Based on European studies, many of the original edaphic characteristics may not be restorable, although restoration has not been attempted in subalpine fens.

As stated above, natural revegetation of mined areas occurs only very slowly, and primarily through vegetative growth. This was evident from examination of current mine conditions, and was confirmed through experimental manipulations intended to reproduce many of the effects of mining. Experiments and observations show that reintroducing the native propagule bank in the upper soil surface can significantly increase the rate and floristic richness of revegetation. Within intact fen areas, the difference between plots with and without the propagule bank intact were greatest. Experimental plots located in previously mined areas reclaimed with stockpiled fen soil, showed rapid recovery to control levels. This indicates that the flora which has colonized the reclaimed mine is one with a relatively high fecundity and seed viability. The experimental plots located in mined areas that had not received post-mining treatment were also quite similar to control plots, but this was because all of the plots had very little vegetation. This again shows the extreme consequences of peat mining especially when coupled with a lack of restoration.

Calcareous fens, like those of South Park, Colorado are one of the Rocky Mountains' great wetland resources. These fens are floristically diverse, environmentally beneficial, aesthetically valuable and extremely fragile, but many have been significantly impacted, perhaps irreparably. Still, there are many sites which are relatively pristine or which may be restorable to a significant degree.

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APPENDICES

APPENDIX 1

Methods of Community Analysis

Although community ecology has been a formal science for more than 100 years, two fundamental questions still lie at the root of most investigations. First, how do species respond to environmental gradients? Second, are there species assemblages which consistently respond to the same complex suite of environmental factors and can these assemblages, therefore, be grouped into vegetation types?

Satisfyingly answering these questions is far from trivial. Biotic communities are inherently complex containing numerous species, each of which responds uniquely to a single, or interaction of many, environmental factors (e.g. Tilman 1982). Such complex interactions exponentially compound analytical contingencies. Ecologists have devised or adopted a number of analytical methods, each of which has its own particular advantages and disadvantages. Suites of analytical methods are generally employed to take advantage of a technique's strong points and compensate for its short comings. For example, ordination and direct gradient analysis can be sequentially applied to community data. Applying these two methods in tandem is a powerful approach to parsing systematic change in community composition from random noise (Gauch 1982, Økland 1996). If description of discrete vegetational types is desired, community classification may also performed to create a triad of methodologies (Gauch 1982). This review will describe the theory and application of ordination, direct gradient analysis and classification, focusing on techniques used in the current study.

It is most desirable to explicitly link changes in community composition to changes in environmental factors. If one or a few species are of interest, a measure of species performance, most commonly abundance, frequency or biomass, can be regressed against measured environmental factors. This type of analysis provides, perhaps, the most straightforward analysis of a species response to an environmental gradient. Whittaker (1967) described this process and dubbed it "direct gradient analysis".

Ordination

The limitations of this individualistic approach quickly become evident as increasing numbers of species and environmental factors are considered. To circumvent this problem, several ingenious numerical methods have been adapted from other scientific fields or developed for ecological problems in particular. The first set of techniques seek to indirectly elucidate causative environmental gradients through changes in species composition (Whittaker 1967). The basic premise of this approach is that species growing in a given habitat are directly coupled to the suite of environmental factors present in that particular locale. Species finding the conditions at a site more amenable to their own physiological requirements will grow larger, more densely, or more consistently in that environment. But species do not respond identically to each environmental factor, or combination thereof. For instance, species x and species y may respond similarly to differences in soil moisture, while responding to pore water calcium in disparate manners. Therefore, each species contains both unique and redundant information about the environment in which they grow.

Indirect analytical techniques seek to take advantage of these ecological attributes. By ordering samples according to their species composition one may subsequently infer the underlying causes of vegetational change. The nature of causative environmental gradients subsequently can be deduced based on the experience of the investigator, or more objectively by using statistical techniques such as regression. Using this approach, the inference of causative environmental gradients is secondary to the quantification of vegetational change; therefore, such techniques are referred to methods of "indirect gradient analysis" (Whittaker 1967). Because sites are ordered during the process, it is also frequently called "ordination" (Gauch 1982).

Ordination methods seek to reduce the dimensionality of ecological data by eliminating the redundancy contained in species data and extracting the most significant axes of variation in species composition. Again, the gradients of vegetational change are assumed to correspond to changes in environmental factors. The gradients are generally not related to a change in a single environmental variable, rather, they represent the subtle interaction of several factors. In this regard, plants are used to integrate and manifest the effects of environmental factors. As such, gradients extracted during ordination are referred to as complex or latent gradients.

Goodall (1954, pg. 322, in Gauch 1982) nicely summed up the utility of ordination methods in reference to ordination with principle components analysis. He said:

"There is much to be said for the view that the complexes of environmental factors determining plant distribution can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements; this is, of course, the idea behind using 'phytometers' in agricultural meteorology"

Examples of currently used ordination techniques are weighted averaging (WA), polar ordination (PO), principal components analysis (PCA), correspondence analysis (CA) and related methods, and non-metric multidimensional scaling (NMDS). The methods by which these techniques reduce dimensionality and order sites are mathematically diverse, although at times conceptually similar. Each of these methods will be considered briefly, except CA which will be described in more depth due to its relevance to this study, and NMDS which will not be discussed because of its methodological dissimilarity to the other techniques.

Weighted Averaging

Weighted averaging was one of the earliest ordination techniques (Whittaker 1948, Curtis and McIntosh 1951). Weighted averaging produces an ordination based on sample species composition and the investigator's knowledge of the species' ecological preferences. The formula for WA is:

$$S_j = \frac{\sum A_{ij} W_i}{\sum A_{ij}} \qquad (1)$$

where A_{ij} is the abundance of the ith species in the jth sample, and W_i is the weight applied to the ith species. The summations are for all species i. Weighted average ordination is almost a hybrid of direct and indirect gradient analysis, because the weights that are applied are generally related to a known environmental gradient. This feature makes axis interpretation relatively straightforward compared to pure indirect techniques (see below). Weighted averaging ordination is not frequently used today due to its subjectivity, however, the basic formula and concept are integral to correspondence analysis and its derivatives; these are most commonly used and powerful gradient analysis techniques available.

Polar Ordination

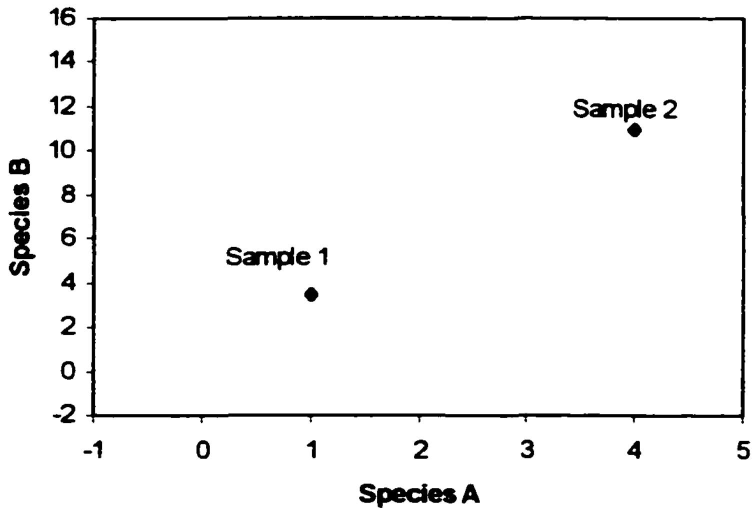
Polar, or Bray-Curtis ordination (Bray and Curtis 1957), orders sites by constructing a species similarity (i.e. distance) matrix for vegetation samples, and then determining the sample distance from two subjectively chosen endpoints. Endpoints are generally chosen through the ecologist's knowledge of the site conditions. Although polar ordination explicitly requires subjective input from the researcher, it has been found to be a robust and useful technique that is not based on assumptions regarding the statistical distribution of the data (Beals 1973, Beals 1985).

Principal Components Analysis

Principal components analysis (Hotelling 1933) is a mathematically elegant method of eigenanalysis that creates linear equations of site (subject) variables, such as species, to designate site placement. Although, PCA was originally developed to meet the statistical needs of social scientists, Goodall (1954) suggested its utility in the ecological sciences. Principal components analysis was revolutionary in that it was the first ordination method that it worked directly on the data matrix and did not require subjective input from the investigator (Gauch 1982). It was also efficient in that it could order species and sites simultaneously.

Reduction of dimensionality is a goal of PCA and ordination methods in general. A simple figure will help illustrate the way in which ordination methods achieve this goal. Figure A1 shows a simple bivariate example of how site placement is accomplished. The abundance of species A in samples one and two form the abscissa values, while the abundance of species B in these samples are the ordinate values. Plotting these values in the ordination diagram gives a graphical representation of site similarity. A third species could easily be added to the diagram by adding an additional axis perpendicular to the paper. Adding this third axis would provide sample placement in three dimensions. Principal components analysis continues this logic into n-dimensions, where n equals the number of species. Note that this type of construction could also be used to order species, by using samples as the axes instead of species.

Continuing the above example, Fig. A1b shows the ordering of samples when the abundance of species A and B are measured in many sample plots. In PCA a least-squares regression is performed on the data in the direction of greatest variance. The sample points are then rotated such that the regression line is parallel to the x-axis. When so arranged, the x-axis becomes the first, most important complex gradient; in PCA, the first principal component. To extract the second gradient, another regression is performed with the constraint that it is orthogonal to the first axis (shown as the short line in Fig. A1b). In this example, no additional axes may be extracted, as the maximum number of axes equals the



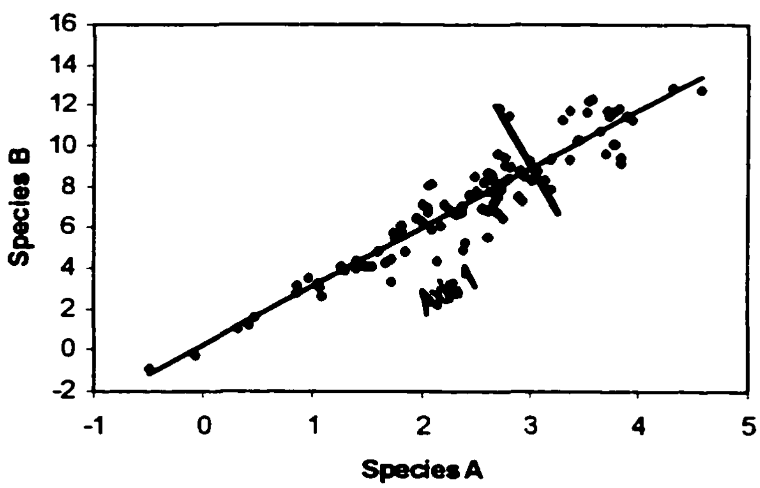


Figure A1a-b. Figure A shows a bivariate ordination of two samples based on the relative contributions of two species. Figure B shows placement of additional samples based on the two species and two orthogonal linear regression lines indicating directions of maximum variance. See text for additional details. After van Groenewoud (1965) and Gauch (1982).

number of variables (species). In actual applications with more than two species, additional axes may be created, although the importance of gradients decreases as the axis number increases. The importance of any given axis is described by its eigenvalue. In PCA, the eigenvalue is equal to the percentage of the total variance accounted for by the given axis.

Although PCA seems a promising tool for ecological analysis, it has certain significant short comings. Most notable is the "horseshoe" or involution of the second and higher axes (Gauch 1982, Peet et al. 1988). When the horseshoe is present, much of the structure of site scores is artificial, driven by the large proportion of zeros in the data (Jackson and Somers 1991). That is, sites at either end of a true gradient are placed relatively close to on another based on the percentage of zero values rather than on composition. To maintain the necessary distance from these extremes, mid-gradient sites are forced upward in the ordination diagram.

This undesirable property of PCA is due to its use of a linear response model, wherein species are assumed to respond monotonically to environmental gradients. If only a small section of a gradient is sampled this might be the case and PCA the appropriate analytical technique (Ter Braak and Prentice 1988, Jongman et al. 1995); however, monotonicity of species response has been found to be the exception rather than the rule in ecological studies. When longer gradients are sampled, species' abundances rise and fall more or less unimodally along those gradients, and PCA cannot be modified to successfully deal with data of this type.

Correspondence Analysis

Correspondence analysis addresses the linearity problem of PCA. It was first developed by Hirschfeld (1935) and Fischer (1940), but was perhaps first applied to ecological problems by Goff (1967, in Gauch 1982). The technique was made popular in ecology by the work of Hill (1973, 1974).

Correspondence analysis is also know as reciprocal averaging. This term more intuitively describes the technique's approach. Correspondence analysis uses the formula for WA (equation 1) to generate sample and species scores, but it additionally employs an iterative (reciprocal) averaging algorithm. CA begins with arbitrary species scores used as weights (W_i in equation 1). With these weights, samples scores are generated. The new sample scores are then used as weights (W_i) and new species scores are calculated. Using this reciprocal averaging algorithm species and sample scores converge on a unique value after a number of iterations. By employing a reciprocal averaging approach, CA is essentially a technique of successive approximation (Gauch et al. 1977). Additional axes are extracted by making axis scores uncorrelated with previous axes, similar to in PCA.

Eigenanalysis is performed on the species by samples matrix to generate eigenvalues also as in PCA. The sum of all eigenvalues in CA is termed the total inertia (Jongmanet al. 1995). Unlike eigenvalues in PCA, CA eigenvalues do not directly give the percentage variance accounted for by an axis. Rather, this variance is calculated by dividing the axis eigenvalue by the total inertia.

As mentioned above, species abundances generally rise and fall unimodally along an environmental gradients. Although this has been known since the beginning of the century

(Ter Braak 1996), Gause (1930) formalized the notion of the species response curve. Gauch (1972) and Whittaker (1956, 1967)stressed the notion of the unimodal species response, and popularized the use of the Gaussian curve as a representation of the response (Ter Braak 1996). Ter Braak (1985) showed that CA approximates the maximum-likelihood solution for fitting unimodal Gaussian response curves to all species simultaneously.

There are four primary assumptions implicit in the use of CA: (1) the entire physiological range of each species is included within the sampled gradient; (2) Species' optima are equally spaced along the environmental gradient; (3) Species have equal tolerances; and (4) Species have equal maximum values. These conditions are those described by Whittaker (1973) as the species packing model. Meeting all of these assumptions is generally not a reality in ecological studies. Fortunately, relaxation of these assumptions does not pose a significant problem for ordination techniques (Ter Braak and Prentice 1988).

Axes in CA can be scaled in units of standard deviation to enhance gradient interpretability. Species abundances rise and fall over approximately four standard deviations (S.D.), so one can expect that plots separated by four S.D. have no species in common. With a difference of one S.D., about50% species in common is expected (Gauch 1982).

Like PCA, an advantage of CA is that it ordinates both species and samples simultaneously. Both species and samples can be displayed in an ordination diagram called a biplot. Biplots have particular rules pertaining to their interpretation, and the rules vary somewhat according to scaling options chosen during the analysis. Primary to ordination interpretation is the centroid rule. The centroid rule states that because species scores are the weighted average of site scores, species scores are located in the centroid of sample points in which that species occurs. That is, samples which contain the species are scattered around the species point (Ter Braak and Smilauer 1998).

The second interpretive rule is the biplot rule, which is interpreted as follows. A species point is connected to the origin with a vector. This vector may then be extended in either direction. Perpendicular lines are then drawn from sample points to this vector. The order of sample point intersection along the species vector ranks the relative abundance of that species in the sample plots. In order for the biplot rule to be in effect, "biplot" scaling must be enacted in the ordination analysis. Usage of biplot scaling and its rule is most attractive and quantitative when gradient lengths are short (<3 S.D.).

The final interpretive rule is the distance rule. The distance rule is an extension of the centroid principle. It states that a sample close to a species point is more likely to contain that species than sample point more distant from the species. The distance rule is applied when Hill's Scaling is in effect and gradient lengths are greater than 3 S.D.

Soon after its adoption, two problems with CA became evident. First, the second axis was found to frequently display structure in the shape of an arch that was not contained in the data. Second, the technique compressed the ends of gradients on all axes. The arch in CA has been described by several authors (Hill 1973, Hill 1974, Gauchet al. 1977, Hill 1979a, Hill and Gauch 1980). The arch arises when the second CA axis is simply a parabolic distortion of the first axis. Higher axes can also show a similar relationship to the first, except that the relationship is based on higher order polynomials. The arch results from the conditions imposed during axis extraction, namely that the higher order axes must not have a *linear* relationship with the first. The arch arises because the second axis meets this criterion, but instead it shows a *non-linear* relationship to the first axis. This contrived axis possesses a relatively high eigenvalue, usually about half the first, and so suppresses lesser, true gradients. Since it is just a permutation of the first axis, the second axis conveys no additional information. It should be noted that although qualitatively similar to the PCA horseshoe, the arch of CA is caused by an entirely different problem (Peetet al. 1988).

The second problem with CA is the compression of gradient ends. This problem is evident on all axes and results from species lying near the gradient ends having their optima outside of the sampled gradient. Essentially only a portion of those species' response curves are found within the sampled gradient; a violation of the first assumption underlying CA. This reduces the relative variance in abundance for those species and causes the compression of sites near the gradient edge.

Hill (1979a) introduced detrended correspondence analysis (DCA), and since then DCA has generally been shown to perform better than CA (Hill and Gauch 1980, Gauch and Whittaker 1981, Ter Braak 1985, Peetet al. 1988). Detrended correspondence analysis was developed to address the two main problems with CA, the arch and gradient end compression. The arch is removed by detrending the second or higher axes. Detrending involves dividing the first axis into a number of segments, then adjusting the axis 2 scores within these segments to have a zero mean. This makes the second and higher axes not just *uncorrelated* with the first, but it allows *no* systematic relationship.

Gradient end compression is overcome by non-linear rescaling of axes. Rescaling is accomplished by dividing an axis into a number of segments. Within these segments, site placement is expanded or contracted such that intra-segment variance is equilibrated across all segments. Detrending and non-linear rescaling indeed remove any hint of arch or gradient end compression, but they are not without their own problems.

The merits and deficits of DCA have been discussed at length and the technique has been variously lauded or panned. Many studies of the method present diametrically opposed results. Such disparate findings can generally be attributed to the use of different test-data structures, different result interpretation, or different personal tolerance of structural distortion. Concerns about DCA mainly surround the "ad hoc, brute force fashion" in which detrending and rescaling take place (Peetet al. 1988). As Beals (1985), Pielou (1984), and Minchin (1987) point out, detrending is effected without regard to structure present in the data, therefore actual arch shaped structure in the data may be destroyed by the process. This is in fact true, however, the potential loss of structure must be weighed against the display of artificial structure.

A series of articles critiquing DCA was begun by Wartenberg et al. (1987). They recommended that DCA not be used since their results showed the method unable to recover structure on axes higher than the first. Minchin (1987) had similar results in his study of DCA, however, his conclusions were not quite as condemning. Peet et al. (1988) pointed out that Wartenberg et al's (1987) artificial data set consisted of only one gradient of variation, so second and higher axes extracted by DCA would not be expected to uncover additional structure. Peet et al. (1988) went on to report that DCA did in fact recover higher gradients when they actually existed in the artificial data set, even if there was some distortion. They concluded that "DCA is one of the most powerful multivariate tools available for representing pattern in communities composed of attributes (species) that vary unimodally along underlying compositional gradients. With multidimensional species data, detrending and rescaling can facilitate interpretations" (Peet et al. 1988; pg. 932-933). They went on to acknowledge flaws in DCA which they considered "minor", and suggested that additional work be directed at improving the detrending and rescaling algorithms.

In the final article of the series, Jackson and Somers (1991) showed that site placement was unstable when differing numbers of segments were employed during detrending and rescaling. They offered no recommendations as to how to remedy this problem or what an optimal number of segments might be.

Van Groenewoud (1992), too, was critical of DCA. Based on complex gradients generated graphically, he found that DCA reconstructed the first gradient of artificial data well, but later axes were only meaningful if their eigenvalues (importances) were much less than the primary axis'. Palmer (1993) contradicted this assertion, finding that DCA did indeed, reconstruct the gradients present in an artificial data set. Palmer (1993) did not offer an explanation for the disparity between the two study's results.

Such antithetic results make evaluation of the technique problematic. DCA has been justifiably criticized by a number of authors, although several complaints have been successfully dismissed (e.g. Peet et al. 1988) . Data gathered during field studies may be more simple or more complex than artificial data sets. Every ecological study investigates a unique situation wherein the structure of vegetation, sampling intensity, and sampling methodology vary in response to site conditions and practical issues. Ultimately, the utility of a statistical modeling approach such as ordination comes down to its performance on the unique qualities of the particular data set in question and the interpretability of its results.

Using real data, I have found that DCA successfully reconstructed the secondary vegetational structure in a fen in Rocky Mountain National Park, Colorado (Johnson 1996). DCA highlighted unobvious vegetational gradients in the current study and so was found to be a highly useful technique (see Chap Two). Detrended correspondence analysis is also handy because of its close relation to other multivariate techniques such as TWINSPAN and CCA (see below). Such a relation makes the results provided by each technique directly comparable (e.g. Allen and Peet 1990, Odland et al. 1990, Prentice and Cramer 1990, Johnson 1996).

Classification

There are several methods of classification available to the ecologist. The most common include ordination space partitioning, cluster analysis and two-way indicator species analysis (TWINSPAN). Ordination space partitioning simply consists of subjectively partitioning the ordination diagram based on a visual assessment of stand placement and the experience of the investigator (Gauch 1982). Ordination techniques appropriate for this type of classification were described in the above section. Cluster analysis was not used in the current study and such a complex subject could not be given just attention in this general overview; therefore the reader is directed to Gauch (1982) or van Tongeren (1996), for a lucid and detailed discussion of the topic.

Two-way indicator species analysis was developed by Hill (1979b) and discussed by Gauch (1981). It is a divisive, hierarchical, polythetic classification technique that was developed for ecological problems in particular. TWINSPAN is based on the ecological precept that vegetational types may be distinguished by differential groups of species that are more prevalent on one side of a dichotomy than the other (van Tongeren 1996). Since the use of such differential species is essentially a qualitative procedure, species abundances must somehow be converted from quantitative percentages to qualitative differential species. Hill cleverly overcame this problem by developing "pseudo-species". For each species abundance, one or more pseudo-species is assigned. Pseudo-species are based on minimum abundances values corresponding to a cut level, therefore, the more abundant a species is, the more pseudo-species will be used to qualify its contribution to community composition. For example, if three pseudo-species cut levels are assigned at 1, 25, and 50 percent cover, than species x with an abundance of 1 percent cover would be represented with one pseudo-species x_1. Species y with a cover of 30 percent would have two pseudo-species, y_1 and y_{25}, and so on. Pseudo-species are also a handy tool for discerning community types in the field and in constructing dichotomous keys because the relative abundance of a species, not merely its presence/absence in a site, can be used as an indicator of group membership. Odland et al. (1990) suggested using cut-levels that correspond to traditional phytosociological scales. Odland et al. (1990)used the Hult-Sernander- Du Rietz scale, although other scales such as Braun-Blanquet or Daubenmire's should be equally meaningful.

TWINSPAN is based on the ordination technique of correspondence analysis (see above) using pseudo-species. What follows is a general accounting of the classification procedure. For a more detailed description see Hill (1979b) and van Tongeren (1996). TWINSPAN starts with a rough CA of the data. The first axis of this ordination is broken in half and the preference of species for either side of the division evaluated. The left side of the division is the "negative side", while the right is the "positive" side. Using calculated preference values as weights, a second more refined ordination is made in a process akin to weighted averaging. The groups determined by this refined ordination are the first two groups of the classification. This process is then performed on both level one groups to produce a total of four clusters. The process is continued until the desired number of divisions has occurred or the number of stands in a group reaches a minimum threshold level.

A few species at each division with the strongest preference are termed "indicator species". This term is a bit of a misnomer, however, because indicator species generation is not the primary goal of the procedure. Hill (1979) suggested alternate names for TWINSPAN to downplay its role as a method for designation of indicator species, but they never caught on. Regarding this issue Hill warns, "Therefore, my dear reader, please do not be confused by the names. The basic method in TWINSPAN is the division of ordination, and not the selection of indicator species" (pg. 7). While indicator species assigned by TWINSPAN may be used in the field or dichotomous keys to discriminate between groups, they alone may well not be indicative of the most important components of the vegetation type.

Surprisingly few evaluations of TWINSPAN's performance have bee undertaken. Divisive, polythetic clustering techniques have theoretical advantages since they use all possible information available when making the initial crucial division (Lambert et al. 1973). But as Belbin and McDonald (1993) point out, this same strength can in some cases be a detriment. If the first division is not placed appropriately, the error cannot be corrected and is carried through subsequent divisions.

Initial tests showed that TWINSPAN generally recovered as much or more of the inherent structure of artificial data as four other hierarchical clustering methods (Gauch and Whittaker 1981). It also performed well on real data in which structure was fairly well known. The utility of TWINSPAN has been demonstrated in many studies wherein the technique recovered vegetation clusters that were observed by investigators or developed using analytical techniques.

Recent studies have called into question the accuracy of TWINSPAN classifications, however. In a harsh critique, van Groenewoud (1992) dismissed the usefulness of TWINSPAN suggesting that it be abandoned for vegetation analyses. He based his recommendation on the results obtained from his artificial data set. He suggested that the root of TWINSPAN's problem resided in the use of the CA algorithm. Within the same paper, van Groenewoud (1992) also minimized the utility of CA and DCA. His results were based on an artificial data set in which four gradients were of equal importance – this situation indeed seems artificial and perhaps some of van Groenewoud's negative conclusions were the result of his choice of unrealistic data structures.

Belbin and McDonald (1993) designed a test of van Groenewoud's conclusions and the performance of several other clustering programs. Belbin and McDonald (1993) likewise, found that TWINSPAN did not perform well when gradients two gradients were of nearly equal lengths, but it was shown to reasonably recreate gradients when a predominant gradient is present. Belbin and McDonald 's (1993) data is more representative of the structure of data collected during field studies, including the current study. TWINSPAN's performance seems clearly to depend on the nature of the data. Based on the above studies, TWINSPAN is deemed an appropriate and useful technique for community classification in this study since a single gradient dominates vegetational change in South Park's fens (Chapter 2).

Direct Gradient Analysis

Indirect gradient analysis leaves the investigator with a difficult question – what are the underlying causes of vegetational change? This is not easily answered since resources can interact in complex ways, with some being essential, some substitutable, and some complimentary (Tilman 1982). Layered on top of this are competitive, historical and stochastic effects. Plants integrate all of these factors, their manifestation being the observed species distributions. Direct gradient analysis seeks to relate changes in species abundance or composition directly to changes in the environment (Whittaker 1967). Through such analyses, causative as well as insignificant factors can be identified. If just a few species are of interest, simple and multiple regression can be used to relate changes in abundance with changes in environmental factors. However, when whole communities are considered this approach becomes impractical and neglects inter-specific effects. In essence this problem is a two-way multivariate problem, relating multiple species to multiple environmental factors.

Canonical correspondence analysis (CCA) was developed to address this complex problem (Ter Braak 1986). It combines techniques of ordination and multiple regression, to provide a direct gradient analysis of species and samples. Canonical correspondence analysis starts with an ordination of data using CA, but then constrains site placement to be a linear combination of measured environmental factors. That is, site placement is adjusted to fit the values predicted by a linear, multiple regression of environmental factors on species composition.

CCA produces an ordination diagram similar to that of CA or DCA, but superimposed upon this diagram are vectors relating environmental factors to vegetational composition (see pg. 102 for an example). Only the relative length and direction of vectors convey information, therefore, vectors may be scaled to best fit the diagram. The relative length of a vector is related to its correlation with changes in species composition, so it is interpreted as describing the importance of the factor in determining species composition. It also allows the ranking of sites or species with regard to the element in question. The ranking is produced using the biplot rule as explained above (pg. 239).

The inter-correlation of environmental factors is described by the angles between vectors. Vectors forming acute angles are positively correlated, with smaller angles indicating a higher correlation. Vectors with obtuse angles are negatively correlated, and orthogonal vectors are uncorrelated. This same relationship exists between vectors and ordination axes.

Canonical coefficients and intra-set correlations provide a somewhat more quantitative description of the relationship between environmental factors and gradient axes. The canonical coefficients define CCA axes as linear combinations of environmental factors (Ter Braak 1986). The strength of the factor in determining site placement is given by the coefficient's absolute value. The sign of the coefficient indicates the direction in which the factor weights the ordination. The intra-set correlations are the correlations between environmental factors and the axis scores which are a linear combination of the environmental data. Another correlation, called the inter-set correlation is also generated in a CCA. The inter-set correlation is the correlation between the environmental factors and the axes derived from the species data, that is, weighted averages scores (see below). Intra-set and inter-set correlations must not be confused since they have different interpretations.

Unlike DCA, CCA produces two sets of site scores. The first set is generated from the weighted average of the species scores. Following Palmer (1983), these scores will be abbreviated as WA scores. The second set of site scores are those estimated from the least-squares multiple regression of site scores on environmental factors. These scores are constrained to be linear combinations of environmental variables and so will be abbreviated as LC scores.

WA scores are not purely based on species data as they are in DCA, and as one might expect. Rather, WA scores are semi-constrained by environmental factors. To explain this, the CCA algorithm needs description. This algorithm is based on that presented by (Ter Braak 1986).

Step1) Start with arbitrary but unequal initial site scores

Step 2) Calculate species scores by weighted averaging of the site scores.

Step 3) Calculate new site scores by weighted averaging of species scores (WA scores)

Step 4) Obtain regression coefficients by weighted multiple regression of the site scores on the environmental variables.

Step 5) Calculate new site scores based on least-squares regression (LC scores).

Step 6) Center and standardize site scores.

Step 7) Stop iteration if site scores are little different from the scores generated in Step 2, otherwise go to step 2 and repeat until convergence.

In considering the algorithm, one can see, in fact, that the species scores used to generate the WA scores are themselves based on the LC scores. This relationship is what causes the minimal constraint of WA scores. In other words, final WA scores are not made to be linear combinations of environmental variables as in step five of the algorithm, but their placement is influenced by environmental factors in initial iterations.

The development of two sets of site scores has created some confusion in the literature – many studies do not report which set of scores they have used, some investigators misinterpret the nature of the scores (usually the WA scores), and there is uncertainty as to which scores are the most appropriate to use. Palmer (1993) was the first to address these difficulties. He noted that initial publications on CCA did not discuss the merits of plotting either WA or LC scores, ordination program documentation did not report which scores were plotted as default, and further, different program versions used different sets of scores.

Palmer (1993) graphically showed the difference between the WA scores produced by DCA and WA scores produced by CCA. Palmer (1993) then showed that LC scores best reconstructed artificial gradients when noise was incorporated into species abundance data. Based on these findings and the uncertain ecological interpretation of WA scores, he strongly suggested the use of LC scores in CCA. Such a suggestion is intuitively appealing, but McCune (1997) showed that WA scores reconstituted an artificial environmental gradient better than LC scores when noise was added to environmental data. This makes sense since

WA scores are less constrained by environmental variables than LC scores, therefore, environmental measurement errors are more pronounced in the maximally constrained LC scores. This situation is basically a case of "garbage in, garbage out". Keeping McCune's findings in mind, I prefer to plot LC scores since, if there is some gradient distortion due to measurement error, at least LC scores have a ready ecological interpretation. Also, as McCune points out, when WA scores are used, a direct gradient analysis is not produced. This fact essentially negates much of the utility of using CCA.

There has also been some confusion as to the nature of ordination diagnostics produced by CCA. McCune (1997) made important observations on the nature of the so called "species-environment" correlation. He noted that the term species-environment correlation is highly misleading and has been generally misinterpreted since the inception of CCA. Species-environment correlations have frequently been used to gauge the quality of a direct gradient analysis using CCA. It has been taken as a measure of goodness-of-fit between changes in species abundances and changes in environmental factors. McCune explained that this correlation is merely the correlation between WA scores and LC scores, and importantly, this correlation rises to 100 percent as the number of environmental variables approaches the number of sites; even if the "environmental factors" are vectors of random numbers! This same phenomenon occurs in standard multiple regression. McCune recommends that the species-environment correlation instead be reported as the LC-WA correlation, if it is even reported at all.

The above discussion begs the question of how to judge the quality of a CCA. Since LC site scores are estimated from a least-squares regression of site vegetation on environmental factors, it follows that if there is a poor correspondence between measured environmental factors and the actual factors responsible for driving changes in species composition, then significant misrepresentation of vegetational patterns would occur. McCune (1997) suggested that randomization tests, such as Monte Carlo Permutation, be used to test the significance of species-environment correlations, because in his study, when random variables were used even very high species-environment correlations were never significant. McCune also suggested using the percent variance of species data accounted for by environmental factors as an even better gauge of ordination success.

Another goodness-of-fit measure that has been suggested is the correlation coefficient of unconstrained ordination scores, from DCA for example, and constrained LC scores (Allen and Peet 1990, Prentice and Cramer 1990, Johnson 1996, Økland 1996). The congruence, or lack there of, between unconstrained and constrained site scores measures the amount of site score displacement due to making sites scores linear combinations of environmental factors.

Conclusion

Ecologists have a number of statistical methods at their disposal for describing vegetational patterns. Uni-variate methods are the most straightforward and accurate, but are of limited use in most studies due to the multitude of species and environmental factors that are usually examined. Multivariate analytical techniques have been adapted or developed to address the complex nature of ecological data. No single approach meets all investigative needs so a blend of techniques is commonly used, including ordination, direct gradient analysis, and classification. Each of these approaches have distinct, but related, goals, strengths and weaknesses.

Each approach can be undertaken using any of several statistical techniques. No analytical technique yet developed is perfect, due to unrealistic assumptions about the nature of ecological data and computational anomalies. But many techniques provide extremely useful graphical representations of vegetational structure when applied in the appropriate circumstances. There is extraordinary disagreement in the literature as to the merits and drawbacks of each method and how statistics should be interpreted. Perhaps the lesson to be learned by these highly variable recommendations is that the results of any method must be highly scrutinized and checked against the perception of the investigator who has closely observed the actual vegetation patterns during the course of investigation.

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APPENDIX 2

This appendix contains plant species composition data for all sample plots. Plots were 5 m in diameter. Data were collected at High Creek Fen on July 7 - 9, 1995, and at Crooked Creek and Fremont's Fen on July 28 - August 3, 1997. Data have been placed into Braun-Blanquet cover classes where, + = <1%, 1 = 1- 5%, 2= 6-25%, 3= 26-50%, 4=50-75%, 5=76-100%. P indicates species presence when abundance data are not present.

Species Abbrev.	Species Name	HC1	HC2	HC3	HC4	HC5	HC7	HC8	HC9	HC10	HC11	HC13	HC14	HC15	HC16	HC17	HC18	HC19	HC20	HC21	HC22	HC23	HC24	HC25	HC26	HC27	HCm	HCDE	HC28	HC29	HC30	HC32	HC33	HC34	HC35
ACHMIL	*Achillea millefolium*																																		
AGRSCA	*Agrostis scabra*																										2					♦			
AGRSTO	*Agrostis stolonifera*																																		
ANTSPP	*Antennaria sp*		♦				♦																												
ALOBOR	*Alopecurus borealis*																																		
ARGANS	*Argentina anserina*	♦					1			♦	♦			♦								♦									2	1	3	5	5
ARTFRI	*Artemisia frigida*																																		
ASTAGR	*Astragalus agrestis*																																		
ASTOCC	*Aster occidentalis*																																	♦	♦
BETGLA	*Betula glandulosa*																																		
CALCAN	*Calamagrostis canadensis*						♦	♦																											
CALSTR	*Calamagrostis stricta*																																		
CALLEP	*Caltha leptosepala*																																		
CAMPAR	*Campanula parryi*																													♦					
CARAQU	*Carex aquatilis*	4	3	2	2	♦		2	♦	1		♦		♦			1			4		1	♦	♦	♦	♦	♦	♦	2			1			
CARAUR	*Carex aurea*																			♦															
CARCAP	*Carex capillaris*																																		
CARHAL	*Carex halli*																														♦				
CARLIM	*Carex limosa*																																		
CARLIV	*Carex livida*													1																					
CARMIC	*Carex microptera*																					♦													
CARMIG	*Carex microglochin*					♦						♦				♦						1	♦	♦											
CARSCI	*Carex scirpoidea*	2	2				2			♦	♦			♦							♦								1						
CARSIM	*Carex simulata*	1	1	2	1	1		2	♦					2		♦				3		1	4	2	1	2		1							
CARUTR	*Carex utriculata*	♦	♦						♦							♦													1	3	1		♦		
CIRARV	*Cirsium arvense*																													♦				♦	♦
CIRCOL	*Cirsium coloradense*						♦																				1								
CONSCO	*Conioselinum scopulorum*																												♦	♦					
CRERUN	*Crepis runcinata*	1	♦	♦						♦																	♦								
DESCES	*Deschampsia cespitosa*	♦	♦				3			♦	2																2		2			1	2	1	1
DISINV	*Distegia involucrata*																																		
DODPUL	*Dodecatheon pulchellum*	♦	♦				♦			♦	♦			♦																					
ELEQUI	*Eleocharis quinqueflora*		♦	3	1	2		1	2	1	♦	2	4	1	2	2	2	3	3	1	3	3	2	3	2	2	♦	2				1	1		
ELYTRA	*Elymus trachycaulus*	♦	1				1																				1		1	2	1		1	1	♦
EPILAC	*Epilobium lactiflorum*			♦	♦																♦									♦					
EPISPP	*Epilobium spp*																																		
EQUARV	*Equisetum arvense*																										♦								
ERILON	*Erigeron lonchophyllus*		♦																																
ERISPE	*Erigeron speciosus*																																		
ERIANG	*Eriophorum angustifolium*																						1			♦									
ERIGRA	*Eriophorum gracile*																																		
GALBOR	*Galium boreale*																													1					
GENFRE	*Gentiana fremontii*		♦								♦			♦																					
GENSPP	*Gentian spp*																																		
HIEHIR	*Hierochloë hirta*						1				♦																♦								
HORBRA	*Hordeum brachyantherum*																													2	3				
HORJUB	*Hordeum jubatum*																														2		1		

Species Abbrev.	Species Name	HC1	HC2	HC3	HC4	HC5	HC7	HC8	HC9	HC10	HC11	HC13	HC14	HC15	HC16	HC17	HC18	HC19	HC20	HC21	HC22	HC23	HC24	HC25	HC26	HC27	HCm	HCDE	HC28	HC29	HC30	HC32	HC33	HC34	HC36
HETPUM	*Heterotheca pumila*																																		
JUNALB	*Juncus albescens*																																		
JUNALP	*Juncus alpinoarticulatus*																																		
JUNBAL	*Juncus arcticus ssp. ater*													♦		♦	♦				♦	♦	1				♦		1	1	1	1			
JONLON	*Juncus longistylis*																																1		
KOBMYO	*Kobresia myosuroides*					♦																							2	1					
KOBSIM	*Kobresia simpliciuscula*	♦	♦	1	♦	1		2	♦		1	1	♦	2	♦	1	1		1		♦	1	♦	1	♦	2		1							
KOLMAC	*Koeleria macrantha*																																♦		
LAPRED	*Lappula redowskii*																																		
LEPRAM	*Lepidium ramosissimum*																																		
LIMHYP	*Limnorchis hyperborea*													♦												♦									
MAIAMP	*Maianthemum amplexicaule*																																		
MOSSPP	*Moss sp.*			1	1				1			1		1	♦	1	1		♦		♦	2	2		1	1		♦		♦					
MUHRIC	*Muhlenbergia richardsonis*																													2					
PARPAR	*Parnassia parviflora*																																		
PASSMI	*Pascopyrum smithii*																																		
PEDCRE	*Pedicularis crenulata*																												♦						
PEDGRO	*Pedicularis groenlandica*			♦	♦	♦		♦	♦	♦	1	♦		1			♦		♦	♦	♦	1	♦	1		♦		1							
PENFLO	*Pentaphylloides floribunda*													1			1			1		♦	1	♦					2	1		♦			
PLAERI	*Plantago eriopoda*						♦																												
POACOM	*Poa compressa*																																1		
POAGLA	*Poa glaucifolia*																																♦		♦
POAPRA	*Poa pratensis*																														1				
POLBIS	*Polygonum bistortoides*																													♦					
POLVIV	*Polygonum viviparum*													♦							♦									♦					
POLFOL	*Polemonium foliosissimum*																																		
POTPEC	*Potamogeton pectinatus*														1		1	1																	
POTPLA	*Potentilla plattensis*																																		
POTSUB	*Potentilla subjuga*																													♦		♦			
PRIEGA	*Primula egaliksensis*	♦	♦	♦	♦			♦	♦		♦		♦	♦		♦	♦		♦	♦	♦	♦	♦	♦	♦										
PRIINC	*Primula incana*	♦	♦								♦																								
PTIPOR	*Ptilagrostis porteri*																																		
RANCYM	*Ranunculus cymbalaria*																																♦		
RUMSPP	*Rumex spp.*																			♦										1					
SALBRA	*Salix brachycarpa*											♦		1		♦	♦			1	♦	♦		♦	♦				2	1					
SALCAN	*Salix candida*								♦			♦		1	♦	♦	♦	♦	♦	1		♦	♦		♦	♦									
SALMON	*Salix monticola*																																		
SALMYR	*Salix myrtillifolia*													1						1									♦						
SALPLA	*Salix planifolia*													♦					♦	♦										1					
SAXHIR	*Saxifraga hirculus*																																		
SEDRHO	*Sedum rhodanthum*																																		
STELON	*Stellaria longipes*																																		
SWEPRE	*Swertia perennis*																																		
SISPAL	*Sisyrinchium pallidum*																																		
TAROFF	*Taraxacum officinale*		♦				1																								1		♦		
THAALP	*Thalictrum alpinum*							♦		♦	♦	♦		♦		♦	1		♦	♦	♦	♦	♦	♦	♦	1			2	1					
TRIPUM	*Trichophorum pumilum*																1				♦														

Species Abbrev.	Species Name	HC1	HC2	HC3	HC4	HC5	HC7	HC8	HC9	HC10	HC11	HC13	HC14	HC15	HC16	HC17	HC18	HC19	HC20	HC21	HC22	HC23	HC24	HC25	HC26	HC27	HCm	HCDE	HC28	HC29	HC30	HC32	HC33	HC34	HC35
TRIMAR	*Triglochin maritima*	1	1	1	+	1	+	1	1	1	+	1	1	1	2	1	1	2	1		1	1	2	2	2	2	+	1	1				1		
TRIPAL	*Triglochin palustris*			+	+	+		1	1	1	2	1	1		1	1	+	+	+		1		+	+	2	1	+	1				1			
UTROCH	*Utricularia ochroleuca*												1		+		1	1																	
VALEDU	*Valeriana edulis*																												+	1					
VIOADU	*Viola adunca*	+																																	
ZYGELA	*Zygadenus elegans*													+							+														
BARGRO	Bare ground	1	1	+	2	2	2	2	3	5	4	3	1	2	3	2	1	1	3	2	3	2	1	2	2	2	4	2	1	1		6	2	1	2
HUMMOK	Hummocks	3	3	2	3	2	3	2	2	+	1	2	+	3	1	2	2	+	1		1	1	2	2	1	2		2	4	3					
Mosses																																			
BRANEL	*Brachythecium nelsonii*																																		
CALGIG	*Calliergon giganteum*																																		
CALSTR	*Calliergon stramineum*																																		
CALTRI	*Calliergon trifarium*																																		
CAMSTE	*Campylium stellatum*																																		
DISCAP	*Distichum capillare*																																		
DISCAP	*Distichum capillare*																																		
DREADU	*Drepanocladus aduncus*																																		
DREREV	*Drepanocladus revolvens*																																		
PHIFON	*Philonotis fontana*																																		
MNIALB	*Mniobryum albicans*																																		
RHIPSE	*Rhizomnium pseudopunctatum*																																		
SCOTUR	*Scorpidium turgescens*																																		
SCOSCO	*Scorpidium scorpioides*																	2																	
WARFXA	*Warnstorfia exannulata*																																		

ID #	SD K	Avg Zn	Sd Zn	Avg Fe	SD Fe	SD Mn	Avg CU	SD CU	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Mn
HC 1	40.84	13.75	4.92	785.33	598.58	9.70	6.85	2.48	9707.13	1211.21	1302.67	345.68	19.17
FS 2	16.26	4.48	0.78	259.00	15.56	4.53	5.10	0.48	10333.40	740.20	589.65	35.85	36.80
FS 3	19.80	8.43	3.36	718.50	259.51	61.16	5.45	1.14	13021.90	1897.73	779.10	31.25	150.25
FS 4	83.44	9.48	4.42	210.00	132.94	25.88	3.82	1.29	14323.85	1473.82	803.35	26.38	30.50
FS 5	12.66	2.46	0.74	436.90	370.67	2.55	6.77	4.09	13593.70	2480.11	1281.65	360.13	32.00
FS 6	47.38	4.29	2.88	171.30	47.66	15.85	13.24	15.85	8905.60	2849.07	686.70	247.06	25.31
FS 7	52.33	3.34	3.70	476.25	139.65	57.42	6.40	2.70	14002.40	3283.24	757.55	62.86	98.90
FS 8	674.58	8.77	5.00	694.00	278.60	11.81	10.59	2.84	7796.10	1009.61	449.00	104.65	69.05
FS 9	31.47	5.05	1.28	1025.00	134.35	183.49	4.58	0.16	11287.25	286.73	373.70	79.62	257.75
FS 10	75.94	4.95	2.74	809.00	496.39	54.16	5.59	1.90	9701.45	880.28	382.15	35.14	119.50
FS 11	48.44	5.80	2.30	655.50	212.84	60.60	4.23	1.58	11119.15	4102.42	379.00	156.98	130.65
FS 12	2.55	1.66	1.14	375.50	194.45	1.27	4.39	0.66	7034.20	595.67	270.15	1.63	36.70
FS 13	3.54	1.40	0.28	591.50	389.62	12.80	3.07	2.76	6671.15	248.69	163.60	33.09	40.25
FS 14	28.99	8.38	0.96	315.25	91.57	27.65	5.85	1.99	8608.15	245.86	471.80	97.86	106.95
FS 15	16.48	1.88	1.70	575.50	443.36	7.28	3.63	1.25	7705.55	598.99	507.00	77.78	57.75
FS 16	12.23	8.55	3.89	234.75	31.47	0.49	3.79	0.76	8589.75	322.79	586.65	27.79	69.15
FS 17	8.84	7.58	0.60	182.50	36.06	2.62	4.30	2.38	9994.65	937.13	570.95	15.63	41.95
FS 18	0.14	5.43	0.11	487.50	154.86	5.23	4.36	0.49	9751.50	1221.17	465.50	65.76	35.70
FS 19	25.17	7.65	7.72	544.50	376.89	2.97	4.83	0.78	10340.50	311.83	339.15	46.88	54.90
FS 20	31.82	4.94	2.84	366.75	294.51	7.11	3.24	0.35	8158.55	127.92	652.80	44.97	44.28
FS 21	21.21	9.56	1.75	428.25	230.16	35.92	7.75	1.56	9584.85	983.09	943.40	531.18	87.60
FS 22	21.92	4.68	0.95	490.25	173.59	5.76	3.67	1.15	8919.10	1.56	397.55	16.33	34.68
FS 23	87.68	13.63	9.93	279.75	6.72	33.66	7.44	1.90	8968.40	2279.15	503.90	131.66	79.20
FS24	45.68	10.54	9.54	337.50	116.67	43.63	3.76	1.32	16252.00	1841.31	1397.85	268.49	46.75
FS25	44.19	13.09	2.11	251.00	137.18	13.93	2.80	1.50	10134.30	809.35	643.40	161.79	48.35
FS26	29.33	19.77	6.97	492.60	222.60	9.12	5.46	2.13	13056.80	810.63	888.35	126.78	63.65
FS 27		40.80		458.00			3.72		14471.80		1154.70		100.40
FF1	57.77	24.05	14.92	867.50	229.81	6.22	3.80	1.05	10808.30	2857.14	571.75	154.50	30.50
FF2	1.27	25.95	4.03	1170.00	919.24	4.60	4.11	1.34	12055.90	5929.66	1235.60	880.49	17.75
FF3	0.28	9.29	5.78	939.00	708.52	6.08	2.91	0.78	15641.00	3180.57	2269.20	732.28	18.10
FF4	4.53	8.95	3.04	734.50	317.49	0.54	2.88	0.40	23102.50	4932.07	1609.60	1730.15	7.74
FF5	95.25	2.92	1.70	1294.50	1549.27	0.13	9.68	5.41	6715.00	4731.96	1153.00	1387.34	3.66
FF6	78.77	15.39	18.40	523.50	16.26	14.30	3.66	1.27	11662.50	5264.41	1467.10	521.70	14.69
FF7	9.40	2.41	0.78	1366.00	1052.17	4.70	2.13	1.24	11653.35	1051.26	770.75	85.91	13.28
FF8	78.91	38.96	43.90	1517.50	399.52	18.94	4.81	0.56	11085.50	741.76	874.80	95.88	17.76
FF9	58.41	29.62	35.04	1224.00	1055.00	6.26	5.23	4.92	8681.30	35.78	787.70	0.99	13.60

Species Abbrev.	Species Name	CC 1	CC 2	CC 3	CC 4	CC 5	CC 6	CC 7	CC 8	CC 9	CC 10	CC 11	CC 12	CC 13	CC 14	CC 15	CC 16	CC 17	CC 18	CC 19	CC 20	CC 21	CC 22	CC 23	CC 24	CC 25	CC 26	CC 27
ACHMIL	*Achillea millefolium*																											
AGRSCA	*Agrostis scabra*																											
AGRSTO	*Agrostis stolonifera*																											
ANTSPP	*Antennaria sp.*																											
ALOBOR	*Alopecurus borealis*																											
ARGANS	*Argentina anserina*															1										2		1
ARTTRI	*Artemisia [illegible]*																								2			
ASTAGR	*Astragalus agrestis*																											
ASTOCC	*Aster occidentalis*																											
BETGLA	*Betula glandulosa*	+		1				+		1			1															
CALCAN	*Calamagrostis canadensis*	+														1	+											
CALSTR	*Calamagrostis stricta*																											
CALLEP	*Caltha leptosepala*																											
CAMPAR	*Campanula parryi*																											
CARAQU	*Carex aquatilis*				4		2	5	4	2	3	2	3	4	2	1	2	3	3	1	4	2	2					
CARAUR	*Carex aurea*		+					+					+				+	+										
CARCAP	*Carex capillaris*																											
CARHAL	*Carex hallii*																					+						
CARLIM	*Carex limosa*				1			1	1																			
CARLIV	*Carex livida*																											
CARMIC	*Carex microptera*																				+							
CARMIG	*Carex microglochin*																											
CARSCI	*Carex scirpoidea*																	1				+						
CARSIM	*Carex simulata*				2		3	+					2	2	4		3	2	3		2		1					
CARUTR	*Carex utriculata*	3	3	3		4	1			4	5	3	3	1		4		1	1	3			3	3				
CIRARV	*Cirsium arvense*																									+	+	
CIRCOL	*Cirsium coloradense*																										+	
CONSCO	*Conioselinum scopulorum*		1																					1				
CRERUN	*Crepis runcinata*																							+			+	
DESCES	*Deschampsia cespitosa*					1	1					1	1	2				2	1	+	1	2		1				1
DISINV	*Distegia involucrata*			1																								
DODPUL	*Dodecatheon pulchellum*												+			+		+										

Species Abbrev.	Species Name	CC 1	CC 2	CC 3	CC 4	CC 5	CC 6	CC 7	CC 8	CC 9	CC 10	CC 11	CC 12	CC 13	CC 14	CC 15	CC 16	CC 17	CC 18	CC 19	CC 20	CC 21	CC 22	CC 23	CC 24	CC 25	CC 26	CC 27
ELEQUI	*Eleocharis quinqueflora*	+			1			1						2			2	2				1						
ELYTRA	*Elymus trachycaulus*																								1	2	1	1
EPILAC	*Epilobium lactiflorum*																											
EPISPP	*Epilobium spp.*	+																										
EQUARV	*Equisetum arvense*	+	1			+	+																					
ERILON	*Erigeron lonchophyllus*																											
ERISPE	*Erigeron speciosus*																											
ERIANG	*Eriophorum angustifolium*																											
ERIGRA	*Eriophorum gracile*												1															
GALBOR	*Galium boreale*		+																					+				
GENFRE	*Gentiana fremontii*																+											
GENSPP	*Gentian spp.*															+		+	+	+	+		+					
HIEHIR	*Hierochloe hirta*																											
HORBRA	*Hordeum brachyantherum*																											2
HORJUB	*Hordeum jubatum*																								1	1	1	2
HETPUM	*Heterotheca pumila*																											
JUNALB	*Juncus albescens*							+																				
JUNALP	*Juncus alpinoarticulatus*							+																				
JUNBAL	*Juncus arcticus ssp. ater*		+			1							+					1							2		3	3
JONLON	*Juncus longistylis*												+															
KOBMYO	*Kobresia myosuroides*				2		2	+					1	2				2	2		2							
KOBSIM	*Kobresia simpliciuscula*							1						1	2		2				2							
KOEMAC	*Koeleria macrantha*																							+				
LAPRED	*Lappula redowskii*																								+	1		
LEPRAM	*Lepidium ramosissimum*																								2	+		
LIMHYP	*Limnorchis hyperborea*												+		+		+		+									
MAIAMP	*Maianthemum amplexicaule*		+																									
MOSSPP	*Moss sp.*	4	+	4	5	2	+	4	5	4	3	3	2	2	3	2	3	1	2	2	2	3	4	4				
MUHRIC	*Muhlenbergia richardsonis*																											
PARPAR	*Parnassia parviflora*												+		+		+	+			+		+					
PASSMI	*Pascopyrum smithii*																								1	2		
PEDCRE	*Pedicularis crenulata*																											

Species Abbrev.	Species Name	CC 1	CC 2	CC 3	CC 4	CC 5	CC 6	CC 7	CC 8	CC 9	CC 10	CC 11	CC 12	CC 13	CC 14	CC 15	CC 16	CC 17	CC 18	CC 19	CC 20	CC 21	CC 22	CC 23	CC 24	CC 25	CC 26	CC 27
PEDGRO	*Pedicularis groenlandica*	+			+			1						1						+				1				
PENFLO	*Pentaphylloides floribunda*		2	1	+	1	+	+		1			2	1	1	2	1	2	2	2	2	2	1	1		1	1	1
PLAERI	*Plantago eriopoda*																											
POACOM	*Poa compressa*																								1			
POAGLA	*Poa glaucifolia*																											
POAPRA	*Poa pratensis*																						+		4	3	4	2
POLBIS	*Polygonum bistortoides*				+	+							+	1	1	1	1	+		+	1		1	+				
POLVIV	*Polygonum viviparum*																											
POLFOL	*Polemonium foliosissimum*																											
POTPEC	*Potamogeton pectinatus*																											
POTPLA	*Potentilla plattensis*																											
POTSUB	*Potentilla subjuga*																								+		1	+
PRIEGA	*Primula egaliksensis*																+	+										
PRIINC	*Primula incana*																											
PTIPOR	*Ptilagrostis porteri*																											
RANCYM	*Ranunculus cymbalaria*													1														
RUMSPP	*Rumex spp.*																											
SALBRA	*Salix brachycarpa*		2	2		2	+			2		1	3			2	1		2	2	1	+	2	2				
SALCAN	*Salix candida*				1		+	1	1	+	+	+		1	1		1	1	1		1	+		1				
SALMON	*Salix monticola*	1	4	1		2							2							1				1	+			
SALMYR	*Salix myrtillifolia*													1		+												
SALPLA	*Salix planifolia*	4		2	+			+	1	1	+	2	2	1	1	1		+	1	3	1	2	1	3				
SAXHIR	*Saxifraga hirculus*																											
SEDRHO	*Sedum rhodanthum*																											
STELON	*Stellaria longipes*																											
SWEPRE	*Swertia perennis*		+	1		+														+		1		1				
SISPAL	*Sisyrinchium pallidum*				+																							
TAROFF	*Taraxacum officinale*																											
THAALP	*Thalictrum alpinum*		+			+	+					+	+		1	1	1	1		+			1					
TRIPUM	*Trichophorum pumilum*						1						1	2	1		1	1	2		1							
TRIMAR	*Triglochin maritima*						1	1	1				+	+	+			+			1							
TRIPAL	*Triglochin palustris*																											

Species	Species Name	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC	CC
Abbrev.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
UTROCH	*Utricularia ochroleuca*																											
VALEDU	*Valeriana edulis*																											
VIOADU	*Viola adunca*																											
ZYGELA	*Zygadenus elegans*																											
BARGRO	Bare ground																								+	1		
HUMMOK	Hummocks	4		4	2	3	4	2	2	2	1	2	3	3	3	2	3	3	3	3	2	3	2	3				
Mosses																												
BRANEL	*Brachythecium nelsonii*			P												P				P			P					
CALGIG	*Calliergon giganteum*	P		P		P					P									P				P				
CALSTR	*Calliergon stramineum*	P		P		P						P								P				P				
CALTRI	*Calliergon trifarium*																											
CAMSTE	*Campylium stellatum*	P						P		P			P	P		P	P	P	P	P		P	P	P				
DISCAP	*Distichum capillare*												P															
DISCAP	*Distichum capillare*													P														
DREADU	*Drepanocladus aduncus*	P							P					P	P	P								P				
DREREV	*Drepanocladus revolvens*	P		P		P		P			P	P		P	P					P				P				
PHIFON	*Philonotis fontana*													P														
MNIALB	*Mniobryum albicans*													P														
RHIPSE	*Rhizomnium pseudopunctatum*	P		P																				P				
SCOTUR	*Scorpidium turgescens*				P			P	P					P	P				P		P							
SCOSCO	*Scorpidium scorpiodes*				P			P	P						P													
WAREXA	*Warnstorfia exannulata*								P	P	P	P		P					P			P	P					

Species Abbrev.	Species Name	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	FF12	FF13	FF14	FF15	FF16	FF17	FF19	FF20	FF21	FF22	FF23
ACHMIL	*Achillea millefolium*	+		1			+			+				1			+	+	1	1			
AGRSCA	*Agrostis scabra*									1		+		1									
AGRSTO	*Agrostis stolonifera*		+																				
ANTSPP	*Antennaria sp.*		1	1																			
ALOBOR	*Alopecurus borealis*					2	+										+						
ARGANS	*Argentina anserina*		2	1		+	1	1		1				1								2	
ARTFRI	*Artemisia frigida*																		+				
ASTAGR	*Astragalus agrestis*					2																	
ASTOCC	*Aster occidentalis*		1	+			1	+									+		+				
BETGLA	*Betula glandulosa*																						
CALCAN	*Calamagrostis canadensis*			2			1					1	1						2			1	2
CALSTR	*Calamagrostis stricta*										1		+	1			1						2
CALLEP	*Caltha leptosepala*																+						
CAMPAR	*Campanula parryi*																						
CARAQU	*Carex aquatilis*	3	+		1		2	2	2	1	3	5	1	4		2	4	3	+	2	2		
CARAUR	*Carex aurea*																						
CARCAP	*Carex capillaris*			1				+															
CARHAL	*Carex hallii*		+																				
CARLIM	*Carex limosa*																						
CARLIV	*Carex livida*																						
CARMIC	*Carex microptera*																						
CARMIG	*Carex microglochin*																						
CARSCI	*Carex scirpoidea*		1																				
CARSIM	*Carex simulata*	2									3	2									5		2
CARUTR	*Carex utriculata*	2	+														1	2					
CIRARV	*Cirsium arvense*		+	+		+													+			+	
CIRCOL	*Cirsium coloradense*			+															+				
CONSCO	*Conioselinum scopulorum*																						
CRERUN	*Crepis runcinata*		1			3	1	1		+				+								1	
DESCES	*Deschampsia cespitosa*	2	2	2		2	4	3	4	2		1	1	2			2	3	5	5	1	2	3
DISINV	*Distegia involucrata*																						
DODPUL	*Dodecatheon pulchellum*								+														

Species Abbrev.	Species Name	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	FF12	FF13	FF14	FF15	FF16	FF17	FF19	FF20	FF21	FF22	FF23
ELEQUI	*Eleocharis quinqueflora*										1												
ELYTRA	*Elymus trachycaulus*		2	2		2	1														+	2	
EPILAC	*Epilobium lactiflorum*																						
EPISPP	*Epilobium spp.*					1							+				+		+				+
EQUARV	*Equisetum arvense*																						
ERILON	*Erigeron lonchophyllus*																						
ERISPE	*Erigeron speciosus*						+		+					+					+			+	
ERIANG	*Eriophorum angustifolium*																						
ERIGRA	*Eriophorum gracile*																						
GALBOR	*Galium boreale*																						
GENFRE	*Gentiana fremontii*						+																
GENSPP	*Gentian spp.*		2														1		1		1	1	
HIEHIR	*Hierochloë hirta*	+																					
HORBRA	*Hordeum brachyantherum*			1																		2	
HORJUB	*Hordeum jubatum*													+									
HETPUM	*Heterotheca pumila*					1																	
JUNALB	*Juncus albescens*																						
JUNALP	*Juncus alpinoarticulatus*																						
JUNBAL	*Juncus arcticus ssp. ater*	2	2	2		2	1	1	1		1						2	+	1			3	2
JONLON	*Juncus longistylis*																						
KOBMYO	*Kobresia myosuroides*	3	1	2				2	3													3	
KOBSIM	*Kobresia simpliciuscula*					2		2			+										2		
KOEMAC	*Koeleria macrantha*	2	2	1		2	1		+													2	
LAPRED	*Lappula redowskii*																						
LEPRAM	*Lepidium ramosissimum*																						
LIMHYP	*Limnorchis hyperborea*																						
MAIAMP	*Maianthemum amplexicaule*																						
MOSSPP	*Moss sp.*								+		+									+	+	+	3
MUHRIC	*Muhlenbergia richardsonis*					2	1																
PARPAR	*Parnassia parviflora*																						
PASSMI	*Pascopyrum smithii*																						
PEDCRE	*Pedicularis crenulata*																						

Species Abbrev.	Species Name	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	FF12	FF13	FF14	FF15	FF16	FF17	FF19	FF20	FF21	FF22	FF23
PEDGRO	*Pedicularis groenlandica*																			+			
PENFLO	*Pentaphylloides floribunda*									+				+									
PLAERI	*Plantago eriopoda*																						
POACOM	*Poa compressa*								1					+									
POAGLA	*Poa glaucifolia*																						
POAPRA	*Poa pratensis*		2	2		2	1											1					
POLBIS	*Polygonum bistortoides*	1							1								+					+	
POLVIV	*Polygonum viviparum*																						
POLFOL	*Polemonium foliosissimum*																	1	1	1			
POTPEC	*Potamogeton pectinatus*																						
POTPLA	*Potentilla plattensis*			1			+															+	
POTSUB	*Potentilla subjuga*													+									
PRIEGA	*Primula egaliksensis*																						
PRIINC	*Primula incana*		+					+															
PTIPOR	*Ptilagrostis porteri*							2															
RANCYM	*Ranunculus cymbalaria*																						
RUMSPP	*Rumex spp.*																	+		+			
SALBRA	*Salix brachycarpa*	2							1								1		+				
SALCAN	*Salix candida*																						
SALMON	*Salix monticola*																						
SALMYR	*Salix myrtillifolia*	+							+														
SALPLA	*Salix planifolia*																						
SAXHIR	*Saxifraga hirculus*																						
SEDRHO	*Sedum rhodanthum*																		+				
STELON	*Stellaria longipes*																		+	1	+		
SWEPRE	*Swertia perennis*																						
SISPAL	*Sisyrinchium pallidum*																						
TAROFF	*Taraxacum officinale*													1				+	+				
THAALP	*Thalictrum alpinum*	1	1	1			2	1	2								1		1			2	
TRIPUM	*Trichophorum pumilum*																						
TRIMAR	*Triglochin maritima*												1										
TRIPAL	*Triglochin palustris*									2						+							

Species Abbrev.	Species Name	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	FF12	FF13	FF14	FF15	FF16	FF17	FF19	FF20	FF21	FF22	FF23
UTROCH	*Utricularia ochroleuca*																						
VALEDU	*Valeriana edulis*						+																
VIOADU	*Viola adunca*																						
ZYGELA	*Zygadenus elegans*																						
BARGRO	Bare ground				5					4	1		5		5	5							
HUMMOK	Hummocks	4		4			5	5	4		2	2					3	3	2	2	2	3	3
Mosses																							
BRANEL	*Brachythecium nelsonii*																						P
CALGIG	*Calliergon giganteum*																						P
CALSTR	*Calliergon stramineum*																						
CALTRI	*Calliergon trifarium*																						
CAMSTE	*Campylium stellatum*																						
DISCAP	*Distichum capillare*																						
DISCAP	*Distichum capillare*																						
DREADU	*Drepanocladus aduncus*																						
DREREV	*Drepanocladus revolvens*								P														P
PHIFON	*Philonotis fontana*																						
MNIABL	*Mniobryum albicans*																						
RHIPSE	*Rhizomnium pseudopunctatum*																			P			
SCOTUR	*Scorpidium turgescens*																						
SCOSCO	*Scorpidium scorpiodes*																						
WAREXA	*Warnstorfia exannulata*										P												P

APPENDIX 3

This appendix contains water chemistry data obtained during this study. Water samples were obtained on August 22-23, 1995 on High Creek Fen and September 13, 1997 at all stations. pH and electrical conductivity were measured approximately bi-monthly throughout the study. All units are in mg/l, except pH which is in standard pH units and electrical conductivity (EC) reported as micro-Siemens. After each mean parameter value the sample standard deviation (SD) is provided.

Station	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Na	Avg K	SD K	Avg P	SD P	Avg Al	SD Al	Avg Fe	SD Fe	SD Na
HC1	288.19		105.43		24.51	1.38		0.15		0.00		0.14		
HC2	197.63		54.50		16.19	1.28		0.10		0.00		0.27		
HC3	60.78	15.11	27.02	2.58	4.87	0.92	0.25	0.08	0.02	0.03	0.04	0.10	0.05	2.36
HC4	94.46	1.36	33.73	2.50	5.54	1.96	1.76	0.09	0.02	0.03	0.04	0.25	0.16	0.48
HC5	87.16	7.02	37.05	5.17	6.51	0.93	0.32	0.09	0.02	0.03	0.04	0.19	0.13	1.99
HC8	116.69	0.44	30.12	1.53	4.47	0.97	0.24	0.08	0.02	0.03	0.04	1.04	1.09	0.24
HC9	151.15	24.81	33.88	0.45	5.84	0.81	0.55	0.06	0.06	0.03	0.04	0.08	0.00	2.88
HC10	241.89	198.70	99.96	47.43	19.70	3.17	1.45	0.26	0.20	0.03	0.04	2.17	2.40	3.81
HC11	98.16	57.05	46.08	35.53	10.69	2.53	1.37	0.13	0.11	0.03	0.04	0.10	0.12	7.37
HC12	126.61	24.48	42.33	0.11	7.99	1.15	0.07	0.13	0.04	0.03	0.04	7.51	9.97	0.43
HC13	114.82	40.75	41.09	13.85	6.76	0.71	0.27	0.13	0.04	0.03	0.04	0.15	0.21	3.20
HC 14	125.82	42.87	52.74	12.36	8.69	0.50	0.71	0.09	0.02	0.03	0.04	0.06	0.08	6.63
HC 15	89.26	14.20	26.38	5.82	6.43	0.65	0.36	0.08	0.03	0.03	0.04	0.15	0.10	3.43
HC 16	129.83	13.47	40.11	1.15	5.43	0.42	0.12	0.08	0.02	0.03	0.04	0.09	0.12	2.31
HC 17	97.26	24.83	41.68	5.97	7.23	1.16	1.33	0.08	0.03	0.03	0.04	0.16	0.01	1.17
HC 18	90.43	31.30	32.15	6.58	5.22	0.65	0.92	0.07	0.04	0.03	0.04	0.03	0.04	2.29
HC 19	107.22	25.63	41.37	3.21	5.76	0.69	0.70	0.11	0.01	0.03	0.04	0.25	0.29	2.91
HC 20	130.79	9.74	40.12	6.76	8.04	0.39	0.27	0.11	0.01	0.03	0.04	0.18	0.13	2.45
HC 21	113.20		38.10		7.60	1.00		0.10		0.05		0.07		
HC 22	92.38	29.52	34.14	6.99	6.77	0.72	0.03	0.10	0.00	0.03	0.04	0.06	0.08	3.92
HC 23	89.36	21.02	35.29	3.52	7.35	0.81	0.13	0.11	0.02	0.03	0.04	0.16	0.23	3.18
HC 24	71.80	18.52	27.61	2.71	6.96	0.94	0.36	0.12	0.03	0.03	0.04	0.31	0.43	1.08
HC 25	47.19	15.43	35.41	32.08	4.33	2.51	1.58	0.14	0.06	0.08	0.05	0.69	0.95	0.24
HC 26	88.48	35.19	28.35	5.58	5.71	0.45	0.64	0.05	0.07	0.03	0.04	0.02	0.03	2.56
HC 27	133.82	44.00	35.41	4.53	7.27	1.18	1.30	0.11	0.02	0.03	0.04	7.39	1.68	1.36
HC 28	162.15		37.47		8.61	0.53		0.06		0.00		0.12		
HC 32	63.66		19.88		5.57	0.76		0.06		0.00		0.08		
HC 34	79.86		27.26		7.22	0.00		0.05		0.00		0.07		
HCDE	62.08	17.79	24.73	3.29	4.52	0.85	0.08	0.06	0.01	0.03	0.04	0.11	0.04	1.02
FS 1	75.06		8.21		2.41	1.26		0.00		0.00		0.08		
FS 3	41.72		4.35		1.57	0.52		0.00		0.00		0.06		
FS 4	83.16		6.62		2.33	0.63		0.00		0.00		0.05		
FS 5	69.21		14.22		4.28	0.00		0.05		0.00		0.10		

Station	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Na	Avg K	SD K	Avg P	SD P	Avg Al	SD Al	Avg Fe	SD Fe	SD Na
FS 6	188.89		26.79		7.40	0.00		0.08		0.00		0.16		
FS 7	97.34		8.75		2.93	0.20		0.00		0.00		0.06		
FS 8	104.28		8.87		3.31	2.83		0.06		0.00		0.47		
FS 9	86.98		8.37		2.62	1.84		0.00		0.00		0.76		
FS 10	116.84		10.84		4.16	1.10		0.04		0.00		1.15		
FS 11	109.26		8.17		2.65	1.71		0.04		0.00		1.74		
FS 13	111.40		9.64		3.60	0.46		0.04		0.00		9.38		
FS 14	84.55		15.42		5.97	2.16		0.09		0.00		0.88		
FS 15	151.79		27.70		8.57	0.55		0.04		0.00		0.91		
FS 16	183.10		23.13		41.55	0.00		0.13		0.00		0.31		
FS 17	162.27		19.64		7.33	0.57		0.17		0.00		0.58		
FS 18	171.93		18.74		7.21	1.28		0.15		0.00		0.72		
FS 19	50.98		46.51		44.87	9.41		0.97		0.95		1.21		
FS 20	167.21		24.46		11.54	0.00		0.04		0.00		0.50		
FS 21	124.82		38.16		23.10	0.28		0.02		0.00		0.17		
FS 22	104.98		10.85		3.44	0.00		0.00		0.00		0.08		
FS 23	165.34		20.46		9.37	0.24		0.07		0.00		0.18		
FS 26	190.52		25.28		9.58	0.26		0.32		0.00		2.86		
MC 7	180.39		29.51		29.34	0.00		0.00		0.00		0.14		
MC 10	44.50		10.09		10.02	1.07		0.00		0.00		0.69		
MC 11	28.63		6.37		26.07	0.15		0.06		0.37		7.77		
MC 12	32.03		7.48		15.72	0.45		0.00		0.21		0.97		
MC 15	35.60		5.51		8.46	1.17		0.00		0.00		0.18		
MC 16	178.86		27.28		49.80	0.23		0.00		0.00		0.27		
MC 17	39.75		5.48		9.98	0.00		0.09		0.90		3.56		
MC 20	31.56		7.62		9.17	1.41		0.04		0.00		1.65		
SC 1	26.87		6.91		12.53	0.75		0.00		0.00		0.27		

Station	Avg Mn	SD Mn	Avg Ti	SD Ti	Avg Pb	SD Pb	Avg Mo	SD Mo	Avg Cd	SD Cd	Avg Cr	SD Cr	Avg Sr	SD Sr	Avg V
HC1	0.02		0.00		0.00		0.00		0.00		0.04		0.83		0.01
HC2	0.07		0.00		0.00		0.00		0.00		0.03		0.48		0.01
HC3	0.01	0.00	0.00	0.00	0.09	0.12	0.01	0.01	0.00	0.00	2.31	3.27	0.26	0.13	0.01
HC4	0.03	0.02	0.00	0.00	0.17	0.24	0.01	0.01	0.00	0.00	3.25	4.57	0.27	0.03	0.01
HC5	0.01	0.01	0.00	0.00	0.15	0.21	0.00	0.00	0.00	0.00	3.05	4.31	0.27	0.03	0.00
HC8	0.08	0.08	0.00	0.00	0.18	0.25	0.01	0.01	0.00	0.00	4.31	6.07	0.31	0.04	0.01
HC9	0.04	0.03	0.00	0.00	0.24	0.34	0.00	0.00	0.00	0.00	3.09	4.36	0.30	0.02	0.00
HC10	0.07	0.10	0.00	0.00	0.04	0.06	0.03	0.00	0.00	0.00	3.96	5.57	0.67	0.33	0.02
HC11	0.01	0.01	0.01	0.00	0.10	0.14	0.03	0.03	0.00	0.00	2.00	2.82	0.28	0.18	0.02
HC12	0.07	0.03	0.00	0.00	0.20	0.28	0.01	0.01	0.00	0.00	3.74	5.26	0.35	0.03	0.01
HC13	0.06	0.01	0.01	0.00	0.11	0.16	0.00	0.00	0.00	0.00	2.79	3.92	0.36	0.13	0.00
HC 14	0.04	0.01	0.00	0.00	0.13	0.18	0.01	0.01	0.00	0.00	3.84	5.41	0.32	0.23	0.00
HC 15	0.07	0.04	0.00	0.00	0.18	0.25	0.01	0.01	0.00	0.00	3.07	4.34	0.21	0.07	0.00
HC 16	0.06	0.00	0.00	0.00	0.20	0.28	0.00	0.00	0.00	0.00	3.80	5.37	0.30	0.01	0.00
HC 17	0.03	0.01	0.00	0.00	0.09	0.12	0.00	0.00	0.00	0.00	3.13	4.40	0.33	0.03	0.01
HC 18	0.01	0.00	0.00	0.00	0.07	0.09	0.00	0.00	0.00	0.00	2.35	3.32	0.27	0.04	0.01
HC 19	0.06	0.00	0.01	0.00	0.11	0.15	0.01	0.01	0.00	0.00	3.85	5.43	0.28	0.11	0.00
HC 20	0.14	0.00	0.00	0.00	0.17	0.24	0.01	0.01	0.00	0.00	5.17	7.29	0.30	0.11	0.01
HC 21	0.12		0.01		0.30		0.01		0.00		6.34		0.65		0.01
HC 22	0.03	0.01	0.00	0.00	0.06	0.08	0.01	0.01	0.00	0.00	2.86	4.02	0.29	0.04	0.01
HC 23	0.02	0.00	0.00	0.00	0.13	0.18	0.00	0.00	0.00	0.00	2.62	3.70	0.27	0.02	0.01
HC 24	0.01	0.01	0.00	0.00	0.13	0.18	0.00	0.00	0.00	0.00	2.80	3.94	0.24	0.02	0.01
HC 25	0.01	0.00	0.03	0.04	0.08	0.11	0.01	0.01	0.00	0.00	2.54	3.55	0.17	0.08	0.02
HC 26	0.01	0.01	0.00	0.00	0.12	0.16	0.00	0.00	0.00	0.00	2.46	3.48	0.28	0.05	0.01
HC 27	0.20	0.02	0.00	0.00	0.22	0.30	0.00	0.00	0.00	0.00	4.91	6.91	0.37	0.05	0.01
HC 28	0.01		0.01		0.00		0.01		0.00		0.03		0.34		0.01
HC 32	0.00		0.00		0.00		0.00		0.00		0.02		0.17		0.01
HC 34	0.00		0.00		0.00		0.00		0.00		0.00		0.23		0.00
HCDE	0.01	0.01	0.00	0.00	0.09	0.12	0.00	0.00	0.00	0.00	2.06	2.90	0.17	0.01	0.00
FS 1	0.00		0.00		0.00		0.00		0.00		0.00		0.15		0.00
FS 3	0.01		0.00		0.00		0.00		0.00		0.00		0.07		0.00
FS 4	0.00		0.00		0.00		0.00		0.00		0.01		0.12		0.01
FS 5	0.01		0.00		0.00		0.00		0.00		0.00		0.14		0.00

Station	Avg Mn	SD Mn	Avg Ti	SD Ti	Avg Pb	SD Pb	Avg Mo	SD Mo	Avg Cd	SD Cd	Avg Cr	SD Cr	Avg Sr	SD Sr	Avg V
HC1	0.02		0.00		0.00		0.00		0.00		0.04		0.83		0.01
FS 6	0.01		0.00		0.00		0.00		0.00		0.01		0.38		0.00
FS 7	0.00		0.00		0.00		0.00		0.00		0.02		0.15		0.01
FS 8	0.01		0.00		0.00		0.00		0.00		0.02		0.16		0.01
FS 9	1.56		0.00		0.00		0.00		0.00		0.01		0.13		0.00
FS 10	2.93		0.00		0.00		0.00		0.00		0.02		0.19		0.01
FS 11	6.64		0.00		0.00		0.00		0.00		0.01		0.01		0.00
FS 13	0.75		0.01		0.01		0.00		0.00		0.02		0.02		0.01
FS 14	4.89		0.00		0.00		0.00		0.00		0.01		0.01		0.00
FS 15	0.69		0.00		0.00		0.00		0.00		0.02		0.02		0.00
FS 16	0.08		0.00		0.00		0.00		0.00		0.01		0.01		0.00
FS 17	0.60		0.01		0.00		0.00		0.00		0.02		0.02		0.00
FS 18	0.52		0.00		0.00		0.00		0.00		0.02		0.02		0.00
FS 19	0.97		0.92		0.00		0.94		0.93		0.94		0.94		0.94
FS 20	0.41		0.00		0.09		0.00		0.00		0.01		0.01		0.00
FS 21	0.04		0.00		0.00		0.00		0.00		0.00		0.00		0.00
FS 22	0.00		0.00		0.00		0.00		0.00		0.00		0.19		0.00
FS 23	0.18		0.00		0.00		0.00		0.00		0.01		0.28		0.00
FS 26	0.47		0.01		0.00		0.00		0.00		0.01		0.35		0.00
MC 7	0.04		0.00		0.00		0.00		0.00		0.02		1.19		0.00
MC 10	2.68		0.00		0.00		0.00		0.00		0.00		0.43		0.00
MC 11	0.09		0.07		0.00		0.00		0.00		0.00		0.22		0.00
MC 12	0.01		0.06		0.00		0.00		0.00		0.00		0.25		0.00
MC 15	0.07		0.00		0.00		0.00		0.00		0.00		0.22		0.00
MC 16	0.02		0.01		0.00		0.00		0.00		0.02		0.91		0.00
MC 17	0.04		0.20		0.00		0.00		0.00		0.00		0.25		0.01
MC 20	0.13		0.01		0.00		0.00		0.00		0.00		0.27		0.00
SC 1	0.00		0.00		0.00		0.00		0.00		0.00		0.21		0.00

Station	SD V	Avg Cu	Sd Cu	Avg Zn	SD Zn	Avg Ni	SD Ni	Avg B	SD B	Avg Ba	SD Ba	Avg Si	SD Si	Avg U	SD U
HC1		0.00		0.00		0.02		0.05		0.17		17.02		0.0176	
HC2		0.00		0.00		0.01		0.03		0.21		14.79		0.0000	
HC3	0.01	0.00	0.00	0.01	0.01	0.01	0.00	0.10	0.09	0.12	0.08	3.54	4.97	0.0040	0.0045
HC4	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.16	0.21	0.16	0.11	4.79	6.76	0.0008	0.0011
HC5	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.16	0.20	0.17	0.17	6.41	9.04	0.0004	0.0006
HC8	0.00	0.01	0.01	0.03	0.04	0.01	0.00	0.26	0.14	0.20	0.15	5.05	7.10	0.0188	0.0187
HC9	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.16	0.21	0.24	0.29	6.20	8.76	0.0012	0.0006
HC10	0.02	0.01	0.01	0.04	0.05	0.03	0.01	0.73	0.97	0.19	0.07	0.40	0.49	0.0950	0.0297
HC11	0.01	0.00	0.00	0.02	0.02	0.01	0.00	0.26	0.35	0.07	0.03	3.47	4.89	0.4310	0.4794
HC12	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.20	0.23	0.25	0.25	12.66	17.90	0.0004	0.0006
HC13	0.00	0.00	0.00	0.04	0.06	0.01	0.00	0.30	0.38	0.16	0.17	7.69	10.84	0.0003	0.0004
HC 14	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.20	0.25	0.19	0.18	5.67	8.01	0.0017	0.0004
HC 15	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.14	0.20	0.13	0.12	2.60	3.65	0.0008	
HC 16	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.18	0.23	0.19	0.22	6.19	8.75	0.0014	0.0011
HC 17	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.20	0.23	0.14	0.07	6.87	9.66	0.0008	0.0011
HC 18	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.14	0.14	0.11	0.07	5.09	7.17	0.0004	0.0006
HC 19	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.18	0.23	0.17	0.15	9.17	12.95	0.0050	0.0054
HC 20	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.26	0.34	0.18	0.17	9.04	12.75	0.0047	0.0066
HC 21		0.01		0.02		0.01		0.60		0.05		0.03		0.0010	
HC 22	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.14	0.18	0.13	0.12	7.97	11.22	0.0004	0.0006
HC 23	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.15	0.21	0.17	0.16	5.90	8.30	0.0031	0.0035
HC 24	0.00	0.00	0.00	0.03	0.04	0.01	0.00	0.12	0.16	0.15	0.17	5.21	7.32	0.0013	0.0007
HC 25	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.13	0.16	0.08	0.04	5.83	8.22	0.0016	0.0023
HC 26	0.01	0.00	0.00	0.01	0.01	0.01	0.00	0.13	0.17	0.16	0.19	4.86	6.81	0.0041	0.0049
HC 27	0.01	0.00	0.00	0.09	0.12	0.01	0.00	0.18	0.24	0.25	0.26	7.95	11.18	0.0100	0.0119
HC 28		0.00		0.00		0.01		0.01		0.37		6.84		0.0700	
HC 32		0.03		0.00		0.01		0.01		0.14		6.40		0.0028	
HC 34		0.00		0.00		0.01		0.01		0.12		5.71		0.0030	
HCDE	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.08	0.11	0.11	0.11	3.78	5.32	0.0022	0.0020
FS 1		0.00		0.00		0.00		0.00		0.21		7.58		0.0012	
FS 3		0.00		0.00		0.00		0.00		0.11		4.36		0.0012	
FS 4		0.00		0.00		0.01		0.00		0.16		4.61		0.0000	
FS 5		0.00		0.00		0.00		0.00		0.23		2.39		0.0300	

Station	SD V	Avg Cu	Sd Cu	Avg Zn	SD Zn	Avg Ni	SD Ni	Avg B	SD B	Avg Ba	SD Ba	Avg Si	SD Si	Avg U	SD U
HC1		0.00		0.00		0.02		0.05		0.17		17.02		0.0176	
FS 6		0.00		0.00		0.00		0.00		0.50		13.17		0.0076	
FS 7		0.00		0.00		0.01		0.00		0.21		5.24		0.0056	
FS 8		0.00		0.00		0.01		0.00		0.24		8.77		0.0000	
FS 9		0.00		0.00		0.01		0.00		0.23		8.63		0.0000	
FS 10		0.00		0.00		0.01		0.00		0.32		6.43		0.0000	
FS 11		0.00		0.00		0.01		0.00		0.43		9.11		0.0000	
FS 13		0.00		0.00		0.01		0.01		0.33		11.20		0.0010	
FS 14		0.00		0.00		0.01		0.00		0.54		16.03		0.0000	
FS 15		0.00		0.00		0.01		0.00		0.51		14.40		0.0016	
FS 16		0.00		0.00		0.00		0.00		0.41		9.65		0.0000	
FS 17		0.00		0.00		0.01		0.00		0.34		9.46		0.0000	
FS 18		0.00		0.00		0.01		0.00		0.47		13.08		0.0000	
FS 19		0.92		0.95		0.93		0.90		0.93		1.23		0.0000	
FS 20		0.00		0.00		0.00		0.00		0.38		10.68		0.0016	
FS 21		0.00		0.00		0.00		0.00		0.21		13.87		0.0000	
FS 22		0.00		0.00		0.00		0.00		0.25		8.42		0.0008	
FS 23		0.00		0.00		0.00		0.00		0.34		7.94		0.0168	
FS 26		0.00		0.00		0.00		0.00		0.23		6.15			
MC 7		0.00		0.00		0.00		0.00		0.04		12.52		0.0006	
MC 10		0.00		0.00		0.00		0.00		0.26		9.80		0.0008	
MC 11		0.00		0.00		0.00		0.26		0.09		17.24		0.0004	
MC 12		0.00		0.00		0.00		0.01		0.10		11.29		0.0010	
MC 15		0.00		0.00		0.00		0.00		0.02		9.81		0.0006	
MC 16		0.00		0.00		0.00		0.04		0.02		13.18		0.0004	
MC 17		0.00		0.01		0.00		0.04		0.08		30.30		0.0004	
MC 20		0.00		0.00		0.00		0.00		0.07		8.71		0.0004	
SC 1		0.00		0.00		0.00		0.01		0.02		11.98		0.0004	

Station	95 Gross alpha	95 Gross beta	Avg pH	SD pH	Avg EC (micro S)	SD EC
HC1			7.07	0.50	1075	682
HC2			7.28	0.51	959	387
HC3			7.79	0.40	426	28
HC4	2.00	5.00	7.16	0.34	577	108
HC5			6.88	0.48	537	102
HC8			7.24	0.30	554	122
HC9			7.09	0.21	657	107
HC10			6.73	0.57	714	353
HC11			7.31	0.68	662	204
HC12			7.49	0.35	526	197
HC13			7.53	0.28	502	93
HC 14	2.00	4.00	7.43	0.45	636	130
HC 15			7.07	0.27	597	138
HC 16			7.24	0.32	651	150
HC 17			7.58	0.40	622	92
HC 18			7.47	0.35	506	100
HC 19			7.30	0.40	575	198
HC 20	9.00	3.00	7.27	0.38	683	151
HC 21	7.00	1.00	7.49	0.53	629	168
HC 22			7.32	0.43	491	76
HC 23	1.00	1.00	7.18	0.39	561	79
HC 24	32.00	17.00	7.05	1.18	477	212
HC 25			7.57	0.57	454	85
HC 26			7.52	0.38	471	157
HC 27			7.52	0.29	592	81
HC 28			7.00	0.37	422	68
HC 32			7.86	0.54	890	240
HC 34			7.59	0.76	660	147
HCDE			7.78	0.32	437	82
FS 1			7.84	0.66	304	66
FS 3			7.53	0.73	318	97

Station	95 Gross alpha	95 Gross beta	Avg pH	SD pH	Avg EC (micro S)	SD EC
HC1			7.07	0.50	1075	682
FS 4			7.81	0.64	346	124
FS 5			7.78	0.21	475	345
FS 6			7.79	0.28	429	246
FS 7			7.97	0.53	256	208
FS 8			7.87	0.47	335	323
FS 9			7.62	0.59	557	164
FS 10			7.74	0.54	369	200
FS 11			7.91	0.72	509	191
FS 13			7.82	0.46	453	291
FS 14			7.79	0.51	493	276
FS 15			7.65	0.43	538	261
FS 16			7.66	0.36	494	281
FS 17			7.91	0.46	620	245
FS 18			8.03	0.45	499	271
FS 19			7.88	0.53	536	261
FS 20			7.51	0.36	527	267
FS 21			7.53	0.41	539	206
FS 22			7.70	0.36	425	173
FS 23			7.49	0.28	581	425
FS 26			7.39	0.07	397	15
MC 7			7.23	0.42	555	252
MC 10			7.74	0.70	220	37
MC 11			7.33	0.50	547	423
MC 12			7.09		320	
MC 15			7.14	0.73	293	96
MC 16			6.40	0.48	870	309
MC 17			6.52	0.82	289	162
MC 20			7.18	0.40	347	122
SC 1			7.24	0.24	445	214

Appendix 4

This appendix contains means of soil chemistry and physical characteristics obtained during this study. Sample standard deviations (SD) follow the column with the means. The chemical analyses are in mg/kg (= parts per million), except pH which is in standard pH units and electrical conductivity (EC) reported as micro-Siemens. Units for physical factors are provided in the column headings.

ID #	Avg pH	pH SD	Avg EC	EC SD	avg N03	SD NO3	Avg P	SD P	Avg K	Avg OM (%)	SD OM
HC 1	7.50	0.2	1.5	0.6	20.33	6.51	16.80	21.03	158.00	41.0	3.4
HC 2	7.47	0.1	1.2	0.2	13.67	4.16	6.67	1.15	143.07	47.8	6.3
HC 3	6.83	0.2	1.1	0.6	8.00	5.29	8.97	7.09	137.47	62.4	19.2
HC 4	6.97	0.3	2.9	0.2	9.00	5.57	4.67	4.60	130.93	41.9	22.3
HC 5	7.10	0.4	2.0	0.3	11.67	2.08	10.60	12.93	94.53	62.0	11.1
HC 7	7.70	0.1	1.4	0.2	15.67	3.21	4.43	1.59	72.80	20.8	3.1
HC 8	7.53	0.1	1.1	0.0	9.67	5.69	4.27	3.78	118.17	53.6	16.9
HC 9	7.13	0.2	2.5	0.4	9.00	6.56	4.27	5.45	53.87	37.9	20.2
HC 10	6.67	1.4	1.6	1.3	15.67	8.50	3.87	3.35	62.97	59.1	15.9
HC 11	7.27	0.3	1.3	1.0	12.33	5.51	5.13	4.31	52.67	58.3	11.3
HC 12	6.87	0.4	2.6	0.4	8.67	6.03	8.40	4.23	157.07	51.1	37.9
HC 13	7.30	0.1	2.1	0.8	15.33	8.50	9.43	5.31	83.57	39.1	0.9
HC 14	6.93	0.7	2.0	0.8	15.00	3.00	13.40	4.80	117.20	61.6	11.3
HC 15	7.23	0.2	2.0	0.8	12.67	2.08	6.73	5.93	130.20	58.4	5.5
HC 16	7.24	0.4	2.2	0.4	6.67	5.51	8.00	3.94	57.07	33.9	19.8
HC 17	7.10	0.1	2.2	0.4	15.67	8.62	16.67	10.52	63.17	36.2	2.5
HC 18	7.30	0.2	2.0	0.7	12.67	3.06	17.27	6.69	117.57	53.8	12.8
HC 19	6.20	2.5	1.8	0.7	12.00	8.72	4.53	2.01	80.73	39.6	21.5
HC 20	7.40	0.1	2.5	0.2	7.00	7.00	5.13	6.47	39.15	40.1	23.1
HC 21	7.30	0.0	2.7	0.4	9.67	9.81	4.67	4.05	108.47	33.0	5.0
HC 22	7.23	0.5	2.1	0.1	13.67	14.57	14.80	8.86	140.57	64.4	19.1
HC 23	7.20	0.4	1.6	0.6	5.33	6.11	14.67	14.36	110.23	45.3	17.3
HC 24	6.73	0.4	1.7	0.8	10.33	3.79	15.33	2.57	152.60	75.3	8.3
HC 25	7.33	0.6	1.2	0.3	15.00	6.24	10.43	3.20	168.00	72.0	4.7
HC 26	7.03	0.3	1.4	0.2	15.67	13.87	15.57	11.60	123.43	71.9	12.3
HC 27	7.07	0.2	1.5	0.1	10.33	4.04	10.00	10.54	162.47	39.8	7.9
HC 28	7.40	0.4	1.0	0.3	17.50	7.78	1.60	2.26	106.45	46.3	3.5
HC 29	7.55	0.1	1.1	0.1	22.00	14.14	14.20	16.69	136.50	51.4	5.4
HC 30	7.90	0.0	1.3	0.1	20.00	22.63	21.60	1.13	220.00	51.7	1.3
HC 32	7.30	0.1	0.8	0.6	5.19	6.80	5.20	6.79	166.60	14.2	1.2

ID #	Avg pH	pH SD	Avg EC	EC SD	avg N03	SD NO3	Avg P	SD P	Avg K	Avg OM (%)	SD OM
HC 1	7.50	0.2	1.5	0.6	20.33	6.51	16.80	21.03	158.00	41.0	3.4
HC 33	7.70	0.0	0.9	0.1	12.50	12.02	5.60	7.92	54.25	29.5	2.1
HC 34	7.85	0.1	1.3	0.3	13.50	7.78	3.40	4.81	72.85	27.9	1.5
HC 35	7.85	0.1	1.3	0.2	17.50	7.78	8.20	11.60	78.85	32.7	4.1
HC DE	6.80	0.6	1.9	1.4	9.33	7.37	3.67	4.04	72.27	70.6	12.7
HC 31	7.90	0.1	1.4	0.6	17.50	7.78	3.10	4.38	50.25	24.5	0.6
FS 1	7.35	0.2	1.3	0.8	17.00	4.24	45.70	18.81	266.50	65.3	6.8
FS 2	7.50	0.4	0.4	0.0	9.00	7.07	6.60	4.24	139.50	38.8	5.7
FS 3	7.00	0.7	0.5	0.1	12.50	3.54	21.45	12.66	209.00	68.7	1.9
FS 4	7.85	0.2	0.4	0.0	21.50	2.12	8.40	9.05	205.00	79.4	10.3
FS 5	7.90	0.4	0.5	0.1	24.00	8.49	5.50	5.23	56.45	51.8	10.8
FS 6	8.10	0.3	0.4	0.0	22.50	3.54	7.40	3.68	83.70	43.2	19.6
FS 7	7.90	0.3	0.4	0.1	10.50	0.71	14.00	0.00	112.50	84.3	1.8
FS 8	7.85	0.4	0.6	0.3	17.50	3.54	23.50	28.99	773.00	83.9	4.5
FS 9	7.75	0.5	0.8	0.0	9.50	6.36	4.80	6.79	100.75	47.3	1.1
FS 10	6.85	0.5	1.2	0.0	14.50	2.12	3.20	4.53	102.30	43.8	4.3
FS 11	8.05	0.2	0.8	0.1	9.00	5.66	5.40	7.64	119.75	39.8	11.7
FS 12	7.95	0.4	0.5	0.0	8.00	2.83	3.60	5.09	51.00	18.8	3.2
FS 13	7.80	0.0	0.6	0.2	8.50	3.54	1.40	1.98	30.70	21.7	3.1
FS 14	7.65	0.4	0.8	0.4	11.50	2.12	8.30	10.89	153.50	37.9	2.1
FS 15	7.95	0.1	0.7	0.2	9.00	4.24	8.70	9.76	52.45	21.8	2.6
FS 16	7.80	0.1	0.9	0.2	15.00	0.00	6.40	9.05	82.35	37.1	0.5
FS 17	7.55	0.5	0.7	0.2	12.50	3.54	4.25	6.01	114.25	29.5	21.1
FS 18	7.50	0.1	0.5	0.1	14.50	0.71	3.40	4.81	82.60	47.6	10.2
FS 19	7.50	0.3	0.6	0.3	48.50	51.62	8.80	7.35	92.60	41.8	5.4
FS 20	7.70	0.0	0.6	0.1	7.50	2.12	4.30	4.67	63.00	36.2	4.3
FS 21	7.55	0.2	0.7	0.2	16.50	4.95	5.30	6.08	89.00	43.4	6.9
FS 22	7.50	0.4	0.7	0.2	20.50	13.44	3.90	4.67	83.00	38.9	1.6
FS 23	7.80	0.3	0.6	0.2	10.00	5.66	7.85	8.13	185.00	23.0	2.2
FS24	7.55	0.4	1.4	0.6	266.50	26.16	13.20	14.71	85.70	74.2	5.0
FS25	7.70	0.1	2.9	3.0	821.50	962.37	16.40	3.96	79.35	31.7	1.8
FS26	7.85	0.2	1.1	0.4	46.75	65.41	7.80	11.03	55.46	47.1	2.4
FS 27	8.10		0.7		66.00		16.20		92.60	64.4	

ID #	Avg pH	pH SD	Avg EC	EC SD	avg N03	SD NO3	Avg P	SD P	Avg K	Avg OM (%)	SD OM
HC 1	7.50	0.2	1.5	0.6	20.33	6.51	16.80	21.03	158.00	41.0	3.4
FF1	6.90	1.0	1.1	0.1	42.50	24.75	7.95	2.76	97.15	52.3	32.9
FF2	6.05	1.1	2.3	1.1	119.00	154.15	10.40	4.24	170.90	67.7	7.5
FF3	7.35	0.1	3.1	0.1	37.50	16.26	5.80	4.81	78.00	59.5	1.6
FF4	5.60	2.5	3.6	0.8	31.00	21.21	3.80	1.98	75.00	57.8	8.3
FF5	6.25	2.1	4.2	2.6	11.50	4.95	13.90	18.81	90.65	28.9	8.2
FF6	7.55	0.2	3.1	0.0	21.00	7.07	6.70	0.71	150.30	38.9	19.9
FF7	6.30	0.6	1.6	0.8	19.50	6.36	7.30	0.14	65.65	59.0	1.3
FF8	6.20	0.3	1.8	0.3	22.00	11.31	3.20	4.53	124.70	72.2	5.5
FF9	6.30	0.7	1.4	0.6	22.00	8.49	4.90	0.14	83.70	56.6	19.3
FF10	6.35	0.6	0.5	0.1	8.50	4.95	7.45	4.31	59.40	37.6	30.4
FF11	6.20	0.7	0.9	0.1	8.50	2.12	4.60	6.51	90.50	47.2	11.8
FF12	6.50	0.7	0.6	0.3	6.50	2.12	3.40	4.81	57.35	31.6	24.7
FF13	6.45	0.8	0.8	0.5	8.50	3.54	1.60	2.26	87.40	27.7	13.0
FF14	5.05	1.9	2.1	1.5	14.00	8.49	4.80	6.79	71.95	42.5	7.6
FF15	4.15	1.5	2.9	0.7	20.00	14.14	12.20	8.77	45.95	53.7	29.6
FF16	7.60		1.2		16.00		3.60		33.36	58.0	
FF17	5.60	0.4	1.4	1.4	13.00	2.83	5.70	4.67	160.00	76.6	3.9
FF18	6.30	0.1	0.7	0.0	16.50	4.95	18.45	8.41	165.00	72.0	8.5
FF20	6.20	0.8	1.0	0.3	16.50	2.12	11.25	1.77	173.70	74.4	11.7
FF 21	5.95	0.2	1.3	0.8	9.50	0.71	20.75	1.06	345.00	69.8	11.9
FF 22	6.95	0.8	2.4	0.4	51.00	55.15	7.95	0.78	134.20	52.9	10.4
FF 23	6.80		0.5		10.00		7.50		311.50		

ID #	SD K	Avg Zn	Sd Zn	Avg Fe	SD Fe	SD Mn	Avg CU	SD CU	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Mn
HC 1	40.84	13.75	4.92	785.33	598.58	9.70	6.85	2.48	9707.13	1211.21	1302.67	345.68	19.17
HC 2	43.45	17.52	11.53	716.00	309.12	12.55	5.70	1.48	10371.70	1705.88	1082.07	327.30	25.77
HC 3	142.94	10.88	3.49	201.00	72.58	7.06	7.30	0.65	10268.73	488.46	1962.20	75.63	5.89
HC 4	112.37	6.95	3.66	572.00	325.72	6.53	3.70	2.25	10324.45	163.41	1267.63	482.57	10.13
HC 5	12.98	10.52	1.20	626.17	338.39	1.27	5.19	1.34	11186.30	2730.70	1783.50	122.36	5.94
HC 7	28.35	3.77	0.66	194.73	177.29	2.08	3.52	0.35	7106.00	529.23	1375.17	193.57	10.27
HC 8	60.77	7.85	3.19	1001.33	415.31	6.69	4.46	0.89	11373.43	2211.83	1053.80	332.06	20.25
HC 9	30.39	3.26	0.77	254.33	98.50	2.12	2.59	0.95	9855.13	1335.58	854.00	191.46	8.84
HC 10	15.91	5.42	1.69	1590.27	1260.68	8.89	3.08	1.57	9833.47	3328.85	1504.70	768.64	8.94
HC 11	23.23	11.35	3.46	854.67	109.46	9.46	4.25	0.85	12663.93	1241.43	1845.20	288.20	6.73
HC 12	115.96	6.48	4.67	561.00	403.43	7.31	4.07	3.46	5200.80	6669.40	657.67	778.35	9.24
HC 13	14.91	7.47	5.85	174.13	50.71	6.39	3.33	1.35	12428.60	4822.87	1529.83	292.65	19.19
HC 14	61.91	9.99	3.94	472.83	430.40	6.64	6.16	1.98	7641.83	6640.61	1373.60	1201.18	19.38
HC 15	25.74	8.64	2.65	473.33	266.84	11.84	4.37	0.46	12803.63	1926.80	1392.37	106.62	31.07
HC 16	31.08	4.28	2.93	157.57	59.70	8.52	2.63	1.80	9961.87	3091.89	1157.50	522.60	14.01
HC 17	21.96	4.05	0.96	188.20	43.43	2.11	2.73	0.55	12244.87	6286.92	1277.63	268.48	9.04
HC 18	42.30	11.42	3.03	340.93	243.79	3.10	4.87	0.58	15595.17	9006.19	1709.67	179.97	9.17
HC 19	43.01	6.64	2.44	199.87	87.12	7.10	4.09	2.40	8378.07	2955.88	1360.90	523.15	13.27
HC 20	34.60	3.68	1.00	411.73	190.84	11.43	2.32	1.09	12321.97	5732.67	1254.27	620.50	27.23
HC 21	40.96	19.17	4.82	382.27	138.32	9.28	5.90	2.11	9849.70	1040.48	1298.00	158.08	29.87
HC 22	93.86	13.97	7.94	542.00	286.13	9.77	4.72	0.93	12058.43	3325.97	1897.43	377.40	12.71
HC 23	93.35	6.19	3.52	352.33	185.19	14.05	4.17	2.19	8117.33	7469.87	1017.57	921.57	15.84
HC 24	81.79	10.94	2.98	175.97	88.40	5.27	2.83	1.35	10905.43	1178.21	1750.23	158.60	6.05
HC 25	57.65	7.93	2.24	421.00	76.37	2.14	3.91	1.15	9110.33	7951.09	1559.07	1372.53	6.42
HC 26	88.40	6.08	2.82	119.73	40.16	6.17	2.95	1.24	15661.00	4751.53	1967.17	464.02	10.84
HC 27	114.69	9.63	5.94	350.53	290.40	4.56	4.75	2.04	9956.33	1648.66	992.70	355.71	9.57
HC 28	36.70	6.50	7.16	742.40	562.29	11.72	5.21	0.47	11428.05	738.15	968.15	31.32	15.56
HC 29	9.19	11.79	9.77	442.90	192.47	35.58	5.64	2.34	11722.45	1127.91	1473.05	181.09	32.84
HC 30	107.48	8.06	7.83	107.60	90.51	20.93	4.10	0.82	8718.80	1569.49	3258.75	496.74	31.20
HC 32	165.46	5.48	1.29	189.46	232.69	24.35	5.86	2.12	4793.70	315.79	939.40	163.48	17.86
HC 33	0.92	5.31	0.08	443.40	515.62	8.22	8.18	2.86	7917.00	427.09	1188.65	61.73	6.89
HC 34	34.44	8.72	2.72	609.80	365.15	2.25	8.07	0.83	7741.85	218.99	1604.95	125.94	12.11
HC 35	3.32	12.21	2.98	624.20	373.07	4.17	6.97	0.86	8468.15	276.97	1674.50	176.07	9.95

ID #	SD K	Avg Zn	Sd Zn	Avg Fe	SD Fe	SD Mn	Avg CU	SD CU	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Mn
HC 1	40.84	13.75	4.92	785.33	598.58	9.70	6.85	2.48	9707.13	1211.21	1302.67	345.68	19.17
HC DE	5.28	9.48	2.00	605.93	446.21	14.06	6.72	2.32	12123.67	316.02	1951.97	176.89	14.07
HC 31	0.92	10.97	8.95	277.10	19.66	6.92	2.76	1.33	8320.55	838.42	1572.15	690.07	7.51
FS 1	94.05	16.05	5.87	1180.00	226.27	41.30	6.02	1.14	11687.75	59.75	791.40	1.98	88.80
FS 2	16.26	4.48	0.78	259.00	15.56	4.53	5.10	0.48	10333.40	740.20	589.65	35.85	36.80
FS 3	19.80	8.43	3.36	718.50	259.51	61.16	5.45	1.14	13021.90	1897.73	779.10	31.25	150.25
FS 4	83.44	9.48	4.42	210.00	132.94	25.88	3.82	1.29	14323.85	1473.82	803.35	26.38	30.50
FS 5	12.66	2.46	0.74	436.90	370.67	2.55	6.77	4.09	13593.70	2480.11	1281.65	360.13	32.00
FS 6	47.38	4.29	2.88	171.30	47.66	15.85	13.24	15.85	8905.60	2849.07	686.70	247.06	25.31
FS 7	52.33	3.34	3.70	476.25	139.65	57.42	6.40	2.70	14002.40	3283.24	757.55	62.86	98.90
FS 8	674.58	8.77	5.00	694.00	278.60	11.81	10.59	2.84	7796.10	1009.61	449.00	104.65	69.05
FS 9	31.47	5.05	1.28	1025.00	134.35	183.49	4.58	0.16	11287.25	286.73	373.70	79.62	257.75
FS 10	75.94	4.95	2.74	809.00	496.39	54.16	5.59	1.90	9701.45	880.28	382.15	35.14	119.50
FS 11	48.44	5.80	2.30	655.50	212.84	60.60	4.23	1.58	11119.15	4102.42	379.00	156.98	130.65
FS 12	2.55	1.66	1.14	375.50	194.45	1.27	4.39	0.66	7034.20	595.67	270.15	1.63	36.70
FS 13	3.54	1.40	0.28	591.50	389.62	12.80	3.07	2.76	6671.15	248.69	163.60	33.09	40.25
FS 14	28.99	8.38	0.96	315.25	91.57	27.65	5.85	1.99	8608.15	245.86	471.80	97.86	106.95
FS 15	16.48	1.88	1.70	575.50	443.36	7.28	3.63	1.25	7705.55	598.99	507.00	77.78	57.75
FS 16	12.23	8.55	3.89	234.75	31.47	0.49	3.79	0.76	8589.75	322.79	586.65	27.79	69.15
FS 17	8.84	7.58	0.60	182.50	36.06	2.62	4.30	2.38	9994.65	937.13	570.95	15.63	41.95
FS 18	0.14	5.43	0.11	487.50	154.86	5.23	4.36	0.49	9751.50	1221.17	465.50	65.76	35.70
FS 19	25.17	7.65	7.72	544.50	376.89	2.97	4.83	0.78	10340.50	311.83	339.15	46.88	54.90
FS 20	31.82	4.94	2.84	366.75	294.51	7.11	3.24	0.35	8158.55	127.92	652.80	44.97	44.28
FS 21	21.21	9.56	1.75	428.25	230.16	35.92	7.75	1.56	9584.85	983.09	943.40	531.18	87.60
FS 22	21.92	4.68	0.95	490.25	173.59	5.76	3.67	1.15	8919.10	1.56	397.55	16.33	34.68
FS 23	87.68	13.63	9.93	279.75	6.72	33.66	7.44	1.90	8968.40	2279.15	503.90	131.66	79.20
FS24	45.68	10.54	9.54	337.50	116.67	43.63	3.76	1.32	16252.00	1841.31	1397.85	268.49	46.75
FS25	44.19	13.09	2.11	251.00	137.18	13.93	2.80	1.50	10134.30	809.35	643.40	161.79	48.35
FS26	29.33	19.77	6.97	492.60	222.60	9.12	5.46	2.13	13056.80	810.63	888.35	126.78	63.65
FS 27		40.80		458.00			3.72		14471.80		1154.70		100.40
FF1	57.77	24.05	14.92	867.50	229.81	6.22	3.80	1.05	10808.30	2857.14	571.75	154.50	30.50
FF2	1.27	25.95	4.03	1170.00	919.24	4.60	4.11	1.34	12055.90	5929.66	1235.60	880.49	17.75
FF3	0.28	9.29	5.78	939.00	708.52	6.08	2.91	0.78	15641.00	3180.57	2269.20	732.28	18.10

ID #	SD K	Avg Zn	Sd Zn	Avg Fe	SD Fe	SD Mn	Avg CU	SD CU	Avg Ca	SD Ca	Avg Mg	SD Mg	Avg Mn
HC 1	40.84	13.75	4.92	785.33	598.58	9.70	6.85	2.48	9707.13	1211.21	1302.67	345.68	19.17
FF4	4.53	8.95	3.04	734.50	317.49	0.54	2.88	0.40	23102.50	4932.07	1609.60	1730.15	7.74
FF5	95.25	2.92	1.70	1294.50	1549.27	0.13	9.68	5.41	6715.00	4731.96	1153.00	1387.34	3.66
FF6	78.77	15.39	18.40	523.50	16.26	14.30	3.66	1.27	11662.50	5264.41	1467.10	521.70	14.69
FF7	9.40	2.41	0.78	1366.00	1052.17	4.70	2.13	1.24	11653.35	1051.26	770.75	85.91	13.28
FF8	78.91	38.96	43.90	1517.50	399.52	18.94	4.81	0.56	11085.50	741.76	874.80	95.88	17.76
FF9	58.41	29.62	35.04	1224.00	1055.00	6.26	5.23	4.92	8681.30	35.78	787.70	0.99	13.60
FF10	29.84	4.30	1.85	794.50	255.27	267.83	3.98	2.03	5886.45	2567.43	694.25	295.92	191.12
FF11	31.82	11.77	7.54	1297.50	159.10	257.99	17.88	18.20	7431.30	2835.92	689.95	50.98	213.58
FF12	2.33	6.70	5.52	921.50	973.69	13.41	8.30	0.09	5875.25	9.55	660.70	75.38	18.22
FF13	48.93	5.54	2.81	530.50	38.89	6.49	6.44	5.03	5521.35	683.56	692.60	34.51	7.97
FF14	73.61	9.00	1.25	1070.00	905.10	35.71	5.58	1.44	14248.55	10992.05	658.30	242.82	37.55
FF15	24.82	17.74	15.43	2297.50	1912.72	25.53	5.36	3.90	5751.15	6241.14	718.95	193.68	34.05
FF16		13.00		242.40			4.36		12469.50		728.90		4.88
FF17	18.38	68.15	6.86	1445.00	289.91	2.12	10.80	4.53	11156.45	2601.52	712.90	236.32	51.50
FF18	25.46	34.20	33.66	1212.50	166.17	17.89	7.84	4.47	9928.10	1501.75	835.80	217.51	61.85
FF20	107.20	12.55	11.39	1590.00	509.12	3.32	7.69	6.80	8558.45	1454.45	909.80	231.65	62.85
FF 21	127.28	21.13	0.18	990.00	42.43	12.73	4.05	1.92	8868.40	2812.02	1110.85	226.06	44.50
FF 22	16.69	19.79	1.99	1011.00	917.82	7.14	4.38	1.78	14579.40	7234.27	758.15	280.23	32.95
FF 23		28.60		980.00			4.80		9387.30		803.00		

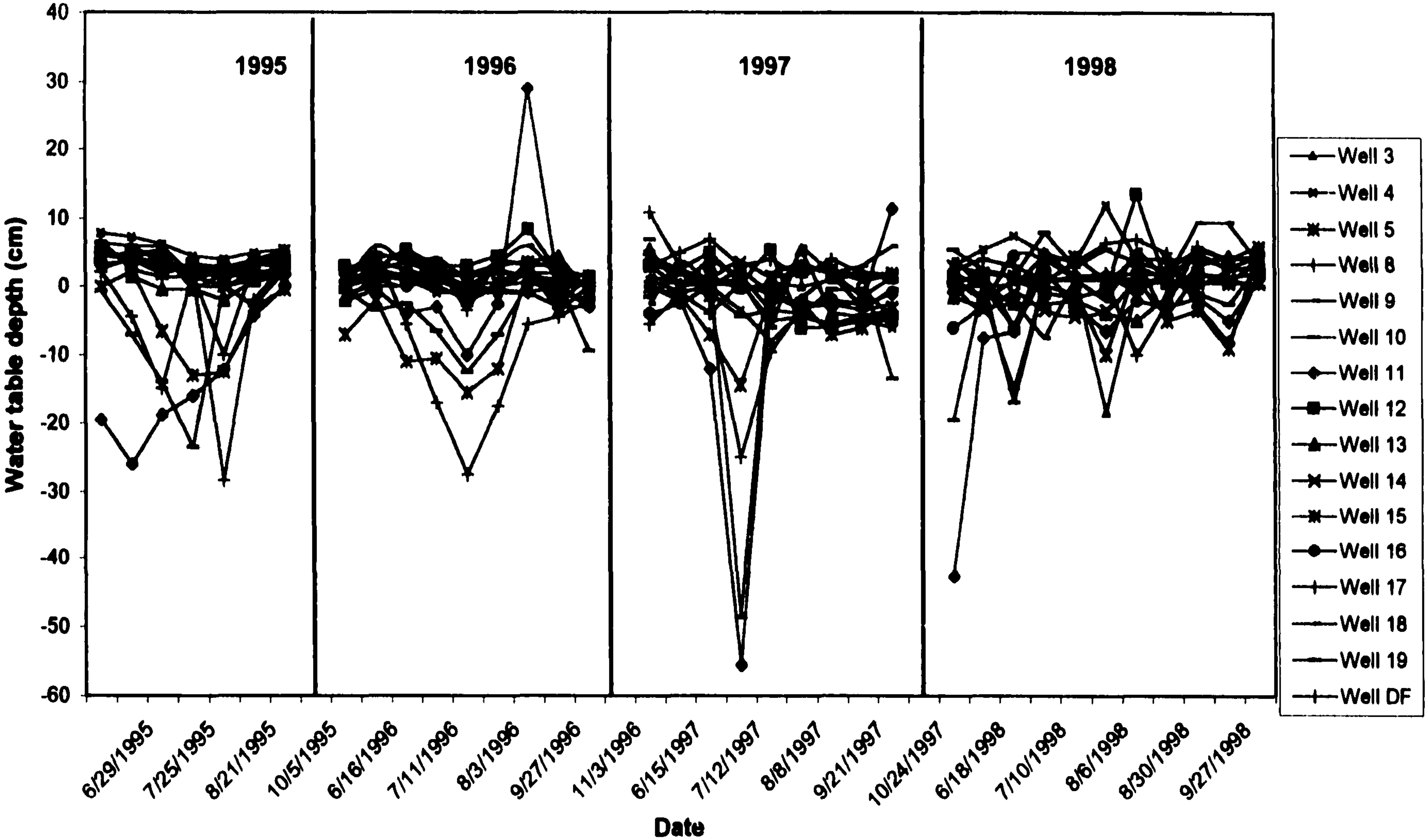
ID #	Avg Na	Sd Na	Avg Sr	SD Sr	Avg Pb	SD Pb	Avg CaCO3	SD CaCO3	95 Cr	Avg U	SD U	dry BD (g/cm^3)	Porosity
HC 1	124.97	76.94	433.37	28.70	44.01	7.79	29.01	18.64	11.00	7.18	4.28	0.33	0.76
HC 2	88.40	95.94	320.07	115.40	39.34	4.87	31.22	23.12	7.30	10.00		0.31	0.75
HC 3	112.47	76.54	48.30	42.07	11.47	12.04	4.97	6.12	20.30	41.00		0.15	0.64
HC 4	73.50	93.62	50.06	16.52	12.39	6.71	3.73	2.58	3.80	21.03	10.95	0.23	0.69
HC 5	100.00	81.96	43.37	39.15	40.20	34.92	12.34	19.55	9.80	39.00		0.14	0.67
HC 7	73.17	32.10	464.13	41.75	28.38	8.12	44.11	31.32	3.80	3.00		0.68	0.70
HC 8	102.13	87.90	224.23	166.91	21.15	2.48	23.92	24.95	5.40	11.00	4.06	0.21	0.70
HC 9	82.90	91.19	117.67	48.59	15.81	8.52	18.78	12.43	5.20	4.10	0.37	0.35	0.70
HC 10	96.03	78.34	152.23	147.38	9.31	4.06	16.13	22.62	8.50	78.32	33.63	0.22	0.56
HC 11	98.03	67.49	106.43	15.14	7.08	2.07	3.72	4.20	16.20	134.35	38.68	0.24	0.71
HC 12	122.63	205.60	35.57	41.39	15.70	22.12	10.18	10.35	3.70	7.50		0.11	0.68
HC 13	88.40	99.32	283.67	49.56	34.85	20.40	38.80	15.94	5.30	15.50		0.23	0.67
HC 14	114.33	118.17	100.96	36.30	25.13	11.49	9.68	6.62	11.90	8.84	2.13	0.16	0.76
HC 15	152.13	90.09	160.03	35.71	37.03	10.11	13.44	3.00	7.10	7.50		0.17	0.69
HC 16	81.70	50.05	50.40	55.57	7.03	8.87	20.23	13.95	6.70	8.50		0.15	0.82
HC 17	91.00	83.57	365.67	84.83	34.68	5.38	34.43	25.97	3.30	4.50		0.25	0.80
HC 18	142.37	137.05	108.50	51.30	51.02	6.88	12.01	13.67	4.40	8.00		0.16	0.60
HC 19	126.73	141.73	168.03	121.89	28.78	23.49	34.08	18.46	5.70	5.50		0.20	0.98
HC 20	154.73	191.65	127.27	65.07	13.61	6.95	15.08	17.07	4.40	5.50		0.16	0.76
HC 21	134.70	79.07	224.37	52.19	62.95	15.97	23.54	7.33	9.00	4.06	1.68	0.24	0.92
HC 22	110.13	37.12	83.43	20.56	59.05	30.06	13.47	14.40	11.20	12.00		0.12	0.82
HC 23	111.17	97.55	33.50	29.01	9.30	9.01	14.60	17.49	6.70	13.50		0.13	0.67
HC 24	152.63	51.78	75.64	10.29	28.24	9.56	5.02	4.80	9.39	37.38	15.30	0.15	0.75
HC 25	98.93	86.43	58.90	51.04	22.53	21.02	8.01	11.28	8.08	55.00		0.19	0.67
HC 26	123.70	40.89	83.14	16.43	60.68	35.84	14.42	18.69	10.40	17.67	3.32	0.14	0.84
HC 27	83.70	27.08	184.57	108.46	55.71	37.62	41.15	4.82	10.40	17.57	10.89	0.22	0.64
HC 28	93.15	22.84	211.75	56.21	20.47	7.74	18.71	10.79		3.44	0.19	0.32	0.92
HC 29	117.30	58.41	295.05	158.46	52.90	10.05	20.38	11.27				0.32	0.71
HC 30	306.85	212.34	282.80	1.13	41.12	4.07	11.69	6.63				0.40	0.81
HC 32	64.25	87.33	53.56	3.45	19.93	0.11	0.04	0.06		43.99	6.68	0.94	0.51
HC 33	82.10	87.54	85.82	19.54	20.43	4.85	4.50	1.02		11.54	1.51	0.62	0.57
HC 34	195.90	73.68	84.17	0.23	27.11	7.23	4.70	2.23		7.97	0.39	0.71	0.57

ID #	Avg Na	Sd Na	Avg Sr	SD Sr	Avg Pb	SD Pb	Avg CaCO3	SD CaCO3	95 Cr	Avg U	SD U	dry BD (g/cm^3)	Porosity
HC 1	124.97	76.94	433.37	28.70	44.01	7.79	29.01	18.64	11.00	7.18	4.28	0.33	0.76
HC 35	167.25	1.06	84.29	3.23	24.67	0.47	2.16	1.51		14.25	1.59	0.68	0.69
HC DE	167.43	111.42	35.13	30.43	21.03	32.12	10.97	18.32	11.90	46.50		0.17	0.73
HC 31	98.85	88.18	290.90	82.17	29.29	1.68	12.89	15.85	6.45	41.00		0.65	0.79
FS 1	142.90	66.61	66.21	5.95	43.89	24.20	8.17	13.89		7.63	3.04	0.17	0.81
FS 2	91.65	82.52	49.93	1.32	29.11	14.30	4.92	8.12				0.62	0.64
FS 3	135.90	51.05	61.77	5.32	50.29	6.67	2.26	3.82		10.93	0.39	0.17	0.80
FS 4	228.10	152.59	37.50	53.03	39.00	55.15	23.88	27.40				0.08	0.59
FS 5	130.15	73.33	182.35	53.25	7.50	10.61	19.53	14.02		20.19	3.14	0.38	0.88
FS 6	122.25	35.00	248.05	90.44	32.00	25.46	41.04	23.98				0.28	0.96
FS 7	197.65	113.63	29.00	41.01	2.00	2.83	2.12	0.67				0.19	0.62
FS 8	91.90	41.15	29.00	41.01	7.00	9.90	4.82	4.43				0.07	0.67
FS 9	105.10	60.67	130.75	9.55	37.27	1.80	29.16	23.81				0.30	0.72
FS 10	108.20	67.60	170.45	10.54	35.16	1.63	29.80	24.76				0.21	0.59
FS 11	113.60	115.12	154.60	48.93	24.63	9.37	36.82	25.70				0.24	0.80
FS 12	36.60	50.06	253.75	122.68	23.19	18.65	35.22	14.81				0.41	0.80
FS 13	47.25	57.63	289.85	35.14	13.46	6.42	49.61	37.61		1.81	0.31	0.41	0.77
FS 14	92.95	69.37	207.90	26.73	27.16	11.54	39.91	24.57				0.23	0.80
FS 15	50.45	19.16	322.90	18.24	3.50	4.95	43.47	33.76				0.75	0.53
FS 16	100.60	45.82	204.15	11.10	31.64	8.99	38.03	25.49				0.32	0.91
FS 17	77.15	42.21	171.65	16.05	17.75	13.08	34.26	19.00				0.25	0.89
FS 18	81.65	65.55	183.05	2.76	22.27	22.25	40.35	17.25				0.29	0.78
FS 19	66.80	38.47	179.35	13.65	27.19	1.68	27.24	22.29				0.31	0.77
FS 20	70.60	61.38	238.10	14.00	20.27	13.77	44.72	26.82		8.22	1.34	0.31	0.75
FS 21	191.80	17.25	222.05	62.30	27.57	3.63	30.68	26.32				0.26	0.78
FS 22	78.60	17.54	257.65	2.33	19.68	6.12	37.02	26.87				0.29	0.77
FS 23	63.85	44.05	77.14	26.68	18.86	10.10	14.62	5.65				0.27	0.87
FS24	95.60	31.68	111.35	2.33	3.50	4.95	8.63	3.91		24.80	3.15	0.23	0.71
FS25	93.65	51.83	124.00	175.36	18.50	26.16	46.41	17.54				0.56	0.61
FS26	178.70	58.97	140.65	17.47	20.89	4.41	12.99	7.77		7.10	0.77	0.60	0.60
FS 27	135.60		147.20		17.00					4.45	1.40	0.45	0.67
FF1	84.95	25.39	185.50	70.00	39.17	3.07	22.18	34.91		8.53	6.97	0.23	0.83

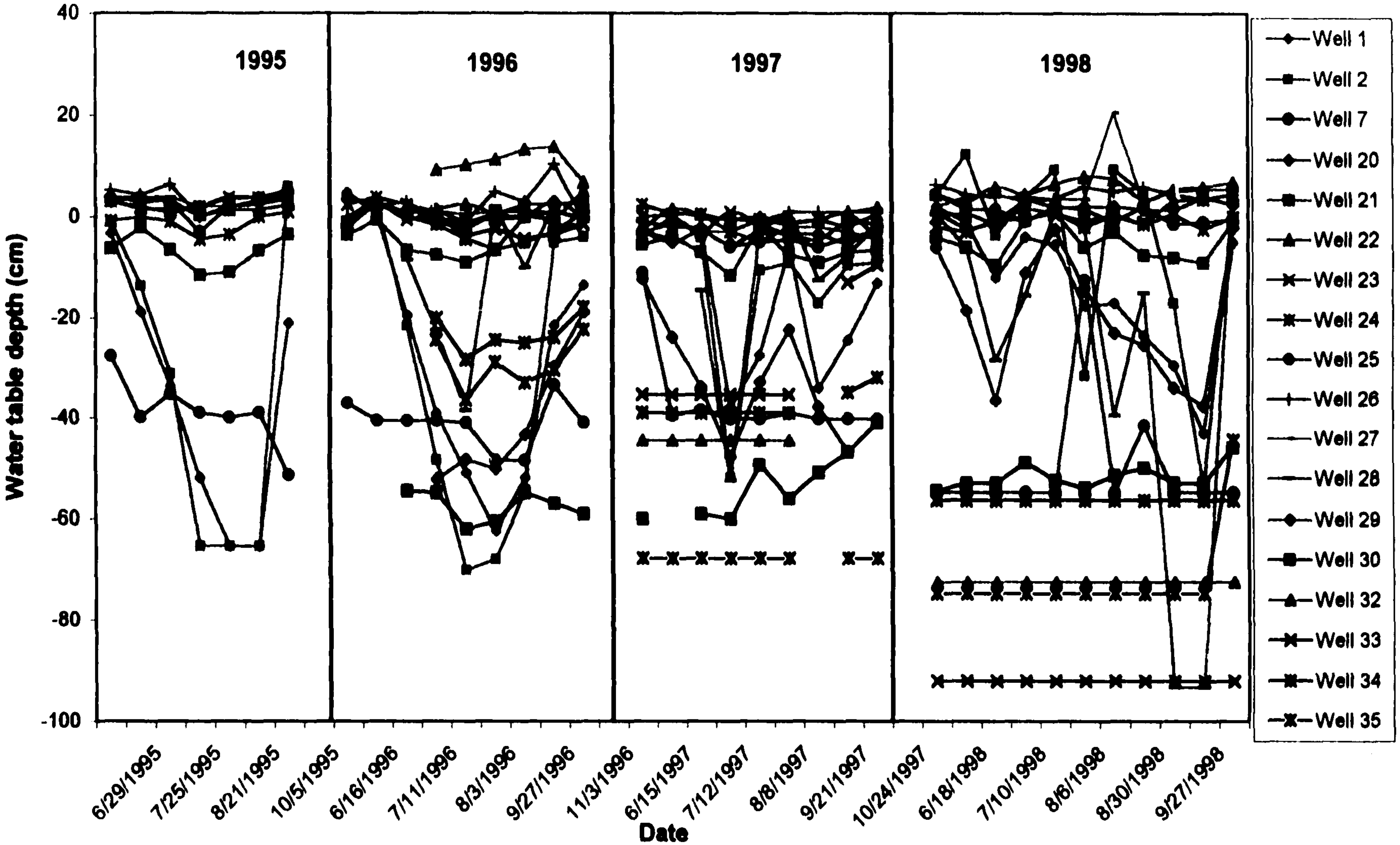
ID #	Avg Na	Sd Na	Avg Sr	SD Sr	Avg Pb	SD Pb	Avg CaCO3	SD CaCO3	95 Cr	Avg U	SD U	dry BD (g/cm^3)	Porosity
HC 1	124.97	76.94	433.37	28.70	44.01	7.79	29.01	18.64	11.00	7.18	4.28	0.33	0.76
FF2	246.45	79.83	147.10	117.52	27.41	1.99	2.45	1.10		7.58	1.41	0.34	0.70
FF3	313.20	83.72	133.50	188.80	8.00	11.31	8.96	5.13				0.50	0.95
FF4	515.80	505.16	234.50	94.05	10.15	1.62	1.79	0.27		21.66	11.60	0.49	0.72
FF5	978.15	1263.10	260.10	229.24	9.50	13.44	8.58	6.20		5.51	2.67	0.50	0.47
FF6	633.30	187.67	378.30	98.57	17.39	0.55	8.90	13.90				0.45	0.70
FF7	170.40	111.16	175.10	12.59	12.60	0.57	0.43	0.38		10.35	3.65	0.36	0.85
FF8	386.80	214.68	145.65	16.05	38.98	19.76	8.69	9.62		10.89	2.08	0.26	0.97
FF9	479.35	236.67	131.80	12.45	28.90	22.77	8.23	12.59		7.67	3.74	0.52	0.89
FF10	151.45	43.20	119.80	36.49	10.90	2.69	1.31	1.21		24.54	16.69	0.74	0.54
FF11	199.00	115.97	117.55	10.54	11.76	2.49	1.98	1.17		8.93	0.71	0.40	0.78
FF12	177.10	33.80	90.33	15.10	15.49	4.97	2.19	2.42		5.22	0.84	0.89	0.59
FF13	245.65	196.08	67.37	46.15	8.00	11.31	4.31	6.09		4.11	2.81	0.72	0.91
FF14	259.25	27.93	191.50	115.26	6.91	2.96	1.59	1.22		6.68	3.68	0.30	0.95
FF15	228.65	115.05	91.80	46.39	8.71	1.83	0.71	0.98		5.82	0.05	0.20	1.08
FF16	179.20		138.80		37.97					3.88		0.46	0.67
FF17	305.40	159.24	112.10	1.56	29.70	34.92	12.57	19.37		3.60	0.39	0.26	0.77
FF18	188.10	0.14	137.65	16.05	37.75	1.77	1.17	0.53		8.41	6.51	0.21	1.00
FF20	225.80	78.06	126.90	8.63	40.07	8.58	3.67	4.31		3.79	3.10	0.52	0.72
FF 21	265.05	25.39	56.00	79.20	13.50	19.09	6.36	11.02				0.17	0.76
FF 22	289.90	31.25	231.40	132.09	23.60	12.16	6.31	5.89				0.36	0.77
FF 23	113.30		112.10		44.41							0.22	0.94

APPENDIX 5

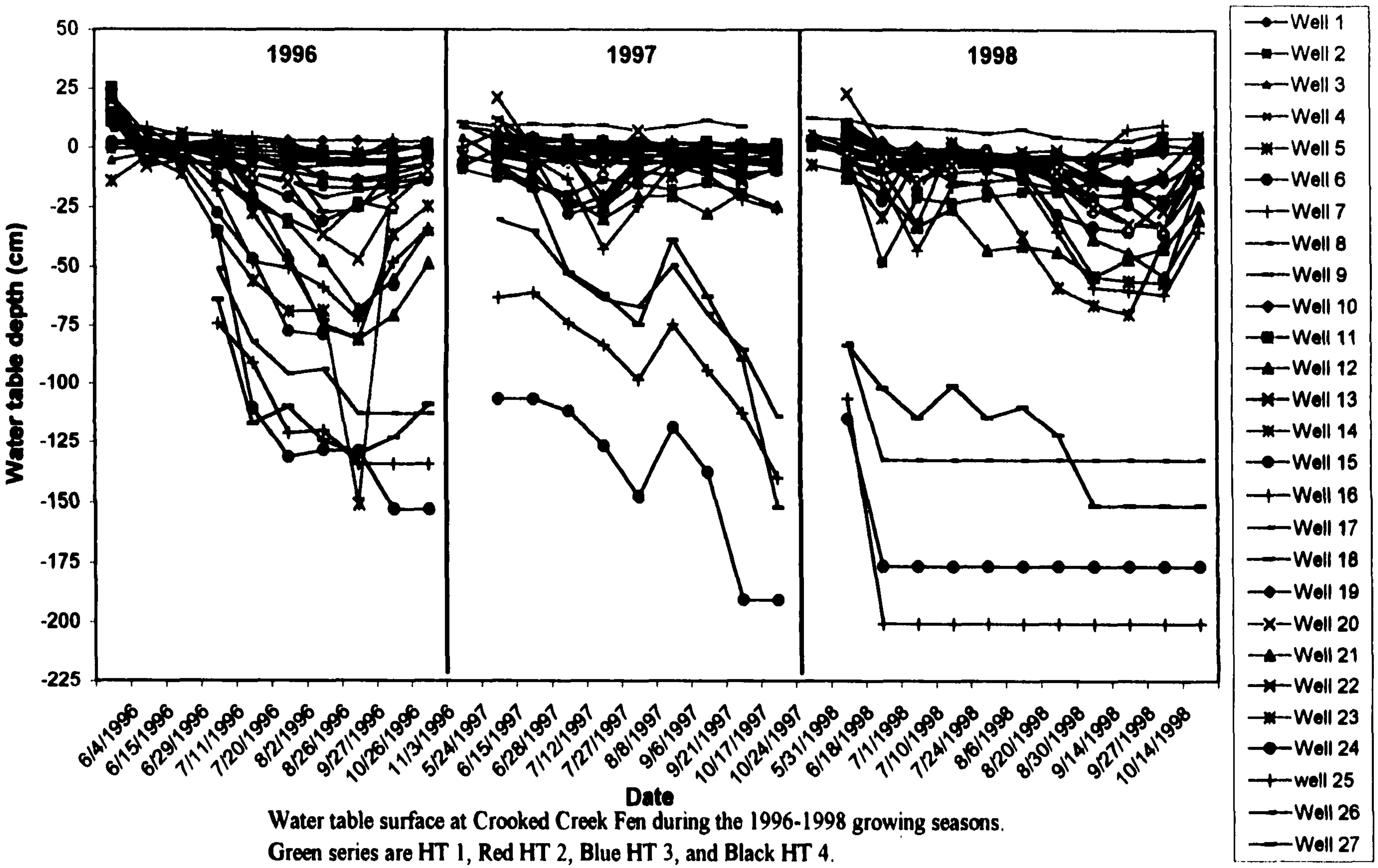
This appendix contains hydrographs for the wells and piezometers installed at the three study sites. The first five pages show well hydrographs and the next four give piezometer hydrographs. Hydrographs have been subjectively grouped into one of four "hydrotypes" (HT). Hydrotype 1 includes areas with relatively stable, high water tables. Hydrotype 2 includes areas with relatively high water tables, that experience a mid-season water table depression followed by a fall recovery. Hydrotype three includes sites which have a relatively high water table which is drawn down during the growing season and restored during the winter. Lastly, hydrotype 4 includes sites which possess fairly erratic water table behavior. These sites are heavily influenced by irregular precipitation events which causes the water table shifts. These hydrotypes will be further developed in an upcoming paper.



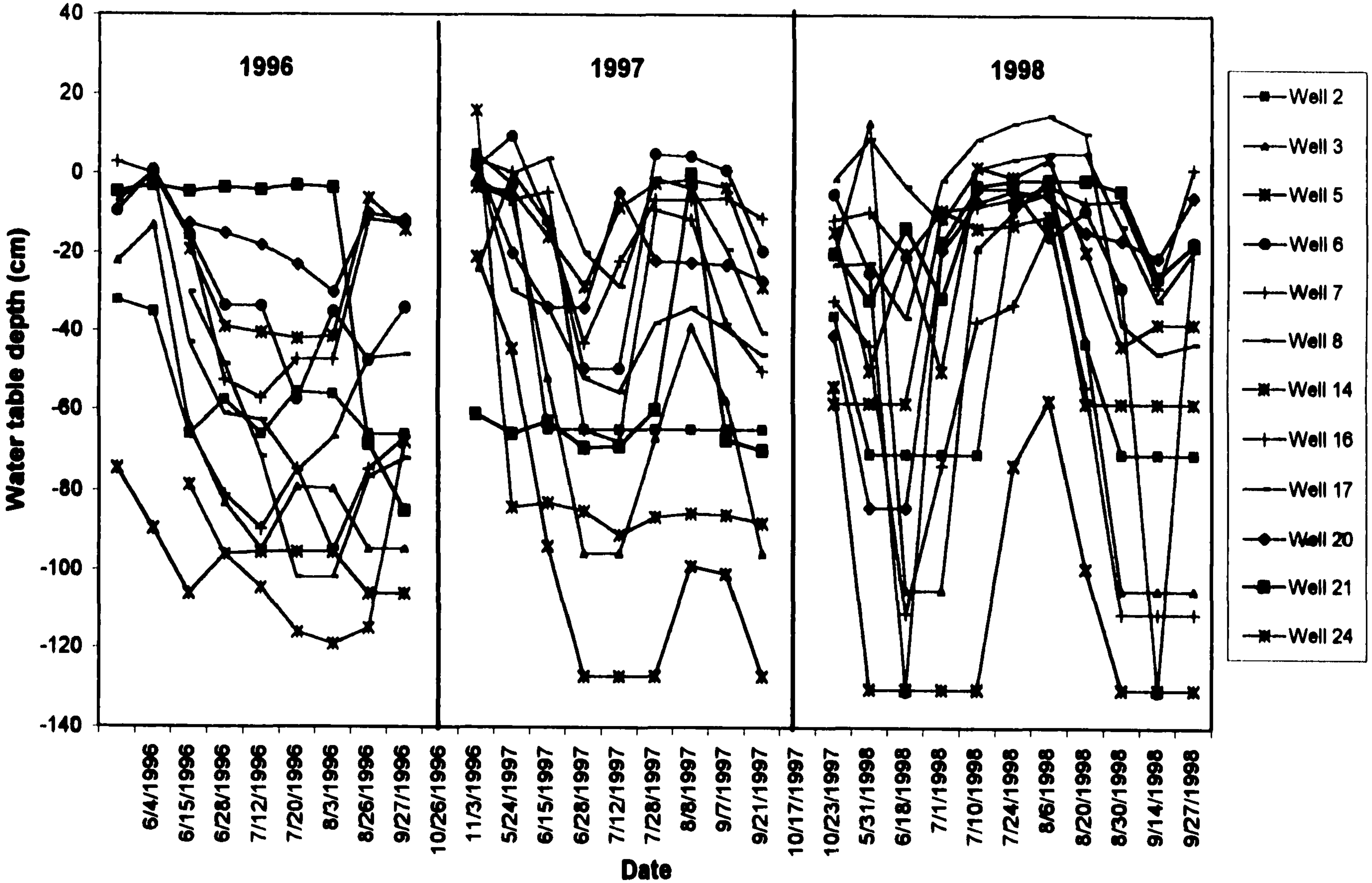
Water table surface at High Creek Fen during the 1995-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



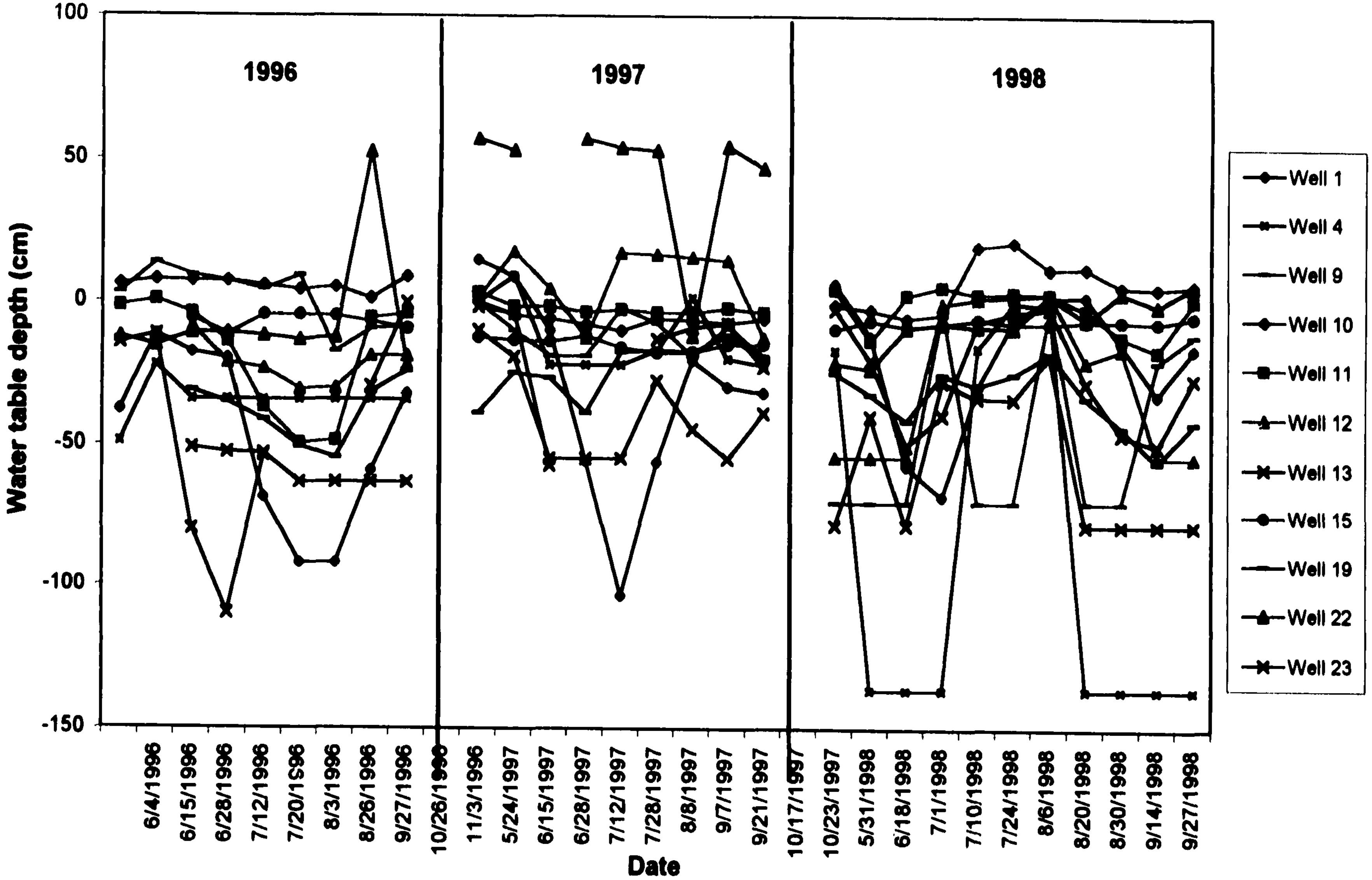
Water table surface at High Creek Fen during the 1995-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT3, and Black HT 4.



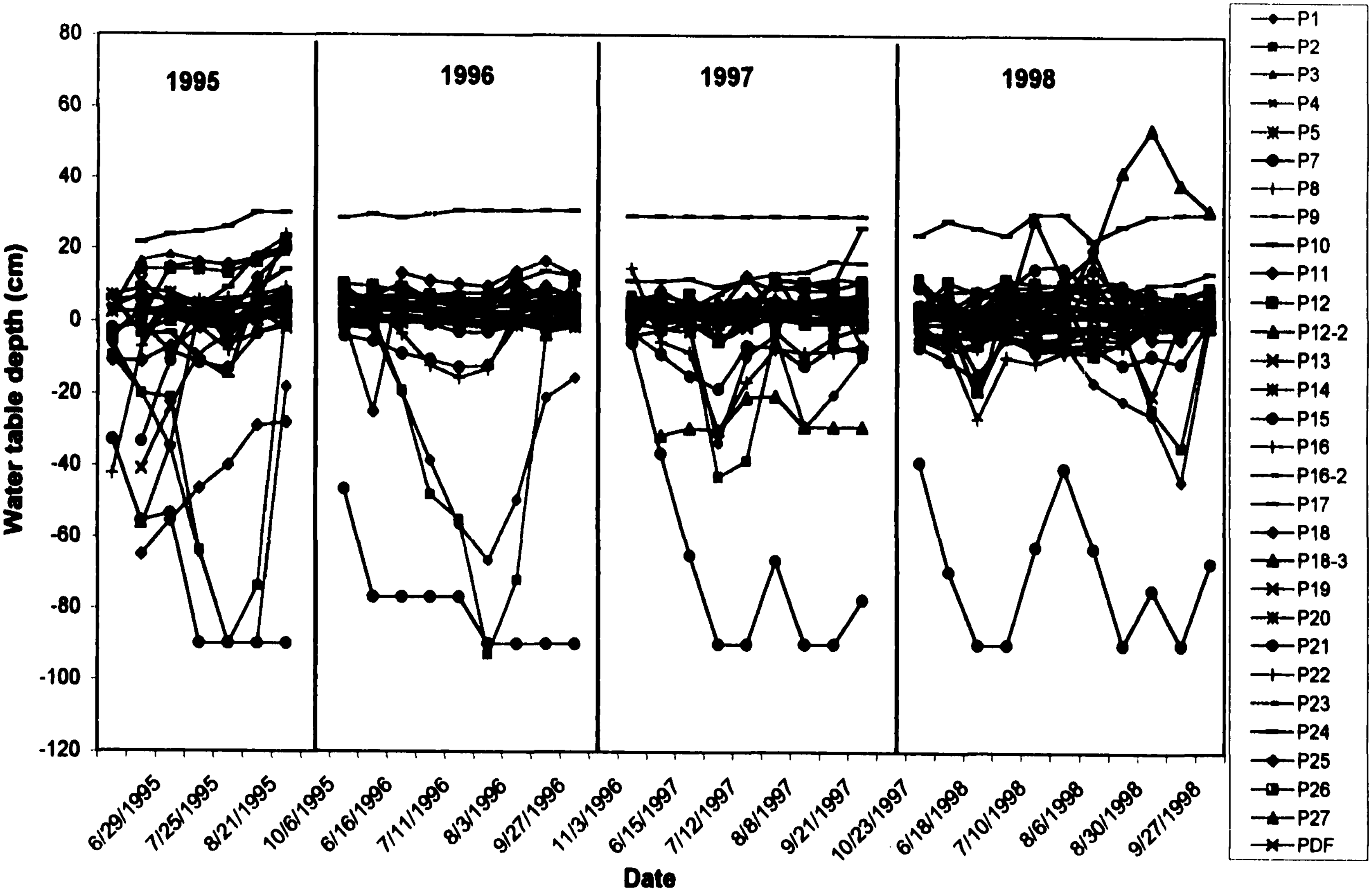
Water table surface at Crooked Creek Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



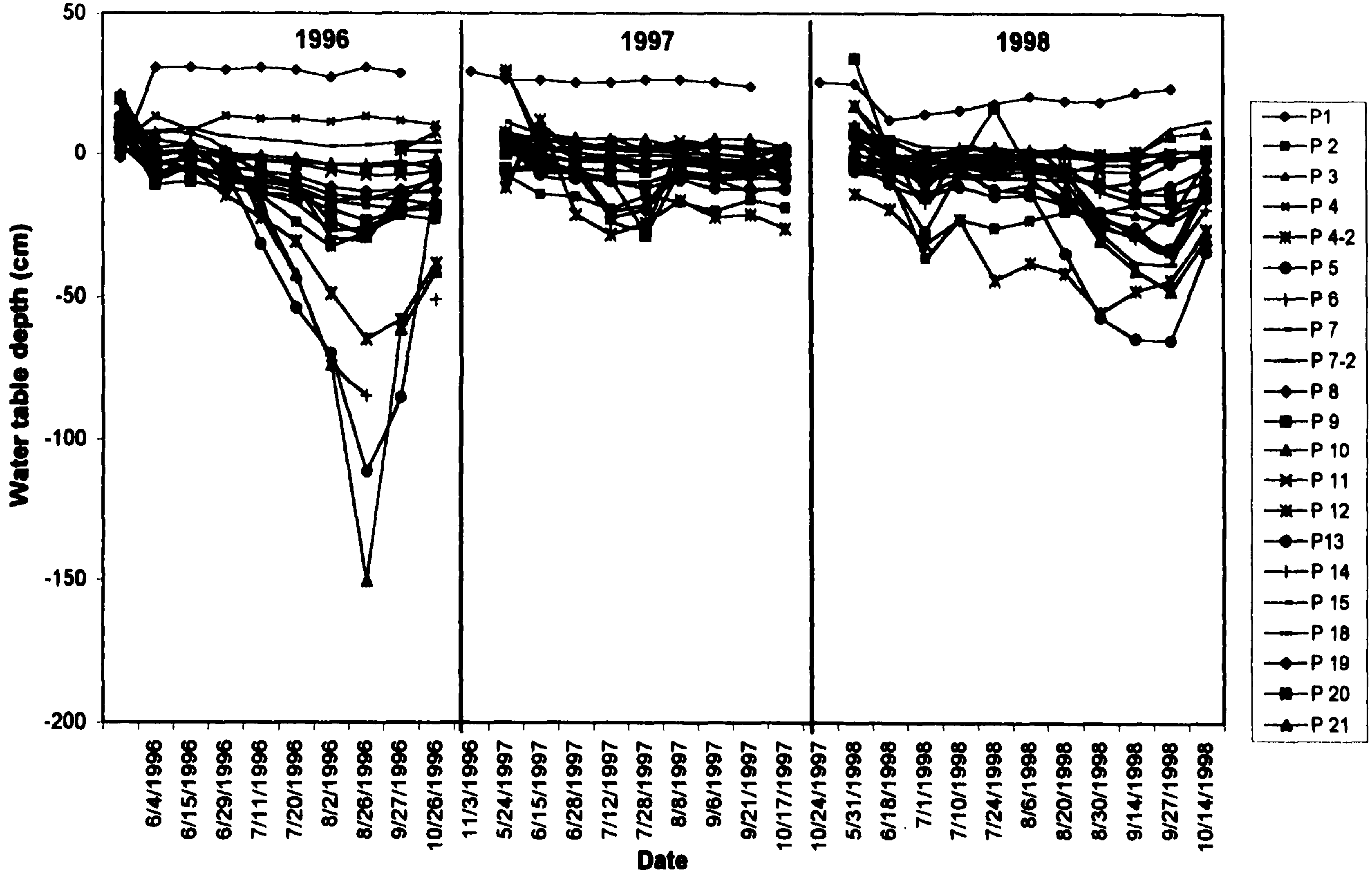
Water table surface at Fremont's Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



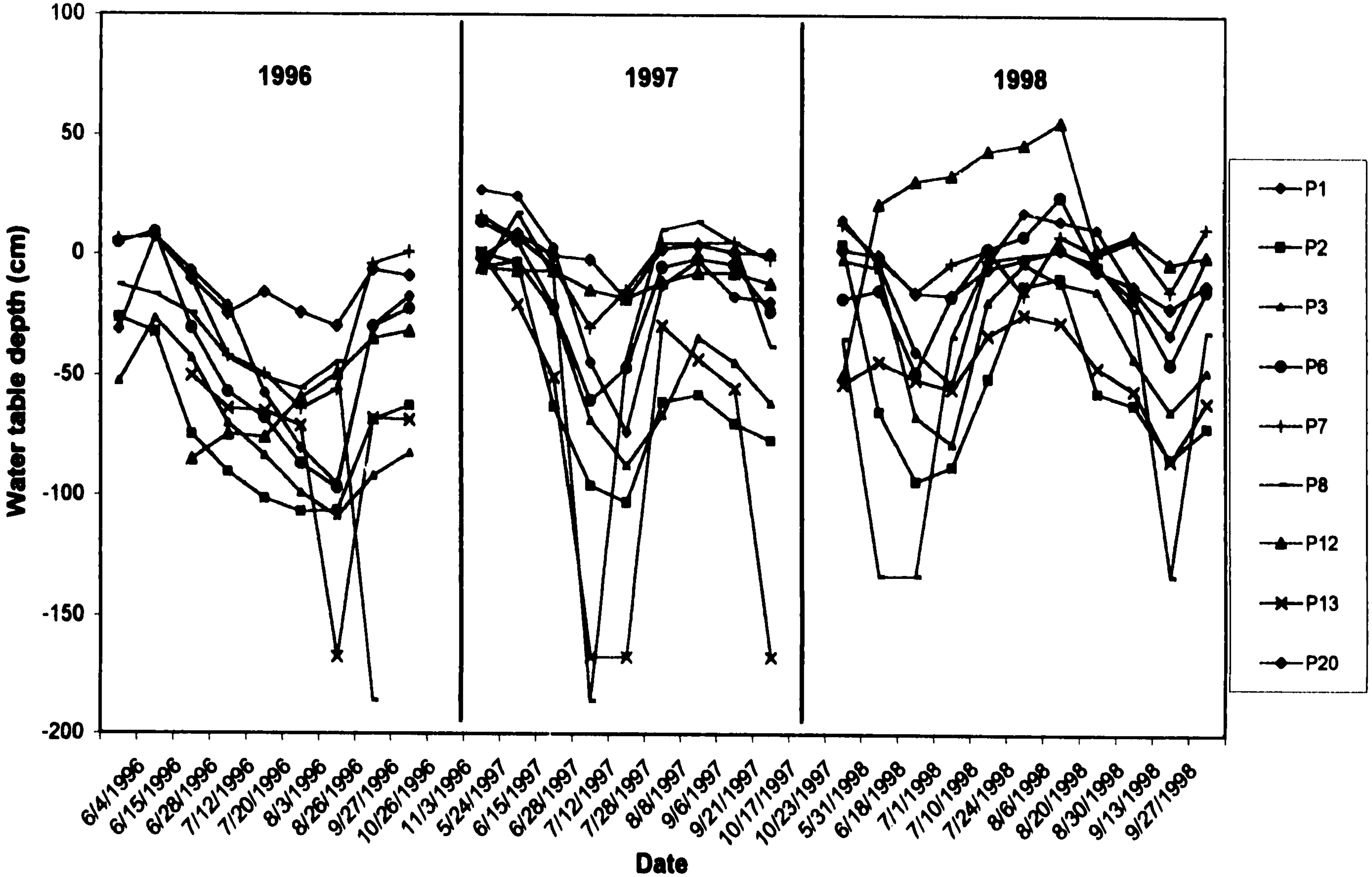
Water table surface at Fremont's Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



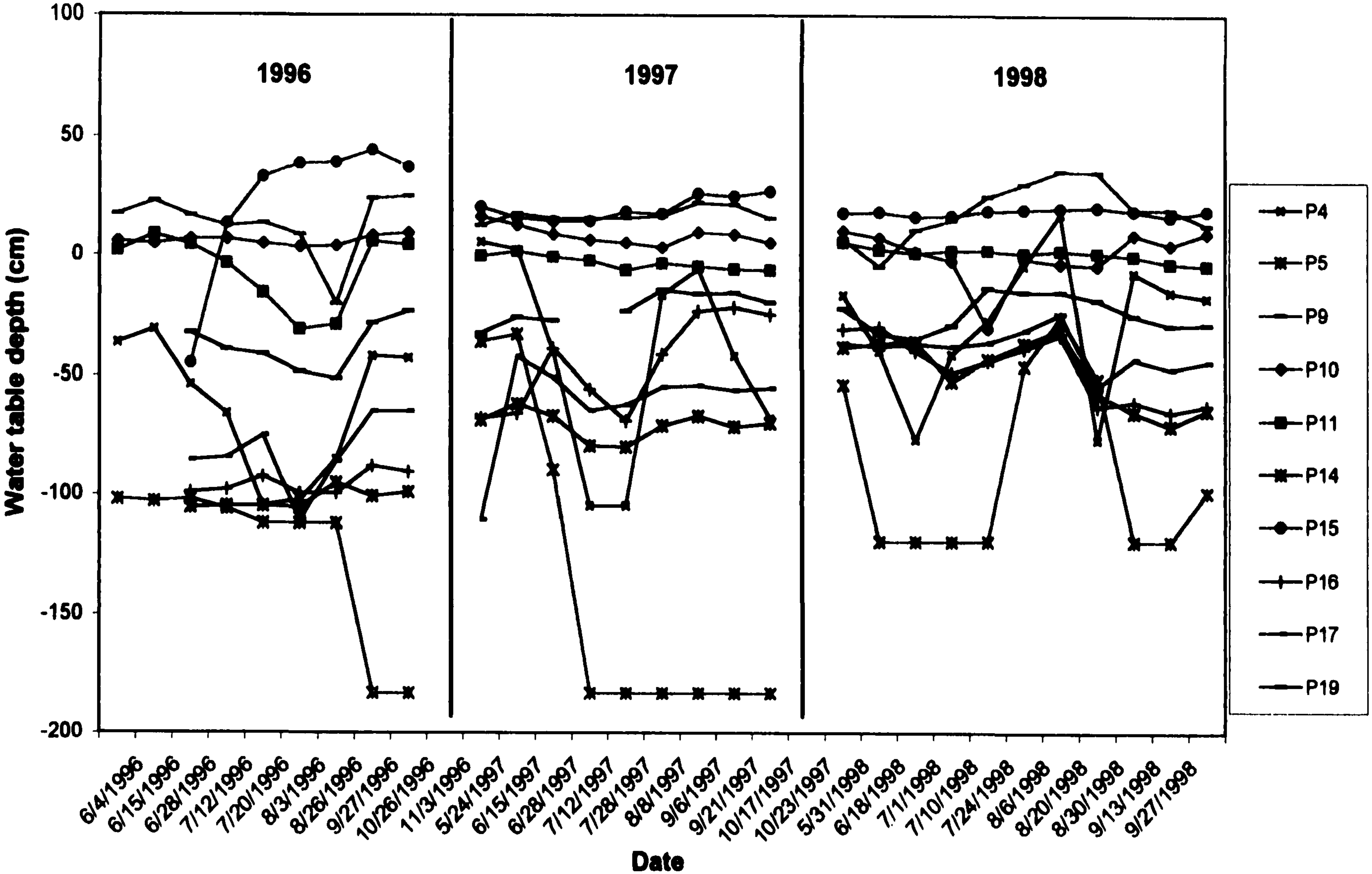
Piezometric surface at High Creek Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



Piezometric surface at Crooked Creek Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT 3, and Black HT 4.



Piezometric surface at Fremont's Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT3, and Black HT 4.



Piezometric surface at Fremont's Fen during the 1996-1998 growing seasons.
Green series are HT 1, Red HT 2, Blue HT3, and Black HT 4.