

THESIS

FENS OF YELLOWSTONE NATIONAL PARK, USA: REGIONAL AND LOCAL
CONTROLS OVER PLANT SPECIES DISTRIBUTION

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WE HERBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JOANNA M. LEMLY ENTITLED FENS OF YELLOWSTONE NATIONAL PARK, USA: REGIONAL AND LOCAL CONTROLS OVER PLANT SPECIES DISTRIBUTION BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

FENS OF YELLOWSTONE NATIONAL PARK, USA: REGIONAL AND LOCAL CONTROLS OVER PLANT SPECIES DISTRIBUTION

Regional and local scale gradients controlling plant species distribution in mountain fens were studied in Yellowstone National Park, Wyoming, USA. Data on vascular and nonvascular plant cover, groundwater and soil chemistry, landforms, microtopography, and regional gradients of elevation, precipitation, and bedrock geology were collected and analyzed for 476 relevés from 166 fens. The pH of groundwater supporting fens ranged from 2.89 to 7.98. Six major bedrock types influence the chemical content of groundwater: three volcanic types, a glacial till complex containing sedimentary deposits, and two rock types altered by geothermal activity. Twenty-eight plant communities were identified through cluster analysis and table methods. Vegetation data were related to environmental gradients using DCA, CCA, and CCA with variance partitioning. The main environmental gradients affecting vascular plant species were site landform and stand topography, which separated fens formed in basins from sloping fens. Bryophytes were more strongly correlated with the acidity/alkalinity gradient of groundwater pH. For all species, the regional variables elevation, annual precipitation, and groundwater chemistry accounted for 40.7% of the total variation explained, while local variables site landform, stand topography and microtopography, and soil characteristics accounted for 43.9%.

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1. INTRODUCTION

Peatlands occur throughout the world wherever the production of organic matter exceeds decomposition due to waterlogging (Moore & Bellamy 1974). An estimated 80% of the world's peatlands occur within boreal regions, particularly Alaska, Canada, Russia, and northern Europe (Wieder & Vitt 2006). But peatlands also occur in temperate and tropical regions at low elevations and in mountain ranges, including the Alps, Andes, and Rocky Mountains.

Peatland vegetation is influenced by several complex ecological gradients (Bridgham *et al.* 1996; Wheeler & Proctor 2000; Rydin & Jeglum 2006). The gradient of acidity/alkalinity and mineral content of peatland water is strongly correlated with species distribution (Sjörs 1950a; Malmer 1986; Vitt & Chee 1990) and is largely controlled by the origin of source water (Fig 1). The primary division among peatlands separates ombrotrophic (rainwater-fed) bogs and minerotrophic (groundwater-fed) fens. Water chemistry and its effects on plant species further differentiates fens along a gradient from poor to extreme rich fens. In boreal regions, the poor–rich gradient is related to the balance of precipitation vs. groundwater. Fed by ample summer rain, boreal bogs and poor fens receive little or no input from regional groundwater, which allows *Sphagnum* moss to lower water pH through cation exchange (Clymo 1963; Andrus 1986). In contrast, rich fens are in contact with local or regional groundwater flow systems and maintain higher pH and water mineral content. Variation within the poor–rich gradient can occur within a single peatland complex from bog center to fen edge (Glaser *et al.* 1990) or across a precipitation gradient from poor fens in high precipitation areas to rich fens in drier regions (Vitt & Chee 1990). In addition to the balance of precipitation vs.

groundwater, bedrock geology has been correlated with the distribution of peatlands along the poor–rich gradient. Bogs and poor fens are more frequent on granite and gneiss while rich fens are more common on calcareous limestone and shale (Halsey *et al.* 1997; Bedford & Godwin 2003).

Gradients related to water table depth and aeration also control peatland vegetation. These include the microtopography gradient, the peatland margin–peatland expanse gradient, and topographic position. The microtopography gradient separates hummocks from hollows and is related to water table depth. Many species, particularly bryophytes, have a narrow tolerance for hydrologic conditions and occur within a specific range of the microtopography gradient (Andrus *et al.* 1983; Glaser *et al.* 1990; Bragazza & Gerdol 1996). The peatland margin–peatland expanse gradient is a complex set of factors related to water table depth and water flow from the surrounding landscape. In general, peatland margin communities have deeper water tables, increased flow rate, and higher mineral content from increased groundwater influence (Sjörs 1950a; Malmer 1986; Økland 1990a), which can lead to the development of woody vegetation. In turn, woody vegetation provides cover for shade tolerant species. Topography is also related to water table depth and the direction of water flow. Fens that develop in depressions or along lakes typically have slow moving, stagnant, or standing water. Sloping fens that occur at springs or hillside seeps can only form where high discharge rates maintain saturated soils throughout the growing season (Rydin & Jeglum 2006).

On a regional scale, gradients related to climate, elevation, and phytogeography have been identified as influencing peatland types and their vegetation across large regions. Mean annual precipitation and mean annual temperature have been correlated to species

richness, floristic assemblages, and the distribution of wetlands across North America (Glaser 1992; Halsey *et al.* 1997; Gignac *et al.* 2000). Elevation was highly significant in a survey of peatlands in the mountains of Australia (Clarke & Martin 1999). In northern Europe, regional variation in peatland vegetation is related to climatic patterns, distance from the ocean, and individual species distributions (Sjörs 1950b; Malmer 1986; Økland 1990b).

In mountainous areas, peatlands form in high elevation valleys, basins, and on sloping hillsides. Most mountain peatlands receive at least some groundwater input, although *Sphagnum*-dominated peatlands floristically similar to boreal bogs occur in the Italian Alps (Gerdol *et al.* 1994; Bragazza & Gerdol 1999) and on the Kosciuszko massif in Australia (Clarke & Martin 1999). The environment of mountain fens differs from that of boreal regions, where most peatland research has occurred. In boreal regions, steep topography and heavy snowfall are uncommon, the frost-free season is short and cool, and most precipitation falls during summer months (Wieder & Vitt 2006). In contrast, mountain landscapes are highly heterogeneous, with pronounced changes in elevation and bedrock across relatively short distances, and summers can be warm and dry. Mountain climates are typically dominated by heavy winter snowfall and spring snowmelt, which replenish groundwater aquifers, lead to peak spring runoff in rivers and streams, and flush wetland systems (Cooper 1990). Given the differences between boreal peatlands and mountain fens, it remains unknown to what extent the same local and regional gradients influence species distribution.

In the Rocky Mountains of the western United States, fens occupy a small fraction of the landscape, but contribute substantially to regional biodiversity (Chadde *et al.* 1998;

Bedford & Godwin 2003). Dry summers prevent the formation of ombrotrophic bogs in the Rocky Mountains. Instead, fens have formed in topographically confined areas connected to surface and/or groundwater, but with wide variation in the chemical content of groundwater driven primarily by bedrock geology. Fens located in watersheds containing sedimentary bedrock are rich or extreme rich fens (Lesica 1986; Cooper 1996; Johnson & Steingraeber 2003). Granite watersheds contain fens with circumneutral pH and extremely low ion levels (Cooper 1990; Cooper & Andrus 1994). And in specific geochemical settings, such as weathering pyrite-rich rocks, fen waters have extreme acidity and high ion concentrations (Cooper *et al.* 2002). In the Rocky Mountains, the water chemistry gradient is a regional gradient controlled by watersheds of different lithologies and not the balance of precipitation vs. groundwater.

The present study was conducted in Yellowstone National Park in the central Rocky Mountains of Wyoming, Montana, and Idaho, a large heterogeneous landscape that allowed the analysis of fens along multiple gradients at different scales. The goal was to examine the role of regional and local scale environmental gradients in controlling plant species distribution and abundance in mountain fens. Vegetation and environmental data were used to address the follow questions: 1) how are ***regional scale*** gradients of elevation, climate, and bedrock geology related to vegetation patterns in mountain fens?; 2) how are ***local scale*** gradients of site landform, stand topography and microtopography, and soil characteristics related to vegetation patterns?; and 3) do environmental gradients affect vascular plants and bryophytes differently?

2. SITE DESCRIPTION

Yellowstone National Park (YNP) covers over 8900 km² in the northwest corner of Wyoming and extending into portions of Montana and Idaho (Fig. 2). The park lies between 44–45° north latitude and 110–111° west longitude at an average elevation of ~2500 m. The heart of YNP is a volcanic plateau circled on three sides by high peaks, the Gallatin Mountains in the northwest and the Absaroka Range in the east. The highest elevation in the park (3521 m) is the summit of Eagle Peak in the southern Absaroka Range and the lowest elevation (1,637 m) is the park's north entrance where the Gardner River flows between the Gallatin and Absaroka Ranges. YNP's southwest corner is the only area not surrounded by mountains. Instead, the Snake River Plain drops more than 500 m below the volcanic plateau and extends beyond the park border. The portion of this lowland within the park is called Bechler Meadows, named for the open landscape within the drainage of the Bechler River, a Snake River tributary. The Continental Divide runs through YNP from the western border towards the southeast, though it does not form a dramatic topographic rise. Lake Yellowstone is the largest lake in the park, with an area of 36,000 ha. The park also contains several major rivers, including the Snake, Yellowstone, Gallatin, and Madison Rivers. Together, lakes and rivers cover approximately 5% of the park (Rodman *et al.* 1996).

2.1 CLIMATE

Yellowstone's climate is representative of the intercontinental Rocky Mountains and is characterized by long, cold winters and short, warm summers. Winters bring heavy snowfall and cold temperatures. Except at low elevations, the frost free season is

typically less than five months. Summer daytime highs are 20–30°C and nighttime lows are commonly below 5°C. There is considerable variability across the park for both temperature and precipitation. Temperature is related to elevation; the highest maximum temperatures occur at the lowest elevations and temperatures drop roughly according to the adiabatic lapse rate of -3°C per 300 m of elevation gain (Dirks & Martner 1982). Mean annual precipitation (Fig. 3) is also affected by elevation. Low elevations in the north, such as the valleys of the Gardiner, Lamar, and Yellowstone Rivers, receive as little as 300–350 mm of precipitation/year. The major mountain ranges average 1250–1500 mm/year. Along with elevation, the exposed southwest corner has a significant impact on precipitation patterns. As the only area not immediately blocked by mountains, this corner experiences heavy winter storms and creates a southwest to northeast precipitation gradient across the park. Low elevations in the southwest corner receive 1000–1250 mm of precipitation/year. The highest annual precipitation exceeds 1750 mm on the Pitchstone Plateau, which rises above Bechler Meadows. Across the park's interior, mean annual precipitation ranges from 500–1000 mm depending on elevation and location within the southwest to northeast gradient (YNP Spatial Analysis Center, unpublished).

Timing of precipitation throughout the year also varies across the park. Despain (1990) identifies two main climatic types: a valley type and a mountain type. The valley climatic type is characterized by peak precipitation in spring and early summer while the mountain climatic type receives peak precipitation in winter, generally in the form of snow. The broad northern river valleys and central volcanic plateau fall within the valley climatic type. The mountain climatic type occurs around the perimeter of the park in the

Gallatin and Absaroka Ranges, along the Continental Divide, and in the exposed southwestern corner. For the northern valleys, the combination of lower elevations, warmer temperatures, and peak precipitation in the spring means half or less than half of total annual precipitation falls as snow. In the park's interior, snowfall can account for half to more than half of the annual precipitation. At high elevations and along the Continental Divide, where the frost free season is short and most precipitation falls in winter, nearly all annual precipitation is snow. Deep snow packs accumulate in the mountains and last well into spring. As the snow packs melt, they recharge regional groundwater aquifers.

2.2 GEOLOGY

Present day YNP is atop the Yellowstone hotspot, one of the largest plumes of molten magma on earth (Fig. 4). The hotspot has been active for over 16 million years, but the center of activity has shifted as the North American plate slowly moves southwest over the plume. Activity has been centered in its current location for ~2 million years, during which time three major eruptions have shaped the landscape. The last eruption, 630,000 years before present (YBP), created the giant caldera 70 by 45 km that is the heart of YNP (Smith & Siegel 2000). The hotspot continues to influence the landscape today, giving rise to an unusually high concentration of thermal features including geysers, hot springs, mudpots, and fumaroles, and inducing both acidic and basic reactions in the groundwater and soils (Rodman *et al.* 1996). Each cycle of volcanism associated with the Yellowstone hotspot produced multiple, successive series of pre- and post-caldera rhyolitic flows and caldera-forming explosions of rhyolitic tuff, making rhyolite the dominant bedrock type throughout the park. In association with rhyolitic volcanism,

minor basaltic flows erupted intermittently around the margins of the calderas. Localized basaltic bedrock can be found in several places in the park, including Bechler Meadows (Christiansen 2001).

Prior to volcanism of the Yellowstone hotspot, older eruptions during the Eocene (50 million YBP) created the Absaroka Volcanic Supergroup, which forms the bulk of the Absaroka Mountains and northern portions of the Gallatin Range. In contrast to the Yellowstone hotspot volcanoes, bedrock of the Absaroka Supergroup is primarily andesite, not rhyolite or basalt (Smedes & Prostka 1972). In addition to volcanic bedrock, YNP contains areas of both metamorphic and sedimentary rocks. Metamorphic basement rocks formed 3.8 to 1.5 billion YBP and are the oldest rocks in the park. Sedimentary rocks—limestones, sandstones, shales, and dolomites—formed 540 to 65 million YBP when the interior of North America was a large inland sea. Both metamorphic and sedimentary rocks were uplifted during the Laramide orogeny (65 million YBP) along major fault lines that stretch north to south. Today, these rocks are exposed in scattered locations throughout the park, concentrated in the Gallatin Range, along the northern border of the park, and in the south. At one time, a chain of uplifted mountains may have connected the Gallatin Range with Mount Sheridan in the south of the park. Collapse of the most recent Yellowstone caldera likely disrupted this chain (Ruppel 1972).

Yellowstone experienced major glaciation at least three different times in the recent past that left carved valleys, glacial till, and the remnants of glacial lakes. During the last glacial maxima (25,000 YBP), Yellowstone was covered by an ice sheet up to 1500 m thick (Good & Pierce 1996). Quaternary deposits from glacial activity, as well as more recent fluvial and alluvial activity, cover valley floors. In many locations, glacial till in

YNP was not transported long distances. The soils formed by till, therefore, are derived from the underlying bedrock. One major exception was a large glacier that flowed from the Beartooth Plateau and filled the northern valleys of the Lamar and Yellowstone Rivers. Glacial till in these valleys is a mixture of granite, andesite, rhyolite, and sedimentary rocks (Despain 1990).

2.3 VEGETATION

Over three quarters of YNP is mixed conifer forest with *Abies lasiocarpa*, *Picea engelmannii*, *Picea glauca*, *Pinus albicaulis*, *Pinus contorta* var. *latifolia*, and *Pseudotsuga menziesii* being most common species. Canopy dominants are largely determined by local conditions such as climate, soil properties, and disturbance history. Several large sagebrush valleys occupy the park's interior. Wetlands likely comprise less than 5% of the landscape and the percentage of wetlands that are fens is unknown. Wetlands with both organic and mineral soil occur in all physiognomic types, i.e. forested wetlands, shrub carrs, and open herbaceous meadows. Wetlands include common Rocky Mountain species and are dominated by species in the genera *Salix*, *Carex*, *Eleocharis*, and *Calamagrostis* (Despain 1990; Rodman *et al.* 1996).

3. MATERIALS AND METHODS

3.1 SITE SELECTION

Using stereo pairs of full color aerial photographs, approximately 500 sites were identified throughout YNP that appeared to have the physical characteristics of fens.

Among those identified, sites were selected for sampling based on confidence in interpretation and across the regional gradients of elevation, climate, and bedrock geology. Data collection took place between June and August of 2004 and 2005. During field visits, sites were determined to be fens based on the presence of saturated soils and an organic soil horizon ≥ 40 cm thick. In total, 166 fens were analyzed (see Fig. 5 for locations).

3.2 VEGETATION DATA COLLECTION

Within each fen, homogeneous stands of vegetation were identified and analyzed using the relevé method (Mueller-Dombois & Ellenberg 1974). Relevé size was determined by the dominant structure of vegetation. A total of 476 relevés were analyzed in the study fens, between one and twelve relevés per fen, depending on size and complexity of the site. Canopy cover was visually estimated for each vascular plant and bryophyte species. Nomenclature for vascular plants follows Dorn (2001). Nomenclature for bryophytes follows Weber & Wittmann (2005) for non-*Sphagnum* species and McQueen & Andrus (2007) for *Sphagnum* species. Voucher collections of vascular plants and bryophytes are housed at the Yellowstone Herbarium (YELL). Duplicate collections of non-*Sphagnum* bryophytes are housed at the University of Colorado, Boulder (COLO), and *Sphagnum* species are housed at Binghamton University in New York (BING).

3.3 ENVIRONMENTAL DATA COLLECTION

Site level variables were collected to characterize each fen. The pH and temperature of groundwater were measured using an Orion Model 250A portable pH meter with combination electrode (Thermo Fisher Scientific, Massachusetts, USA). All pH

measurements were taken from a 40 cm pit after letting it fill for 15 minutes. Values for pH are more reliable if sampled from subsurface rather than surface water, which has considerable diurnal variation (Tahvanainen & Tuomaala 2003). One water sample was collected from each fen in two 20 ml vials, sealed immediately, and frozen until analyzed at the Soil, Water, Plant Testing Lab at Colorado State University. In the lab, electrical conductivity (EC) was determined using an Accumet two-cell conductivity probe (Thermo Fisher Scientific, Massachusetts, USA) and corrected for H⁺ ions. Concentrations of Ca²⁺, Mg²⁺, Na⁺, and K⁺ were determined by inductively coupled plasma emission spectrography (US EPA 1983); HCO₃⁻ by titration; and Cl⁻ and SO₄²⁻ by ion chromatography (Pfaff *et al.* 1989).

Sites were categorized by landform into basin fens, gently sloping fens, steeply sloping fens, and spring mounds. Basin (topogenous or limnogenous) fens originate as topographic depressions or ponds and gradually fill with organic matter (Rydin & Jeglum 2006). Basin fen vegetation may either form a floating mat that extends over open water or emergent vegetation in shallow standing water. Sloping (soligenous) fens form in several geomorphic settings. Gently sloping fens (slopes < 10°) occur at a break in slope, on the edge of valleys, or at the base of alluvial fans where groundwater discharges to the ground surface. Steeply sloping fens (up to 25° slope) can form below hillside springs at bedrock discontinuities (Patterson & Cooper 2007). Spring mound fens form around localized points of upwelling groundwater, can be several m in diameter, up to 2 m higher than the surrounding landscape, and can occur in meadows with mineral soils. For gradient analysis, landforms were converted to a three point scalar: 1 = basin fens; 2 = gently sloping fens; and 3 = steeply sloping fens and spring mounds. Spring mound fens

were grouped with steeply sloping fens because they both experience high discharge rates.

Several additional variables were collected at the stand level. Stand slope was measured with a compass and converted to an index of stand topography: 0 = concave topography; 1 = flat topography (slope = 0°); 2 = gently sloping topography (slope > 0° and < 10°); and 3 = steeply sloping topography (slope ≥ 10°). Concave topography was determined by the presence of deep standing water and aquatic or semi-aquatic plant species. To capture microtopography, stands were noted as hummocks if they were raised above the dominant vegetation matrix. Soil samples were collected at 198 of the 476 stands—at least one sample from each fen—from between 30–40 cm in the soil profile, placed in paper bags, and air dried. In the laboratory, samples were oven dried at 60°C for three days, ground with a ball grinder, and analyzed for carbon and nitrogen using a Truspec CN Analyzer (LECO Corp., Michigan, USA). Soil C:N ratios were calculated from the results. Soil chemistry values from neighboring stands were applied to stands not sampled. Peat thickness was estimated at each stand by inserting a 240-cm steel probe into the soil until the tip reached the first non-organic soil layer, indicated by a change in soil texture.

Regional variables were determined for each site in ArcGIS (ESRI 2005) from UTM coordinates obtained at each site and GIS layers provided by YNP staff. Elevation was determined on USGS 1:24,000-scale topographic maps and rounded to the nearest 10 m. Mean annual precipitation and mean annual snowfall were determined from isohyetal maps of YNP and rounded to the nearest 10 mm for precipitation and 100 mm for snowfall. Dominant watershed bedrock geology was determined from a digital geologic

map based on USGS (1972) and Christiansen (2001). See Table 1 for a list of environmental variables used in the analysis.

3.4 STATISTICAL ANALYSIS

Prior to statistical analysis, species recorded in < 5 relevés were removed from the dataset to reduce noise produced by rare plants. Cover values were converted to a modified Braun-Blanquet cover class system (Table 2) and analyses were run using the midpoint of the cover classes. Water chemistry variables were tested for normality (PROC UNIVARIATE: SAS Institute 2002) and all but pH were lognormally distributed and log transformed. No other environmental variables were transformed.

To characterize the influence of bedrock and parent material on groundwater chemistry, six major categories (hereafter referred to as bedrock types) were identified within fen watersheds: 1) rhyolite and rhyolitic tuff; 2) basalt; 3) andesite; 4) a glacial till complex containing granite, andesite, rhyolite, and sedimentary rocks; 5) rock altered by acidic geothermal activity; and 6) rock altered by neutral, high chloride geothermal activity. Because of the complexity of YNP's geology and the difficulty in determining the path of groundwater movement, the dominant bedrock type was more certain for some fen watersheds than others. A subset of water samples was selected for each bedrock type where the dominant bedrock type was unambiguous. Differences in mean pH and EC between bedrock types were determined by ANOVA with Tukey's HSD multiple comparison test, $P < 0.05$ (PROC GLM: SAS Institute 2002). Dominant groundwater ions for each bedrock type were identified by trilinear Piper diagram (Deutsch 1997). Dominant groundwater ions for each bedrock type were identified by trilinear Piper diagram (Deutsch 1997).

3.4.1 *Vegetation classification*

The purpose of the classification was to create plant communities that would be recognizable in the field based on species composition and dominance and that could be used by YNP staff for other purposes, such as interpretation and future ecological research. This aim was similar to that described by Wheeler (1980) in his large scale classification of the plant communities of rich fens in England and Wales. Relevés were analyzed by hierarchical agglomerative cluster analysis (van Tongeren 1995) in PC-ORD (McCune & Mefford 1999) and by table methods (Mueller-Dombois & Ellenberg 1974). Cluster analysis was performed on vascular plant data using Sørensen distance measure and flexible beta linkage method with $\beta = -0.25$ (McCune & Grace 2002). Indicator species analysis was used to determine the optimum number of clusters produced by the dendrogram (Dufrene & Legendre 1997; McCune & Grace 2002). Bryophytes were then added to the dataset and each cluster was analyzed by table methods using species of intermediate constancy (10–80%). Within each cluster, differential species were identified for further divisions (Mueller-Dombois & Ellenberg 1974).

3.4.2 *Ordination*

Patterns in species distribution were related to environmental variables using detrended correspondence analysis (DCA: Hill & Gauch 1980) and canonical correspondence analysis (CCA: ter Braak 1986) in CANOCO (ter Braak & Smilauer 1997). DCA is a method of indirect gradient analysis that ordines sample units based on species composition. Environmental data can be compared with the resulting ordination scores to evaluate correlation, but are not directly involved in the algorithm. CCA is a

method of direct gradient analysis in which species and stand scores are constrained to be linear combinations of environmental variables, thus ignoring variation not associated with the measured variables. The two methods provide different, but complementary results (Økland 1996). For DCA ordinations, rare species were downweighted and detrending by segments was enforced using the default 26 segments. Separate DCA ordinations were run on (a) all species, (b) vascular plants only, and (c) bryophytes only. Spearman's rank correlation coefficients of environmental variables with samples scores on axes 1 and 2 were calculated for all DCA ordinations. For CCA ordinations, rare species were downweighted, axis scaling was set to bi-plot scaling, and the inter-species distance option was selected. Site scores were plotted as linear combinations of the environmental variables (LC scores of Palmer 1993). Manual forward selection of environmental variables was performed by Monte Carlo test with 199 permutations; only variables significant at $P \leq 0.01$ were included in the analysis. CCA ordination was run on all species.

3.4.3 *Variance partitioning*

The fraction of explained variation attributed to individual environmental variables was obtained by CCA using each variable as the only constraining variable (ter Braak 1986). Significance was calculated by Monte Carlo test with 199 permutations ($P \leq 0.01$). Results were calculated as a percent of total variation explained (TVE), the sum of all constrained eigenvalues from a CCA using all explanatory variables (Økland 1999). Individual variables were tested for (a) all species, (b) vascular plants only, and (c) bryophytes only.

CCA with variance partitioning was carried out on several combinations of two variables sets following the approach of Borcard *et al.* (1992) and Økland & Eilertsen (1994). For each combination, the fraction of explained variation attributed to one set of variables and not shared with the other was obtained by partial CCA using variables of the first set as constraining variables and variables of the second set as covariables. See Fig. 6 for a representation of the components of variation. Each environmental variable subset (Table 1: A–F) was analyzed against all other variables, quantifying the variation attributed exclusively to that subset. Each variable subset was first subjected to manual forward selection (Monte Carlo test, 199 permutations, $P \leq 0.01$) and only significant variables were included. Results are calculated as percent of TVE (Økland 1999).

4. RESULTS

4.1 REGIONAL CHARACTERISTICS OF YNP FENS

4.1.1 *Distribution of fens across the regional gradients*

Nearly two-thirds of fens sampled were located on the central volcanic plateau at 2200–2500 m elevation. The lowest elevation sites occurred along the Lamar and Yellowstone Rivers in the north and within Bechler Meadows in the southwest. Fens at higher elevations were sampled in the Gallatin Range and within the park's interior. Mean annual precipitation at sampled fens ranged from 380 to 1400 mm, and precipitation totals increased with increasing elevation and decreased from southwest to northeast across the study area (Fig. 7). Low elevation fens in the northern range received

the least precipitation, 380–480 mm per year, while fens at similar elevations in Bechler Meadows received 1140–1400 mm.

Fens located within the park's central plateau were predominantly within rhyolite watersheds. Geothermal sites, both acidic and neutral, high chloride, were also located within the park's central plateau in watersheds that were otherwise rhyolite-dominated. Fens in the northern Gallatin Mountains and the southern Absaroka Mountains were located in andesite watersheds. Fens in Falls River Basin were located in basalt watersheds on the edge of the central rhyolite plateau. Sites along the Lamar and Yellowstone Rivers and at the base of the Gallatin Mountains were influenced by the glacial till complex containing sedimentary rock.

4.1.2 *Water chemistry and bedrock geology*

Groundwater pH in study fens ranged from 2.89–7.98 (Table 1) and was significantly different in watersheds of different bedrock types ($F_{5,44} = 47.66$, $P < 0.0001$). Mean pH in glacial till was significantly higher than the three volcanic bedrock types, but not significantly higher than neutral, high chloride geothermal sites. The three volcanic types were not significantly different from each other, but mean pH in acidic geothermal fens was significantly lower than all other bedrock types (Table 3, Fig. 8).

Electrical conductivity (EC) ranged from 7.8–1250.0 $\mu\text{S}/\text{cm}$ and was also significantly different between bedrock types ($F_{5,44} = 16.39$, $P < 0.0001$). Neutral, high chloride geothermal sites had significantly higher EC than all other bedrock types (Table 3, Fig. 9) and the dominant ions were Na^+ and Cl^- (Fig. 10). Mean EC of glacial till groundwater was not significantly different than acidic geothermal groundwater, but both were significantly higher than the volcanic bedrock types. HCO_3^- was the dominant anion

in both glacial till and all three volcanic types, while acidic geothermal water was dominated by SO_4^{2-} .

For most Yellowstone fens, pH was positively correlated with both EC and Ca^{2+} (Fig. 11) with a relationship similar to the one shown in Fig. 1, which has been documented for peatland water chemistry in Europe and North America (Sjörs 1950a; Glaser *et al.* 1981; Malmer 1986; Mullen *et al.* 2000; Glaser *et al.* 2004; Tahvanainen 2004). However, acidic geothermal fens can have $\text{pH} < 5$ and yet high electrical conductivity ($\text{EC} > 100 \mu\text{S}/\text{cm}$) and Ca^{2+} concentrations ($\text{Ca}^{2+} > 20 \text{ mg}/\text{L}$), a combination of water chemistry parameters not described for boreal fens. These water chemistry conditions can only occur where groundwater discharges through highly mineralized rock or geothermal activity.

4.2 LOCAL CHARACTERISTICS OF YNP FENS

4.2.1 *Landforms*

Gently sloping fens were the most common landform surveyed in YNP. Of the 166 surveyed fens, 109 were gently sloping fens, 34 were basin fens, 16 were steeply sloping fens, and only 7 were spring mound fens. Across most of the park, landforms were well distributed, with the following exceptions: 1) spring mound fens were only found on the central volcanic plateau and only in the northern half of the park, and 2) all but one fen in the southwestern Falls River Basin were basin fens.

4.2.2 *Stand topography and microtopography*

Within study fens, individual stands were located on variable topography. Stands on fen margins often had greater slope than stands within the fen center, which were often level or concave. String and flark formation (Rydin & Jeglum 2006) was also evident in a number of sites where parallel ridges of vegetation (strings) alternated with shallow depressions of standing water (flarks). It was evident in the field that this within-site topographic variability was associated with changes in vegetation.

Hummock formation occurred in ~15% of stands. Hummocks were most common in either basin or gently sloping fens where *Sphagnum* dominated the vegetation, but also occurred in areas dominated by *Aulacomnium palustre*. Many hummocks supported shrub or tree species, particularly *Kalmia microphylla* and *Pinus contorta* var. *latifolia*.

4.2.3 *Soil characteristics*

Of the 198 stands sampled for soil chemistry, soil carbon ranged from 10.36–52.60% with a mean of $31.88 \pm 9.69\%$. Soil nitrogen ranged from 0.51–3.66% with a mean of $1.77 \pm 0.66\%$. Soil carbon was not strongly correlated with slope or peat thickness, but was positively correlated to soil nitrogen ($R^2 = 0.45$, $P < 0.0001$).

Peat thickness was measured at all 476 stands and 100 stands had peat > 240 cm thick, the limit of the sampling tool, while the remaining had peat > 40 cm. The thickest peat layers occurred on slopes $\leq 5^\circ$ and few stands with $> 5^\circ$ slope had peat > 120 cm.

4.3 VEGETATION CLASSIFICATION

Using cluster analysis and table methods, 28 plant communities were identified from the 476 relevés (Table 4). The classification was organized into seven groups of communities based on physiognomy of the dominant species, which best reflects the primary floristic gradient within vegetation data (see DCA below). The most common dominant species found in YNP fens, *Carex utriculata*, *Carex aquatilis*, *Eleocharis quinqueflora*, and *Salix planifolia* showed wide tolerances for water chemistry values and therefore the vegetation classification did not naturally break into classes along the poor–rich gradient. One exception is the bryophyte-dominated group of communities, which was primarily associated with acidic environments, such as acidic geothermal fens. Mean cover values and constancy class (II–V) for dominant and differential species in each community are presented in Table 5. A key to the plant communities is in Appendix A. Descriptions of the environmental setting and floristic characteristics of each community are in Appendix B.

4.4 ORDINATION

4.4.1 *Indirect gradient analysis*

Eigenvalues for DCA axes 1 and 2 based on all species were 0.623 and 0.516, respectively (Fig. 12). Several environmental variables were significantly correlated with axis 1 at $P < 0.0001$ (Table 6). Variables most negatively correlated with axis 1 include stand topography (-0.39), SO_4^{2-} (-0.35), and site landform (-0.34). Those most positively correlated with axis 1 include precipitation (0.24), water temperature (0.24), and snowfall (0.22). The correlated variables and stand placement along axis 1 indicate a complex

floristic gradient associated with two different environmental gradients. Stands classified within semi-aquatic and floating mat communities are clustered on the right side of axis 1 while stands within shrub and forested communities are clustered on the left side of axis 1, a gradient linked to site landform and topography. However, stands on the far left of the ordination are classified within bryophyte-dominated communities that occur primarily within acidic geothermal fens, where SO_4^{2-} is often a dominant ion. This far end of axis 1 is linked to an extreme end of the water chemistry gradient. Axis 2 is also related to water chemistry. Groundwater pH, EC, Ca^{2+} , Mg^{2+} , HCO_3^- , SO_4^{2-} are all negatively correlated with axis 2 at $P > 0.0001$. Regional variables precipitation, snowfall, and elevation are among those positively correlated with axis 2 at $P > 0.0001$.

Eigenvalues for DCA axes 1 and 2 based on bryophytes were 0.906 and 0.787 (Fig. 13). At $P < 0.0001$, axis 1 is negatively correlated with pH (-0.38) and HCO_3^- (-0.28) and positively correlated with hummocks (0.44) and soil C:N ratio (0.27) (Table 6). This axis represents the acidity/alkalinity gradient of YNP fen waters. Many species of *Sphagnum* and *Polytrichum*, as well as acid tolerant *Gymnocolea inflata* and *Drepanocladus polygamus* are plotted on the right side of the diagram. Rich fen mosses such as *Scorpidium scorpioides* and *Campyllum stellatum* occur on the left. Axis 2 separates stands that contain *Sphagnum subsecundum* and other species that were found only in the southwest corner of the park. This axis is also correlated with pH and peat C:N ratio, but with lower correlation coefficients than for axis 1. The DCA ordination of only vascular plants produced a diagram similar to the ordination using all species, indicating that gradients affecting all species reflect the gradients affecting the vascular plant species, due to their much higher total canopy cover in most stands than bryophytes.

4.4.2 Direct gradient analysis

Eigenvalues for CCA axes 1 and 2 are 0.364 and 0.305, respectively. The first three CCA axes account for 6.0% of the total variance in the species data and explain 58.4% of the species-environment relationship. Not all physiognomic groups have high fidelity within the CCA diagram, indicating separate plant communities within the groups are associated with different environmental conditions, but several trends are evident from the ordination. CCA axis 1 is driven by the presence of hummocks, high soil C:N, and high elevation (Fig. 14; Table 7) and is longer on the right (positive) side than the left (negative) side. Stands on the right of axis 1 are within the bryophyte-dominated communities that occur in acidic geothermal fens. In the species diagram, *Sphagnum lindbergii*, *Gymnocolea inflata*, *Kalmia microphylla*, *Sphagnum russowii*, *Drepanocladus polygamus*, *Polytrichum commune*, and *Polytrichum strictum* characterize this acidic extreme (Fig. 15). *Pinus contorta* var. *latifolia*, *Vaccinium occidentale*, and *Sphagnum warnstorffii*, which occur in less acidic conditions, fall closer to the center of the axis.

Axis 2 is driven by climate, topography, and water chemistry variables. The upper left portion of the stand diagram contains semi-aquatic, floating mat, and some large sedge and small sedge plant communities, mostly of basin fens. In the species diagram, this area is characterized by *Nuphar lutea* ssp. *polysepala*, *Potamogeton* spp., *Carex lasiocarpa*, *Menyanthes trifoliata*, *Typha latifolia*, and *Carex limosa*. These species are associated with high precipitation, thick peat bodies, relatively warm temperatures of standing water, and low values for topographic index and slope. The lower left portion of the stand diagram contains shrub communities, the *Picea*-dominated community, and several coarse sedge and small sedge stands, particularly sloping and spring-fed communities.

The species diagram shows *Salix pseudomonticola*, *Veronica americana*, *Symphyotrichum eatonii*, *Salix boothii*, *Marchantia polymorpha*, and *Senecio triangluaris* are associated with this extreme. These are sloping fens with high water mineral content, high pH, occurring in low precipitation regions of the park.

4.5 VARIANCE PARTITIONING

For each subset of the species data, 19 of 20 variables were significant in individual tests (Table 8). Among regional scale variables, water chemistry parameters accounted for the highest percent of total variation explained (TVE) in each species subset. Groundwater pH accounted for 12.6% TVE for all species and 17.6% for bryophytes, but Mg^{2+} and Ca^{2+} both accounted for slightly higher %TVE than pH for vascular plants. Elevation and climate variables also accounted for a greater proportion of TVE for vascular plants than bryophytes. Among local scale variables, hummocks accounted for 15.3% and 16.2% TVE for all species and vascular plants, respectively. For bryophytes, soil C:N ratio accounted for 19.7% and hummocks 13.6%. For vascular plants, local scale variables related to a stand's physical position (hummocks, stand topography, and site landform) were associated with the greatest proportion of variation. For bryophytes, soil C:N ratio, pH, and hummocks were the most important variables.

When variable subsets were analyzed for their unique contribution to TVE (Table 9), groundwater chemistry accounted for the highest %TVE of all variable subsets (20.8%). Other regional scale subsets, climate and elevation, explained only 7.0% and 8.2% of TVE, respectively. Of the local scale subsets, stand topography and microtopography accounted for 18.8% of TVE, soil characteristics 16.0%, and site landform only 3.4%. The remaining 25.7% of TVE was shared variation not attributed to any one subset.

When combined, regional scale variables accounted for 40.7% of TVE, while those controlled on a local scale accounted for 43.9%. The variation shared by these two sets ($Y \cap Z$) was only 15.4%, indicating that regional and local factors account for approximately the same amount of variation and appear to affect the distribution of plant species in different ways.

5. DISCUSSION

5.1 GRADIENTS AFFECTING VEGETATION IN YNP FENS

Previous research on peatland vegetation and environmental gradients has shown that peatland vegetation responds simultaneously to multiple gradients. Principal gradients recognized in the literature include the poor–rich gradient of peatland water chemistry, the microtopography gradient, the gradient of peatland margin–peatland expanse, and regional floristic gradients related to climate and phytogeography (Sjörs 1950b; Malmer 1986; Bridgham *et al.* 1996; Wheeler & Proctor 2000). In YNP, major gradients affecting fen vegetation occur on both regional and local scales. Regional gradients, such as bedrock-influenced water chemistry, are strongly associated with vegetation patterns, but specific local factors, particularly topography and microtopography, are equally important in determining the composition of individual stands. Certain results from this analysis confirm common relationships between environmental gradients and peatland vegetation, while others suggest relationships specific to YNP.

5.1.1 *Water chemistry, bedrock geology, and the poor–rich gradient*

Fens in YNP are minerotrophic and receive mineral input from surface and groundwater. Dry summers in the Rocky Mountains preclude the development of ombrotrophic conditions that are found in other parts of the world. In YNP, water chemistry is tied closely to regional scale patterns of bedrock geology and changes across the park. Fens in glacial till watersheds generally have pH between 6.0–8.0, EC > 100 $\mu\text{S}/\text{cm}$, and Ca^{2+} > 20.0 mg/L, while fens in volcanic watersheds have pH between 5.0–7.0, EC < 100 $\mu\text{S}/\text{cm}$, and Ca^{2+} < 20.0 mg/L, and acidic geothermal fens can have pH < 5.0, EC > 100 $\mu\text{S}/\text{cm}$, and Ca^{2+} > 20.0 mg/L. Bedrock controlled water chemistry has been previously documented in Rocky Mountain fens (Cooper & Andrus 1994; Cooper 1996; Cooper *et al.* 2002) and bedrock has been correlated with peatland type elsewhere in North America (Halsey *et al.* 1997; Bedford & Godwin 2003).

Bedrock controlled water chemistry is a major driver of species distribution in YNP fens, accounting for the highest portion of explained variation in the species data (Table 10). Water chemistry values can be used to classify YNP along the poor–rich gradient, which describes change in vegetation associated with pH and ion concentrations. For peatlands around the world, the poor–rich gradient is among the most important controls on species distribution (Sjörs 1950a; Malmer 1986; Glaser *et al.* 1990; Vitt & Chee 1990; Økland 1990a; Bragazza *et al.* 2005). However, this gradient is a continuum of both water chemistry and vegetation patterns. Clear breaks are not defined, particularly for fens in the Rocky Mountains where limited research has been conducted. While individual water chemistry parameters in YNP fens span the poor–rich gradient, the

relationship between pH and ion concentrations does not follow previously described categories, complicating the classification of YNP fens.

Plant species known to indicate particular water chemistry conditions are often used to interpret a fen's classification along the poor–rich gradient (Sjörs 1950a; Wheeler & Proctor 2000). However, the usefulness of these species as indicators may vary regionally (Johnson & Steingraeber 2003). YNP contains several indicator species that are widespread in boreal regions and previous studies of extreme rich fens in the Rocky Mountains contribute additional indicators specific to this region. Selected vascular and bryophyte plant species from YNP fens and their known distribution along the poor–rich gradient in boreal and Rocky Mountain fens is show in Table 10. It is evident from this table that many species, particularly vascular plants, occur across a wide range of conditions in YNP. While research on extreme rich fens in the Rocky Mountains has identified key indicators of the most alkaline and calcareous fens, more work is necessary to identify indicators across the entire poor–rich gradient for Rocky Mountain fens. However, the listed species, along with water chemistry data and descriptions of fens from the literature, help to place Yellowstone's fens within the context of previous peatland work.

Based on water chemistry and vegetation, YNP contains a range of rich fens, but few, if any, poor fens. In addition, YNP's acidic geothermal fens are a separate category of fens that does not fit along the poor–rich continuum. Fens in glacial till watersheds, with the highest pH and ionic concentrations, are the richest fens in the park. Three plant communities showed high fidelity to glacial till fens with high pH and mineral ions: 1) *Picea (engelmannii, glauca)* - *Equisetum arvensis*, 2) *Salix boothii* - *Salix*

pseudomonticola, and 3) *Carex simulata* - *Epilobium palustre*. However, no fens in YNP match the floristic descriptions of extreme rich fens in Colorado or Wyoming, which occur in watersheds with limestone and dolomite (Fertig & Jones 1992; Cooper 1996; Johnson & Steingraeber 2003). Several important indicator species of extreme rich fens are absent from the Yellowstone flora, including *Carex scirpoidea*, *Kobresia myosuroides*, *Kobresia simpliciuscula*, *Salix myrtilifolia*, and *Trichophorum pumilum* (Table 10). Of the extreme rich fen indicators found in YNP only *Salix candida* appeared to reliably indicate high pH and high Ca^{2+} fens, although it was not present in all high Ca^{2+} sites.

Fens within YNP's volcanic watersheds are also rich fens. These sites have lower pH and ionic concentrations than those found in glacial till watersheds, but still contain a number of bryophyte species considered rich fen indicators, including *Tomentypnum nitens*, *Sphagnum warnstorffii*, and *Campylium stellatum*. Plant communities with high fidelity to rich fens of volcanic watersheds include: 1) *Pinus contorta* var. *latifolia* – *Aulacomnium palustre* – *Sphagnum warnstorffii*, 2) *Carex livida* – *Drosera anglica*, and 3) *Carex buxbaumii* – *Campylium stellatum*. Similar rich fens with low ionic concentrations have been found in granite watersheds of Wyoming and Colorado (Cooper 1990; Cooper & Andrus 1994). Though groundwater within these sites is low in mineral ions, they are subject to seasonal or summer-long flushing by snowmelt and groundwater discharge and the total annual flux of ions creates rich fen conditions. Highly mineralized rich fens also occur where neutral, high chloride geothermal water produces high concentrations of Na^{2+} and Cl^- , but these sites could not be distinguished from other rich fens by vegetation alone.

YNP appears to have few, if any, poor fens. When pH is plotted against EC for YNP fens (Fig. 11a), there are few sites with pH < 4.5 and EC < 50 μ S/cm. Compared to the general ranges found in peatlands around the world (Fig. 1), this area of the poor–rich gradient in YNP is relatively empty. Though YNP contains a number of *Sphagnum* species, those strongly associated with poor fens are either lacking, such as *Sphagnum rubellum*, *Sphagnum fallax*, *Sphagnum magellanicum*, and *Sphagnum jensenii* (Chee & Vitt 1989; Slack 1994), or occur in acidic geothermal environments. Only a few sites, located in basin fens in volcanic watersheds with low ionic strength water and minimal water flow, have water chemistry conditions similar to poor fens. At this time, it is unclear what would constitute a poor fen in the Rocky Mountains, but they appear to be limited or absent from YNP.

The *Sphagnum*-dominated vegetation in YNP's acidic geothermal fens resembles poor fens, but these sites contain far greater ion concentrations than boreal poor fens. The acidity of geothermal fens is produced when hydrogen sulfide gas from geothermal vents enters groundwater and is oxidized to form sulfuric acid (Mosser *et al.* 1973). Fens with similar water chemistry and flora occur in the San Juan Mountains of Colorado, the Black Hills of South Dakota, the Warner Mountains of California, and the Andes of Peru, where the oxidation of iron pyrite creates groundwater rich in sulfuric acid (Cooper *et al.* 2002). In acidic geothermal and iron pyrite watersheds, acid production is driven by geochemical characteristics, not autochthonous production by *Sphagnum* moss, but species composition is similar to poor fens because of the highly acidic environment. In YNP, *Sphagnum russowii* is the most frequent dominant in acidic geothermal fens. Based on data collected in New York peatlands, *Sphagnum russowii* occurs most frequently in

pH ~3.8–5.2 (Andrus 1986), similar to the pH of YNP's acidic geothermal fens. These sites also contain *Sphagnum lindbergii*, *Sphagnum fimbriatum*, and *Sphagnum riparium*, all new records for the state of Wyoming (Lemly *et al.* 2007). On the margins of pools within acid fens in YNP, the pH can be as low as 2.9, which may be lower than the *Sphagnum* species present can tolerate. Highly acidic areas supported carpets of *Polytrichum commune* and *Gymnocolea inflata*, a liverwort species that commonly inhabits bogs and poor fens (Chee & Vitt 1989; Slack 1994). A similar bryophyte community of *Polytrichum commune* and *Gymnocolea inflata* was recently described from acidic, mineral-rich waters draining a volcanogenic massive sulfide deposit in Alaska (Gough *et al.* 2006). Acidic geothermal fens of YNP, along with acidic iron fens elsewhere in the western Hemisphere, represent an additional category of fens distinct from the poor–rich gradient. These sites are not yet well understood and deserve further attention.

Fens in YNP and throughout the central and southern Rocky Mountains appear to have a different range of pH and ionic concentrations than peatlands in other areas of the world. Based on data from YNP fens and other studies of Rocky Mountain fens, a general representation of water chemistry in Rocky Mountain fens is presented in Fig. 16. Bogs are lacking completely and poor fens are rare. Most Rocky Mountain fens are rich fens, but water chemistry conditions range from lower pH and ionic concentrations in volcanic or granite watersheds, which some have called transitional rich fens (Cooper & Andrus 1994), to extreme rich fens in calcareous limestone watersheds. Acidic geothermal fens and acidic iron fens add an additional element to the poor–rich gradient in Rocky Mountain fens.

5.1.2 *Climate and elevation*

Regional gradients of climate and elevation have less influence on vegetation than water chemistry in YNP. In the CCA diagram (Fig. 14), high precipitation and snowfall are associated with thicker peat bodies, basin sites, level topography, warmer water temperatures, and lower water chemistry values. However, climate alone accounts for only 8.2% of explained variation (Table 10), largely because there is considerable overlap between climate and water chemistry. Variance partitioning of climate and water chemistry variables illustrates that more than half (53.5%) of the variability explained by climate is also explained by water chemistry (data not shown). Although there is a distinct climatic gradient across the park, the gradient covaries with bedrock geology, which is a stronger driver of vegetation patterns because of its influence on water chemistry. The driest areas of YNP are within glacial till, which produces alkaline groundwater, and the wettest are located on volcanic bedrock, which produces groundwater with lower ionic concentrations.

Climate can be among the most important controls on species distribution in peatlands, however, results vary by region and method of study. Studies showing the greatest correlation between climate and vegetation were conducted across very large geographic areas (ranging from the province of Manitoba to all of eastern North America) and included multiple climatic variables (Gignac & Vitt 1990; Glaser 1992; Halsey *et al.* 1997). Large scale studies compare maritime to continental climates, and boreal regions subject to permafrost to more mild temperate regions. These climatic gradients are steeper and more complex than the precipitation gradient across YNP. But even across the Mackenzie River Basin in northern Canada, which is $> 1,000,000 \text{ km}^2$ in

area, Nicholson *et al.* (1996) found that water chemistry was more important in determining species composition than climate, similar to the results for YNP.

Like climate, elevation alone accounts for a low proportion of explained variability. Low elevations sites occurred at either end of the precipitation gradient and in watersheds of different bedrock geology and therefore do not share uniform characteristics. The highest elevation sites were in volcanic watersheds and included acidic geothermal fens and rich fens with hummocks of *Sphagnum warnstorfi*. As a result, high elevation is associated with low pH, hummocks, and high soil C:N in the CCA diagram (Fig. 14), but these variables are more influential than elevation itself. The mountain topography of YNP is very steep, with bare slopes in many regions, and no fens were surveyed above 2800 m. In the granite Wind River range of Wyoming, ~300 km south of YNP, fens occur in high elevation valleys between 2970–3200 ft (Cooper & Andrus 1994) and contain several high elevation species rarely or never encountered in the surveyed YNP fens. It is likely that fens occur at similarly high elevations in the Gallatin Mountains and Beartooth Mountains beyond the border of the YNP, but were not sampled. Higher elevation fens might support several species not found within YNP and strengthen the relationship between elevation and species distribution. Elevation was found to be significantly correlated to species distribution in Australian peatlands (Clarke & Martin 1999), but the relationship in YNP appears to be limited by the landscape and complexity of other gradients.

5.1.3 *Local scale gradients*

Site landform and stand topography were both strongly correlated with the primary floristic gradients of all species and vascular plants in DCA (Fig. 12, Table 7), which

separated semi-aquatic and floating mat communities from shrub and forested communities. Because stand topography controls finer scale topographical variation, it was more strongly correlated with stand vegetation than site landform and explains a greater percent of the variability in variance partitioning. However, certain communities had high fidelity to either basin or sloping sites, likely linked to hydrologic regime. In general, basin fens have slow moving or stagnant water, restricted inflow and outflow, and seasonally deep standing water in many areas. Floating mat communities, which were far more likely to occur in basin fens than sloping fens, establish on the edges of ponds or small lakes that gradually fill with peat over thousands of years. Two YNP basin fens analyzed in previous paleoecological studies (Buckbean and Cygnet Lake Fens) illustrate this process (Baker 1976; Whitlock 1993). Both originated as lakes and their stratigraphy grades from basal mineral sediments to organic soil at ~7 m deep (aged at $11,500 \pm 350$ YBP) and ~5 m deep (aged at $8,520 \pm 80$ YBP). In contrast, sloping fens have flowing water at or below the peat surface and the steepest slopes appear to limit the build-up of thick peat. This may occur for three reasons: peat may flow downslope due to gravity, large amounts of mineral sediment may be deposited in the fen from upslope sources, and higher discharge rates may mean the soil is more oxygenated than in basin fens. Certain species and communities, such as *Philonotis fontana* – *Carex utriculata* and the shrub communities, have high fidelity to sloping fens.

Both landforms and stand topography influence site variation related to wetness, specifically water table depth and water retention. Variation related to wetness has long been recognized a major driver of peatland vegetation patterns (Sjörs 1950b) and studies from the Rocky Mountains (Cooper & Andrus 1994; Johnson 1996) and elsewhere (Slack

et al. 1980; Økland 1990a; Bragazza *et al.* 2005) confirm this relationship. Depth to water table and duration of standing water were not measured in YNP fens because sites were sampled only once between June and August of two different years and water tables typically vary seasonally and between years (Økland 1989; Cooper 1990). However, these variables likely contribute to the differences between common plant communities dominated by *Carex utriculata*, *Carex aquatilis*, and *Salix planifolia*, which preferentially inhabit different hydrologic regimes. Of the three species, *Carex utriculata* occupies the wettest sites, can tolerate deeper and more prolonged flooding, but can also withstand dry soils in late summer. *Carex aquatilis* also occupies wet sites, but typically where standing water is shallow and the soil remains anaerobic throughout the growing season. *Salix planifolia* can occur with both *Carex utriculata* and *Carex aquatilis*, but extends into much drier habitats where the water table drops 30 cm or more below the surface (Cooper 1990).

The importance of stand topography may also reflect the peatland margin–peatland expanse gradient. In basin and sloping fens, stands located on the margins often had steeper slopes than the central peatland expanse and were more likely to be dominated by shrubs or trees. The peatland margin–expanse gradient is an expression of several underlying changes in hydrology and water and soil chemistry (Sjörs 1950b). Groundwater flowing into the fen margin has been in direct contact with mineral soil and may contain higher concentrations of minerals. As water moves through peat soil towards the fen center, mineral concentrations decrease due to plant uptake and adsorption to the peat (Johnson & Steingraeber 2003). Margins may also have higher discharge rates, leading to an increased delivery rate of minerals (Malmer 1986). In certain locations,

margins may experience greater water table fluctuations, which may raise soil decomposition rates and make soil nutrients more available.

A high proportion of explained variation was also associated with stand microtopography. In YNP, bryophyte species dominate well developed hummocks, primarily species of *Sphagnum*, *Polytrichum*, and to a lesser extent *Aulacomnium palustre*. In addition, the woody species *Pinus contorta* var. *latifolia*, *Kalmia microphylla*, and *Vaccinium occidentale* were associated with hummocks in the CCA species ordination (Fig. 15). Variation in species composition along the microtopographic gradient can occur for several reasons. Hummocks are raised above the surrounding vegetation matrix and water table, are typically drier, and provide favorable microsites for tree seedlings and other species less tolerant of saturated soil (Vitt *et al.* 1975; Glaser *et al.* 1981; Andrus *et al.* 1983; Johnson 1996). Water and soil properties can also differ between hummocks and hollows, such as the oxidation-reduction potential, pH, and cation concentrations (Moore & Bellamy 1974). In YNP fens, hummocks occurred in a low percentage of stands and may actually indicate site level characteristics that are conducive to hummock formation. Variance partitioning showed that 46.0% of the variability explained by hummocks is shared with water chemistry (data not shown), indicating site level water chemistry may produce an environment suitable for hummock-forming bryophytes, such as species of *Sphagnum*. This may be true for soil C:N ratios as well, which also explain a high percent of variability, particularly within the bryophyte data. Variance partitioning of water chemistry and soil characteristics indicated that 33.2% of the variation explained by soil characteristics is also explained by water chemistry. These results suggest that certain water chemistry conditions are suitable for

Sphagnum moss, which often forms hummocks, and these hummocks have very high soil C:N ratios.

5.2 RESPONSE OF VASCULAR PLANTS VS. BRYOPHYTES

The acidity/alkalinity gradient of fen water appears to be more important to the distribution of bryophytes than vascular plants in YNP. For vascular plants, topographic variables related to wetness were most important in the DCA ordination (Fig. 12). Only the extreme end of the water chemistry gradient, represented by high concentrations of SO_4^{2-} , was strongly correlated with axis 1 and the correlation of pH with axis 1 was not significant. In variance partitioning, local topographic variables accounted for a higher proportion of explained variability in the vascular plant dataset than most water chemistry parameters (Table 8). For bryophytes, pH, HCO_3^- , and hummocks were strongly correlated to the primary DCA axis and in variance partitioning, pH, soil C:N ratio, and hummocks account for the highest proportion of explained variability. Throughout the northern hemisphere, bryophytes have high specificity to certain water chemistry conditions, often more so than vascular plants, and are more indicative of the poor–rich water chemistry gradient (Chee & Vitt 1989; Slack 1994). Vitt & Chee (1990) and Bragazza & Gerdol (2002) found the distribution of vascular plants within a broad range of fens was more closely associated with nutrient levels (available N and P), while acidity and mineral elements were more important to bryophyte species. Vascular plants, which are larger and more complex organisms with extensive root systems, may have adaptive mechanisms for tolerating a range of water chemistry conditions, while bryophyte species are restricted to the chemical conditions of their immediate environment.

6. CONCLUSION

Fens are complex ecosystems with a high degree of variation across multiple ecological gradients. Within the heterogeneous landscape of YNP, variation in fen vegetation is driven by characteristics at both regional and local scales. Two main gradients affect Yellowstone's fen vegetation: 1) site landform and stand topography, which are linked to variation in hydrologic regime, and 2) a complex water chemistry gradient. Landforms and topography can vary on a local scale between adjacent fens or within a single fen, while water chemistry is largely a regional gradient driven by bedrock type. While most fens in YNP are rich fens, there is a wide range of water chemistry values. Depending on watershed geology, three main water chemistry regimes characterize fens in YNP: 1) glacial till produces groundwater with high pH and high ionic concentrations, 2) volcanic bedrock creates groundwater with low pH and low ionic concentrations, and 3) acidic geothermal activity produces groundwater with low pH and high ionic concentrations. Differences in water chemistry between glacial till and volcanic bedrock can be interpreted as variation along the poor–rich gradient documented in peatlands around the world, but acidic geothermal fens are a different category of peatland that does not fit into the poor–rich gradient. Additional regional gradients of elevation and climate also relate to patterns in fen vegetation in YNP, but these patterns are likely linked to particular aspects of YNP's geography and are not universal for peatlands across the Rocky Mountains. Among all gradients, the bryophyte component of YNP's fens is most strongly correlated with acidity/alkalinity, while vascular species are more strongly controlled by hydrologic variation.

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8. FIGURES AND TABLES

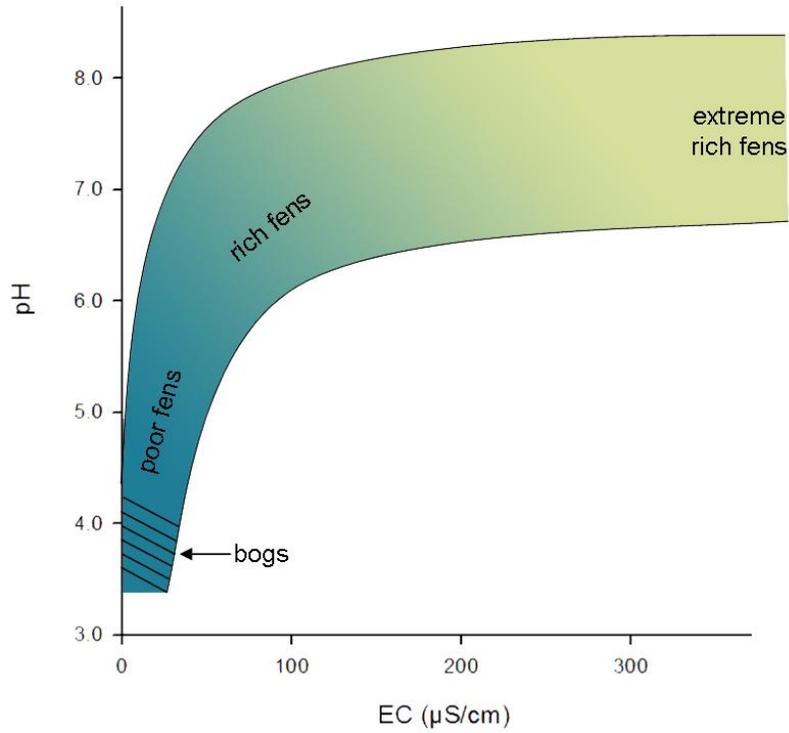


Fig. 1 Range of pH and EC along the poor–rich gradient in peatlands. Adapted from Malmer (1986).

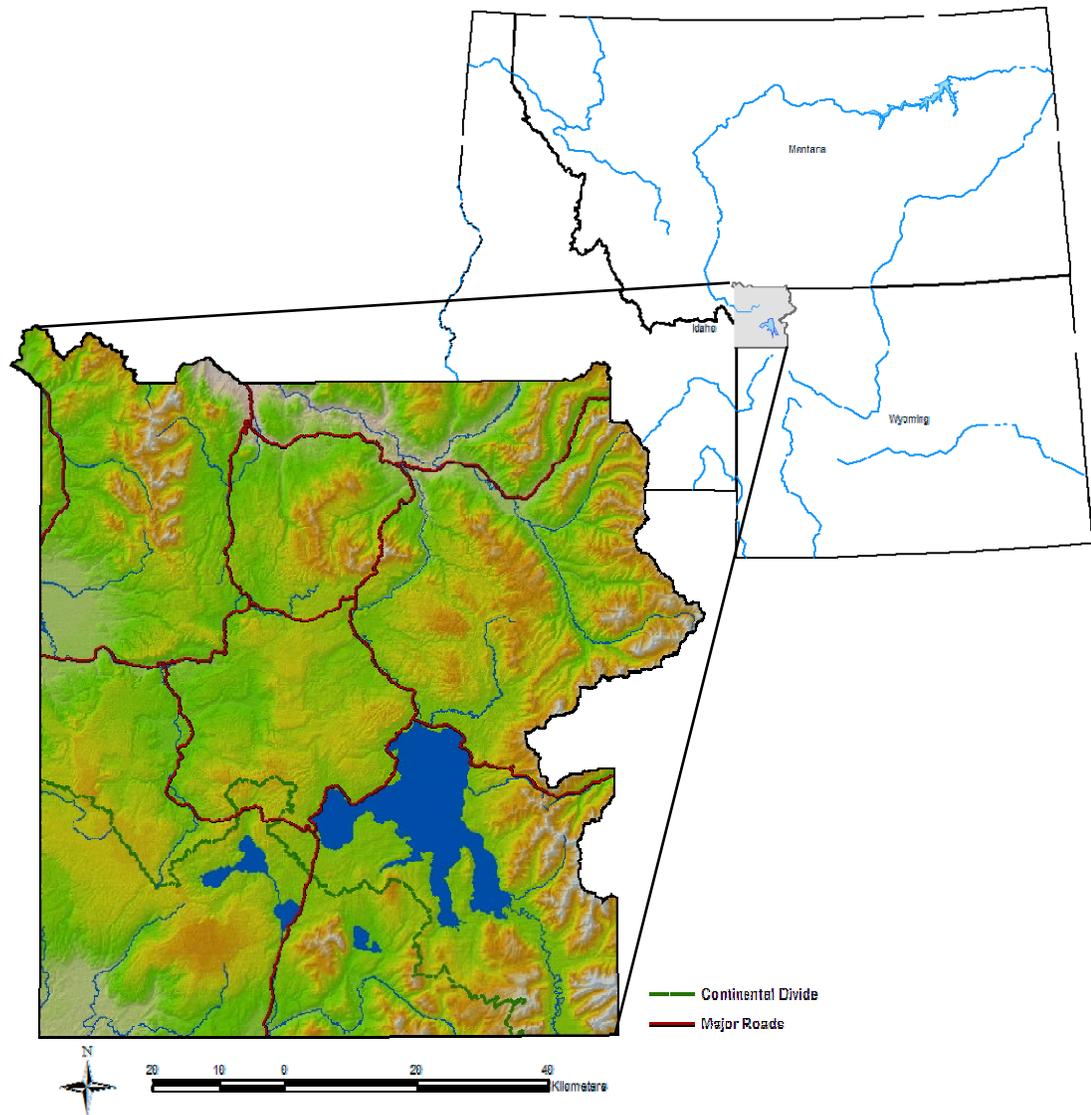


Fig. 2 Map of Yellowstone National Park (YNP), located within Wyoming, Montana, and Idaho. Elevation colorshade ranges from gray-green at low elevations, through green, yellow, orange, and white for high elevations.

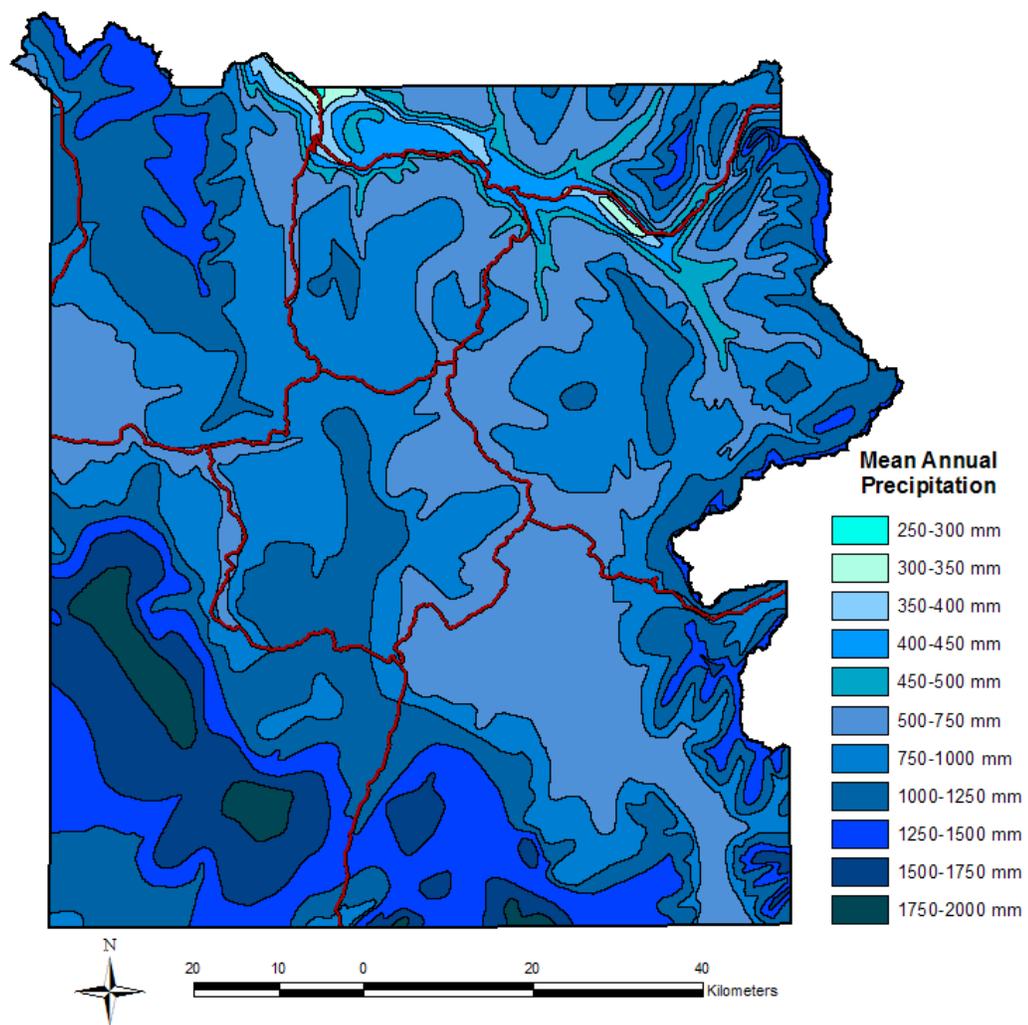


Fig. 3 Isohyetal map of mean annual precipitation across YNP (YNP Spatial Analysis Center, unpublished).

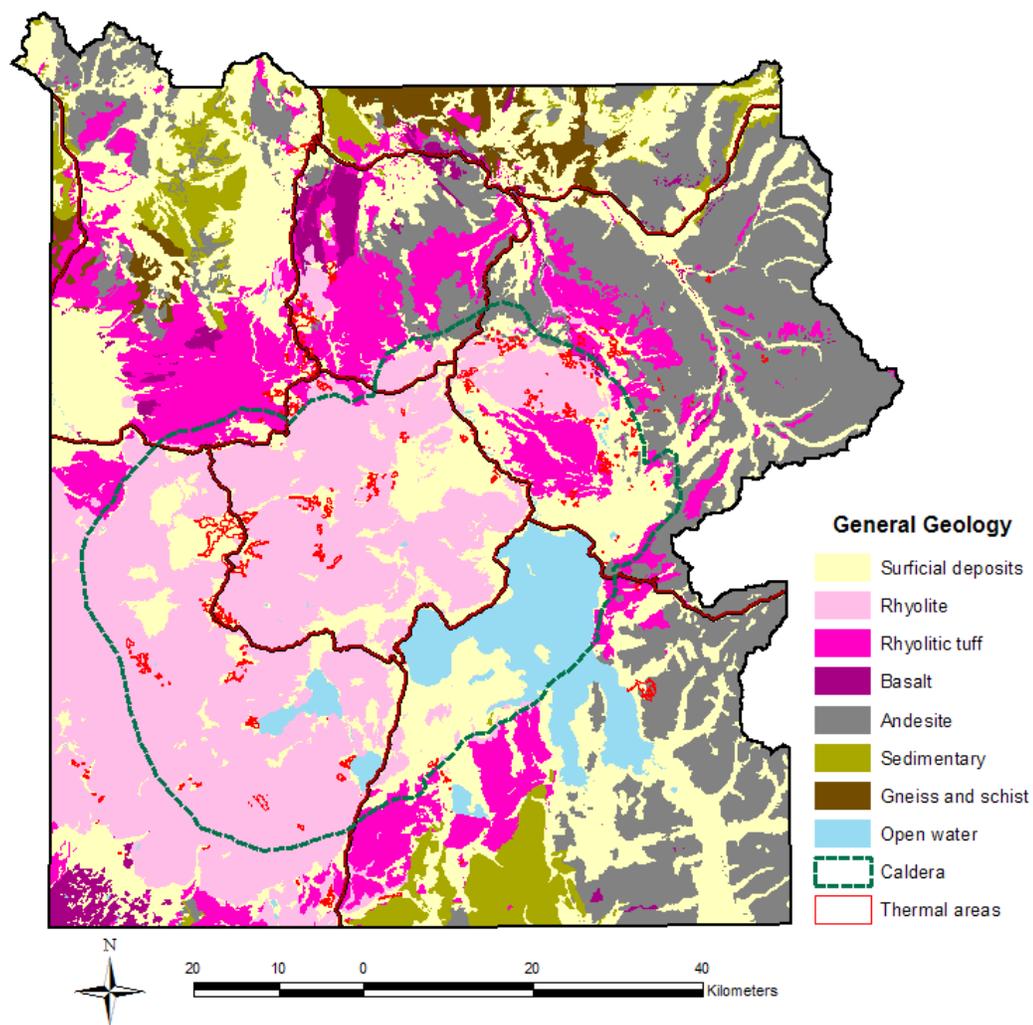


Fig. 4 Generalized bedrock geology of YNP. Adapted from USGS (1972) and Christiansen (2001).

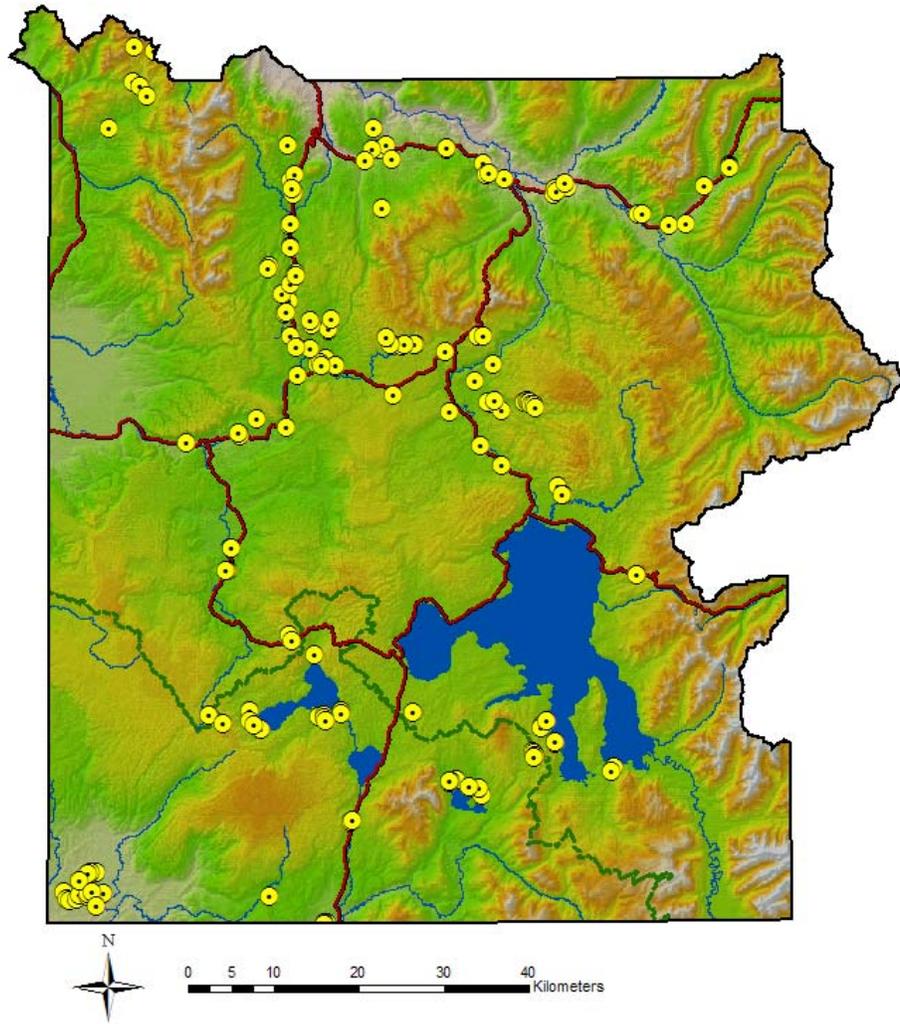


Fig. 5 Locations of 166 analyzed fens in YNP.

Table 1 Environmental variables by regional and local designation and by subset. Abbr. = abbreviation used in tables elsewhere. Observed mean, standard deviation, minimum, and maximum are by site for regional variables and by stand for local variables, except site landforms. Asterisk (*) = values shown are possible values and number of sites or stands in each category. Double asterisk (**) = mean and standard deviation are not shown for peat thickness because maximum peat thickness is not known.

Variable	Abbr	Units	-----Observed-----			
			Mean	St Dev	Min	Max
Regional variables						
A. Climate						
Precipitation	PPT	mm	847	287	380	1400
Snow	Snow	mm	5914	2832	1900	14000
B. Elevation						
Elevation	Elev	m	2264	188	1880	2710
C. Water chemistry						
pH	pH	n.a.	6.13	0.99	2.89	7.98
Temperature	Temp	° C	17.3	5.4	5.9	39.0
Electrical conductivity	EC	µS/cm	141.7	150.4	7.8	1250.0
Ca ²⁺	Ca ²⁺	mg/L	12.7	13.6	0.3	67.3
Mg ²⁺	Mg ²⁺	mg/L	4.1	7.2	0.0	39.6
Na ⁺	Na ⁺	mg/L	11.0	22.2	0.3	193.8
K ⁺	K ⁺	mg/L	2.7	3.6	0.0	23.9
HCO ₃ ⁻	HCO ₃ ⁻	mg/L	68.5	77.4	0.5	390.0
Cl ⁻	Cl ⁻	mg/L	7.6	21.7	0.2	161.0
SO ₄ ²⁻	SO ₄ ²⁻	mg/L	8.5	21.9	0.2	190.0
Local variables						
D. Site landforms						
Site landform*	Landform	n.a.		1 / 2 / 3		34 / 109 / 23
E. Landforms and microtopography						
Stand topography*	StandTopo	n.a.		0 / 1 / 2 / 3		25 / 169 / 219 / 64
Hummocks*	Hum	n.a.		0 / 1		407 / 69
F. Soil characteristics						
Soil carbon	Car	%	31.88	9.69	10.36	52.60
Soil nitrogen	Nit	%	1.77	0.66	0.51	3.66
Soil C:N ratio	C:N	%	19.77	8.30	11.87	63.26
Peat thickness**	Peat	cm	n.a.	n.a.	40	240+

Table 2 Modified Braun-Blanquet cover class.

Class	Range (% cover)	Midpoint (% cover)
+	< 1	0.5
1	1-5	3
2	5-10	7.5
3	10-25	17.5
4	25-50	37.5
5	50-75	62.5
6	75-100	87.5

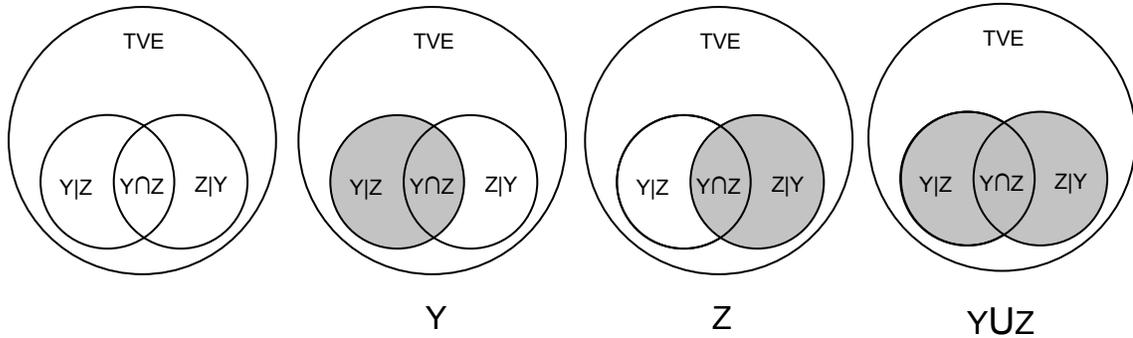


Fig. 6 Components of variation for two sets of environmental variables, $\{Y\}$ and $\{Z\}$, and their relationship to TVE. Y = variation explained by $\{Y\}$ and is the sum of all constrained eigenvalues from a CCA using variables in $\{Y\}$. $Y|Z$ = variation explained by $\{Y\}$, not shared by $\{Z\}$, and is found by partial CCA using variables in $\{Y\}$ as constraining variables and variables in $\{Z\}$ as covariables. The reverse is used to find Z and $Z|Y$. YUZ = variation explained by $\{Y\}$ and $\{Z\}$ together and is the sum of all constrained eigenvalues from a CCA using variables in both $\{Y\}$ and $\{Z\}$. $Y \cap Z$ = variation shared by $\{Y\}$ and $\{Z\}$ is calculated as $Y - Y|Z$ and recalculated as $Z - Z|Y$ to insure accuracy.

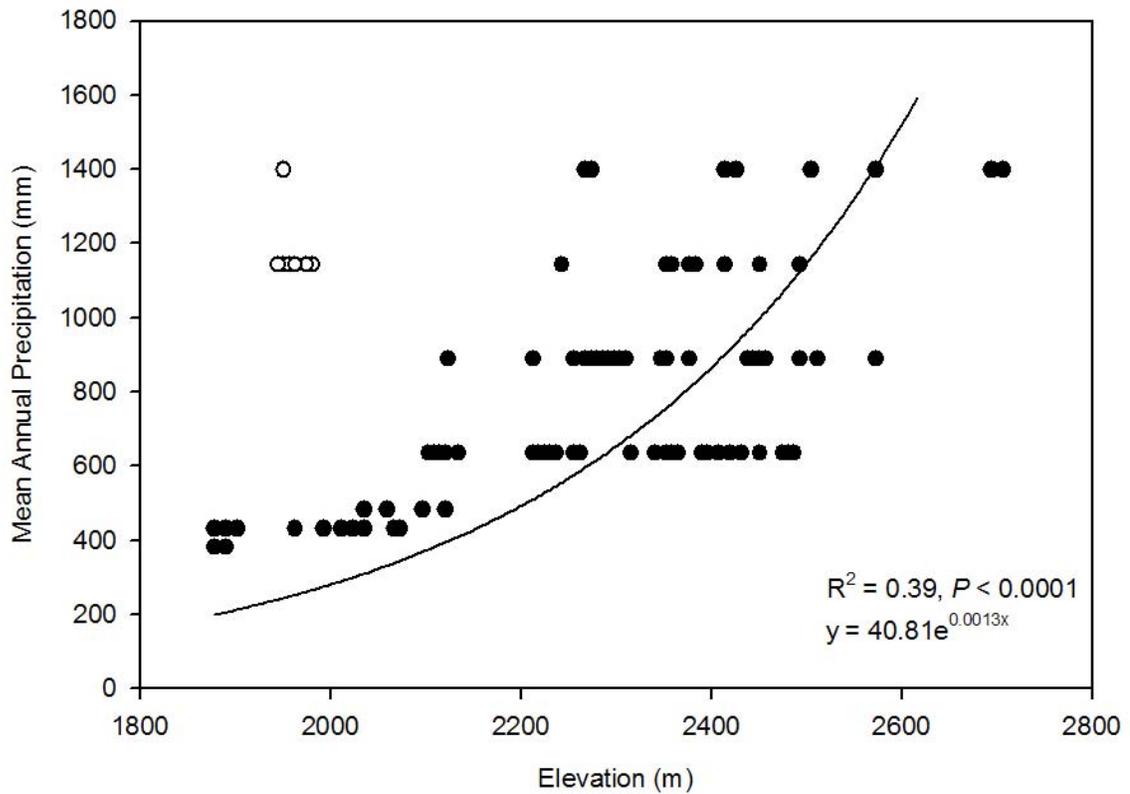


Fig. 7 Elevation vs. total mean annual precipitation for fens in YNP. Black circles represent all fens except those in the southwestern Falls River Basin, which are represented by white circles. Regression line fits only the black circles.

Table 3 Mean (± 1 SE) of groundwater chemistry parameters by bedrock type.

Bedrock type	n	pH	EC	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	HCO ₃ ⁻	Cl ⁻	SO ₄ ²⁻
Glacial Till	10	7.32 +/- 0.13	233.46 +/- 27.01	25.05 +/- 3.97	12.89 +/- 2.18	11.43 +/- 3.04	1.86 +/- 0.50	157.48 +/- 21.02	2.97 +/- 0.97	7.38 +/- 2.39
Chloride	5	6.49 +/- 0.14	642.00 +/- 168.11	19.47 +/- 6.68	1.21 +/- 0.46	103.44 +/- 31.60	14.01 +/- 2.84	153.35 +/- 50.92	103.32 +/- 22.6	22.68 +/- 11.94
Rhyolite	10	5.92 +/- 0.19	67.91 +/- 9.75	6.32 +/- 1.18	1.27 +/- 0.50	3.33 +/- 0.81	1.75 +/- 0.40	32.45 +/- 7.49	1.77 +/- 0.24	1.47 +/- 0.29
Basalt	10	5.26 +/- 0.15	70.06 +/- 8.15	5.52 +/- 0.91	0.98 +/- 0.20	2.68 +/- 0.36	1.51 +/- 0.48	26.35 +/- 4.48	2.12 +/- 0.61	0.97 +/- 0.19
Andesite	5	5.11 +/- 0.20	60.58 +/- 9.80	5.06 +/- 0.66	0.55 +/- 0.19	2.23 +/- 0.51	1.75 +/- 0.42	23.16 +/- 3.46	1.78 +/- 0.54	0.56 +/- 0.15
Acidic	10	3.79 +/- 0.24	212.06 +/- 47.40	19.38 +/- 5.62	2.75 +/- 1.50	16.24 +/- 5.41	6.23 +/- 2.29	30.67 +/- 15.00	7.88 +/- 3.36	63.95 +/- 19.31

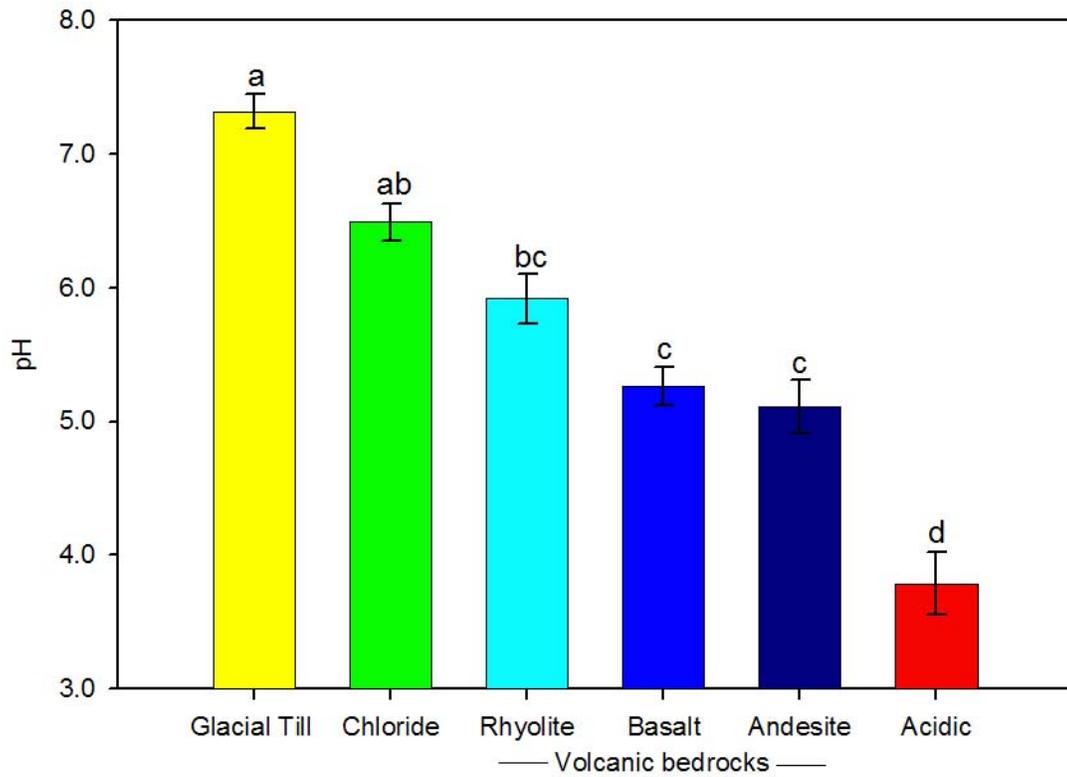


Fig. 8 Mean (± 1 SE) of groundwater pH by bedrock type. Different letters indicate significant differences (ANOVA, Tukey's HSD, $P < 0.05$).

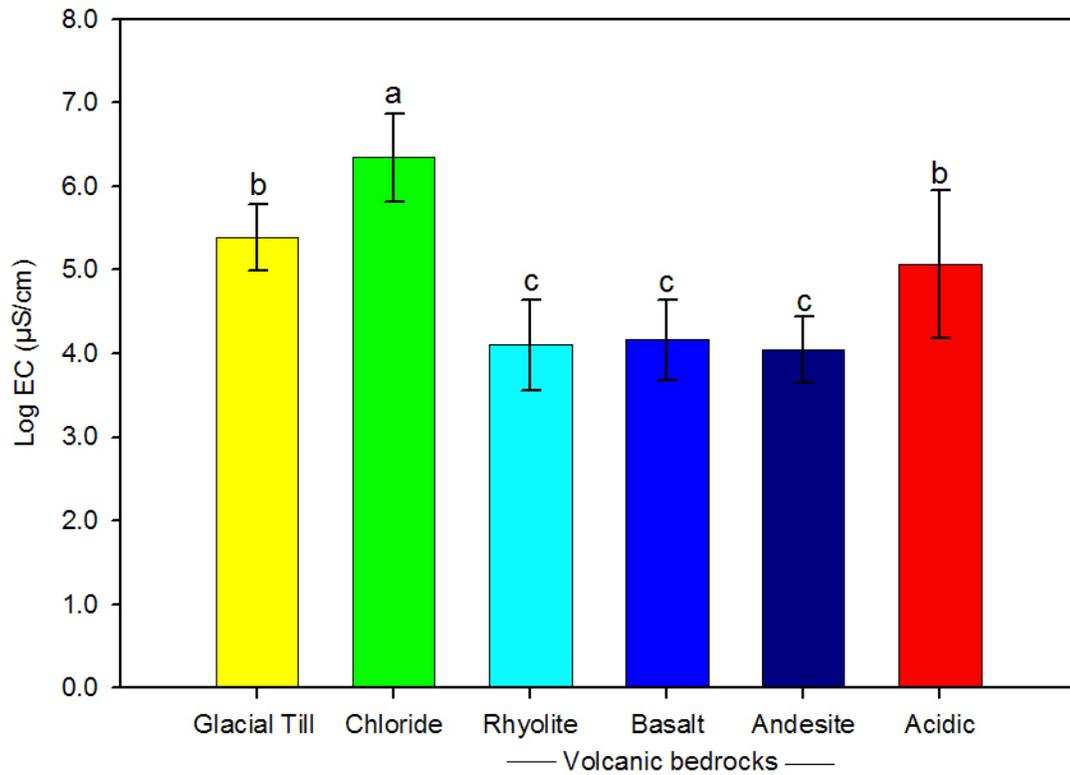


Fig. 9 Mean (± 1 SE) of groundwater EC (log scale) by bedrock type. Different letters indicate significant differences (ANOVA, Tukey's HSD, $P < 0.05$).

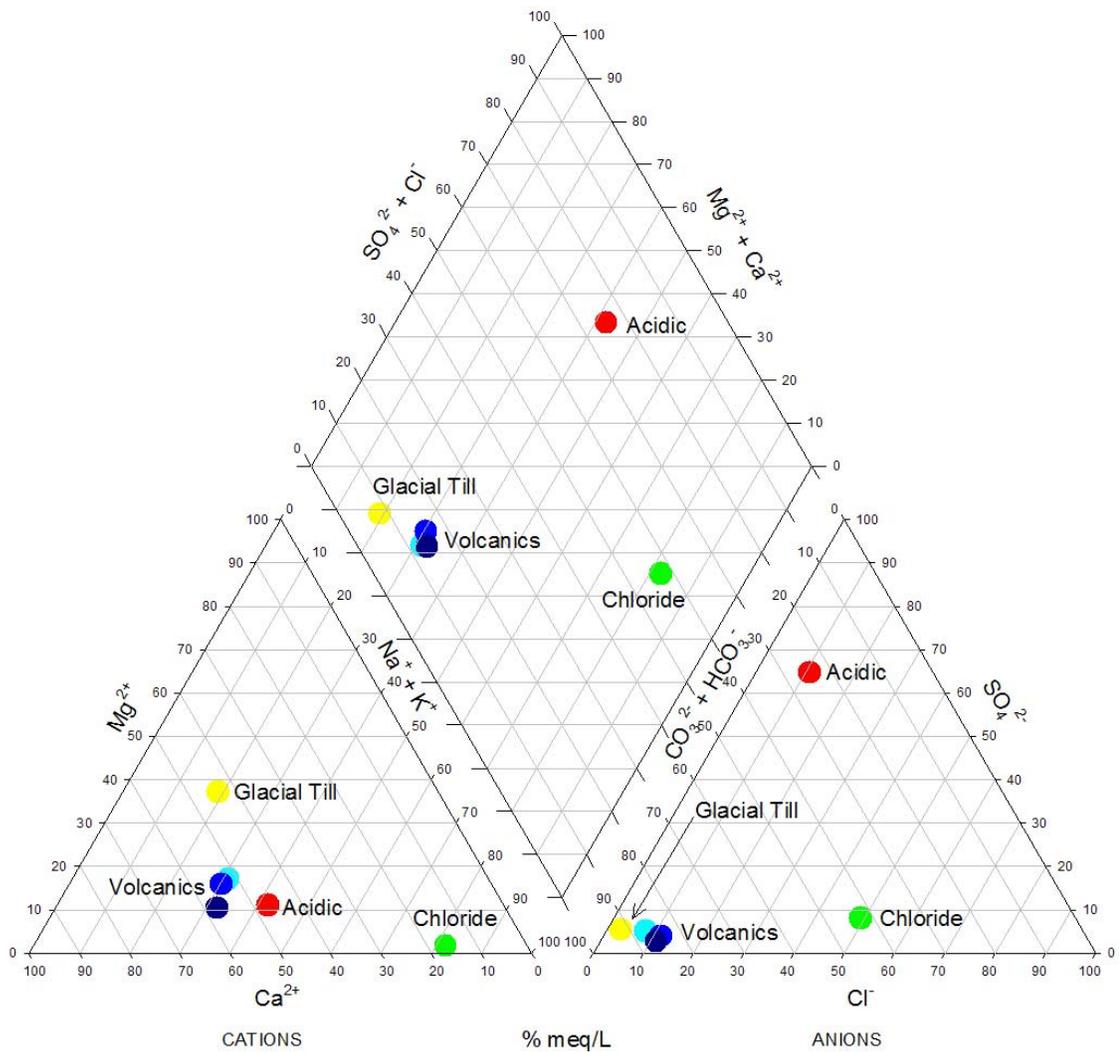


Fig. 10 Trilinear Piper diagram showing relative concentrations of major groundwater ions by bedrock type. Points are mean values shown in Table 3, presented as percent milliequivalents/liter (meq/L). Each bedrock type appears once in each plot. Lower left plot is cations, lower right plot is anions, upper plot is combined cations and anions.

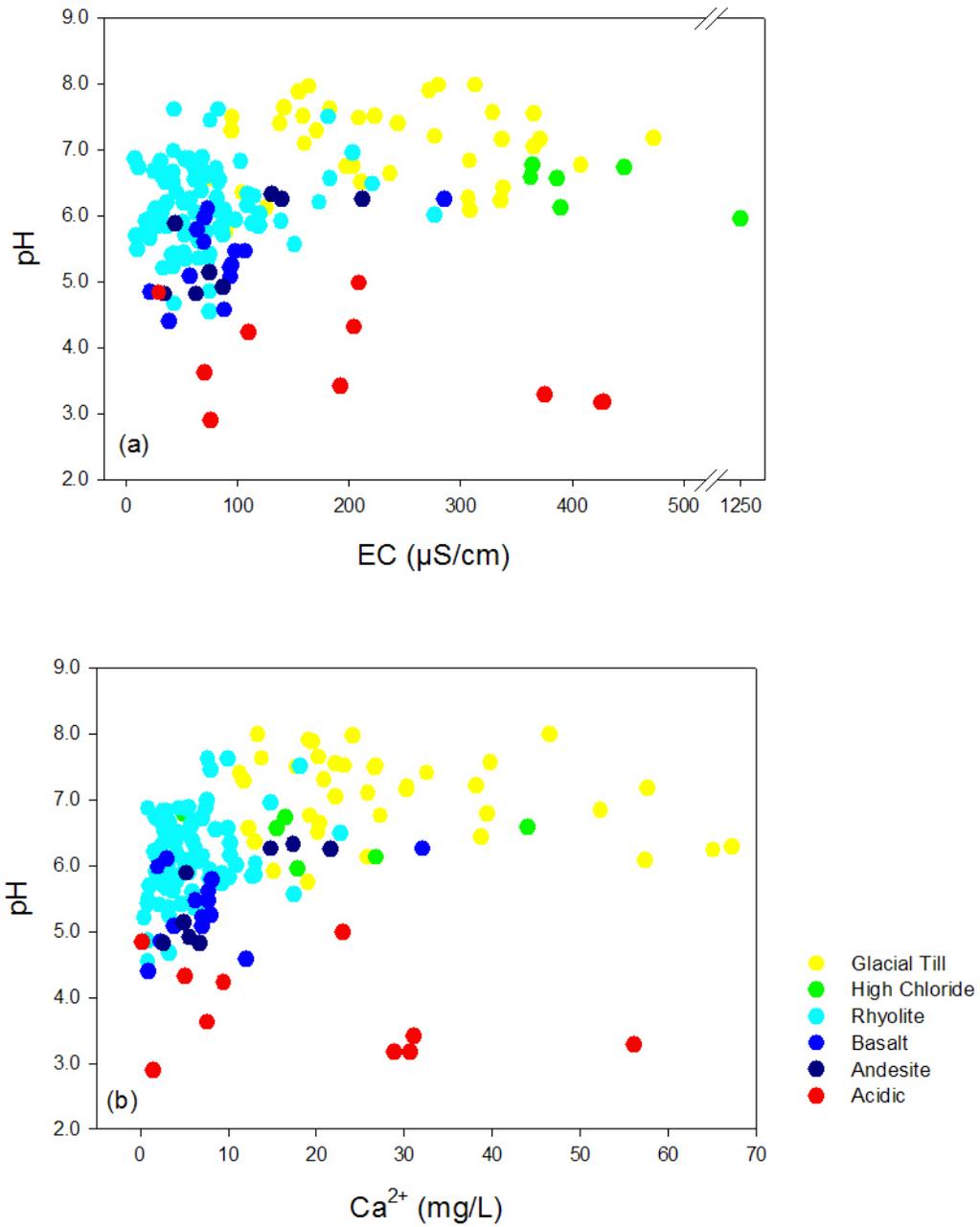


Fig. 11 Groundwater pH vs. (a) EC and (b) Ca^{2+} concentrations by bedrock type.

Table 4 Plant communities of YNP fens, organized by physiognomic group. Code = plant community code used elsewhere in this paper.

Group	Code	Plant Community
A. Semi-aquatic communities		
	A.1	<i>Eleocharis palustris</i> – <i>Utricularia minor</i>
	A.2	<i>Nuphar lutea</i> ssp. <i>polysepala</i> – <i>Potamogeton</i> spp.
	A.3	<i>Schoenoplectus acutus</i> var. <i>occidentalis</i> – <i>Carex utriculata</i>
	A.4	<i>Typha latifolia</i> – <i>Carex utriculata</i>
B. Floating mat communities		
	B.1	<i>Carex lasiocarpa</i> – <i>Potentilla palustris</i>
	B.2	<i>Carex limosa</i> – <i>Menyanthes trifoliata</i>
C. Large sedge communities		
	C.1	<i>Carex vesicaria</i> – <i>Carex aquatilis</i>
	C.2	<i>Carex utriculata</i> – <i>Galium trifidum</i>
	C.3	<i>Philonotis fontana</i> – <i>Carex utriculata</i>
D. Small sedge communities		
	D.1	<i>Calamagrostis canadensis</i> – <i>Plagiomnium cuspidatum</i>
	D.2	<i>Carex aquatilis</i> – <i>Carex urticulata</i>
	D.3	<i>Carex aquatilis</i> – <i>Pedicularis groenlandica</i>
	D.4	<i>Carex buxbaumii</i> – <i>Campyllum stellatum</i>
	D.5	<i>Carex livida</i> – <i>Drosera anglica</i>
	D.6	<i>Carex nebrascensis</i> – <i>Ptychostomum pseudotriquetrum</i>
	D.7	<i>Carex simulata</i> – <i>Epilobium palustre</i>
	D.8	<i>Eleocharis flavescens</i> var. <i>thermalis</i> – <i>Mimulus guttatus</i>
	D.9	<i>Eleocharis quinqueflora</i> – <i>Carex aquatilis</i>
	D.10	<i>Eleocharis quinqueflora</i> – <i>Muhlenbergia filiformis</i>
	D.11	<i>Eleocharis rostellata</i> – <i>Utricularia minor</i>
E. Shrub communities		
	E.1	<i>Salix boothii</i> – <i>Salix pseudomonticola</i>
	E.2	<i>Salix planifolia</i> – <i>Carex aquatilis</i>
	E.3	<i>Salix wolfii</i> – <i>Pentaphylloides floribunda</i>
F. Forested communities		
	F.1	<i>Picea (engelmannii, glauca)</i> – <i>Equisetum arvensis</i>
	F.2	<i>Pinus contorta</i> var. <i>latifolia</i> – <i>Aulacomnium palustre</i> – <i>Sphagnum warnstorffii</i>
G. Bryophyte communities		
	G.1	<i>Gymnocolea inflata</i> – <i>Drepanocladus polygamus</i>
	G.2	<i>Sphagnum</i> spp. – <i>Carex aquatilis</i>
	G.3	<i>Sphagnum russowii</i> – <i>Kalmia microphylla</i> – <i>Pinus contorta</i> var. <i>latifolia</i>

Table 5 Mean cover value and constancy class (II-V) for dominant and differential species by plant community. Species with low constancy (class I) are not shown in the table for readability. Plant community codes are those shown in Table 4.

Species	Semi-aquatic				Floating mat		Large sedge			Small sedge											Shrub			Forested		Bryophyte				
	A.1	A.2	A.3	A.4	B.1	B.2	C.1	C.2	C.3	D.1	D.2	D.3	D.4	D.5	D.6	D.7	D.8	D.9	D.10	D.11	E.1	E.2	E.3	F.1	F.2	G.1	G.2	G.3		
<i>Eleocharis palustris</i>	56.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.5/II	---	---	---	---	---	---	---	---	---	---	---		
<i>Utricularia minor</i>	6.4/II	6.7/V	1.5/II	1.8/III	---	---	---	---	---	---	---	---	---	2.0/II	2.5/II	---	---	2.6/II	---	10.0/III	---	---	---	---	---	---	---	---		
<i>Nuphar lutea</i> ssp. <i>polysepala</i>	---	20.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Potamogeton</i> spp.	2.1/II	6.7/IV	2.6/III	---	0.9/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Schoenoplectus acutus</i>	---	1.7/II	48.6/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Typha latifolia</i>	---	---	---	50.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Carex lasiocarpa</i>	---	---	---	---	46.7/V	---	---	---	---	---	---	---	---	1.7/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Potentilla palustris</i>	---	---	---	---	3.7/III	5.7/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Carex limosa</i>	---	---	---	---	---	39.5/V	---	---	---	---	---	---	---	2.0/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Menyanthes trifoliata</i>	---	0.3/II	---	---	2.0/II	14.5/IV	---	---	---	---	---	---	---	0.4/II	1.3/II	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Carex vesicaria</i>	---	---	---	---	---	---	50.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
<i>Carex utriculata</i>	---	---	6.2/V	5.8/V	3.4/IV	3.3/III	5.0/II	60.6/V	23.0/V	---	7.6/IV	1.9/II	2.0/IV	2.4/II	2.5/II	4.3/V	---	1.7/II	2.4/III	---	20.7/V	10.6/IV	9.9/V	14.1/III	3.5/III	---	---	0.8/II		
<i>Galium trifidum</i>	---	---	---	---	---	---	---	0.9/III	0.5/III	1.2/IV	0.6/III	1.6/IV	0.7/III	---	---	0.9/V	---	---	---	---	0.5/IV	1.2/IV	0.8/IV	1.2/IV	0.5/II	---	---	---		
<i>Philonotis fontana</i>	---	---	---	---	---	---	---	---	28.8/IV	---	---	1.2/II	---	---	3.8/III	---	2.5/II	---	5.5/III	---	---	---	---	---	---	---	---	---		
<i>Epilobium ciliatum</i>	---	---	---	---	---	---	---	0.4/II	6.5/V	---	---	---	---	0.8/IV	0.3/II	---	---	---	---	---	0.4/II	---	0.3/II	0.4/II	0.2/II	---	---	---		
<i>Plagiomnium cuspidatum</i>	---	---	---	---	---	---	---	6.4/II	9.7/IV	9.0/IV	5.0/II	5.8/II	---	---	2.5/II	11.6/II	---	---	---	---	18.1/IV	4.6/II	10.2/V	27.0/V	---	---	---	---		
<i>Symphyotrichum eatonii</i>	---	---	---	---	---	---	---	---	9.0/IV	---	---	---	---	---	---	---	1.8/III	---	---	0.6/IV	---	---	---	---	---	---	---	---		
<i>Calamagrostis canadensis</i>	---	---	---	---	---	---	1.3/III	---	---	46.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2.2/II	4.5/IV	5.8/III	0.2/II		
<i>Carex aquatilis</i>	---	---	---	2.8/III	1.3/II	0.9/II	2.4/IV	4.3/III	9.9/IV	14.0/IV	47.8/V	20.8/V	2.5/II	---	---	7.0/IV	---	6.1/IV	4.6/III	---	13.8/V	21.1/V	19.5/V	8.0/III	11.5/V	8.5/V	48.3/V	19.2/V		
<i>Pedicularis groenlandica</i>	---	---	---	---	---	---	---	---	---	---	---	4.8/V	1.1/III	1.4/III	0.3/II	---	---	0.7/II	---	---	0.4/II	1.4/III	1.6/IV	1.1/III	0.4/III	---	---	---		
<i>Packera subnuda</i>	---	---	---	---	---	---	---	---	---	---	---	4.6/IV	1.1/III	---	---	---	---	---	---	---	---	0.6/II	---	---	---	---	0.5/III	---		
<i>Aulacomnium palustre</i>	---	---	---	---	---	---	---	---	3.9/II	---	---	20.0/IV	---	---	---	---	---	---	---	---	5.0/II	13.4/III	17.3/IV	15.0/V	19.6/IV	---	---	---		
<i>Ptychostomum pseudotriquetrum</i>	---	---	---	---	3.6/II	---	---	1.2/II	4.8/II	26.0/II	4.6/II	10.4/IV	---	---	1.9/IV	4.1/II	---	3.3/II	4.9/II	---	3.1/II	5.5/III	6.8/III	---	3.2/II	---	---	---		
<i>Caltha leptosepala</i>	---	---	---	---	---	---	---	---	---	---	---	9.6/III	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Tomentypnum nitens</i>	---	---	---	---	---	---	---	---	---	---	---	8.8/II	---	---	5.0/II	---	---	---	---	---	---	5.3/II	7.4/II	2.6/II	---	---	---	---	---	
<i>Carex buxbaumii</i>	---	---	---	---	---	---	---	---	---	---	---	30.0/V	1.2/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Campyllum stellatum</i>	---	---	---	---	---	---	---	---	---	---	---	---	43.3/V	---	---	---	2.5/II	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Carex livida</i>	---	---	---	---	---	---	---	---	---	---	---	2.0/II	5.2/IV	28.8/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Drosera anglica</i>	---	---	---	---	---	4.4/II	---	---	---	---	---	---	4.1/IV	---	---	---	---	2.6/II	1.1/III	---	---	---	---	---	---	---	---	---		
<i>Eriophorum angustifolium</i>	---	---	---	---	---	---	0.3/II	---	---	---	---	2.0/II	1.3/III	3.9/III	0.5/II	---	---	1.0/II	1.3/II	---	---	1.2/II	---	---	0.5/II	---	---	---		
<i>Eleocharis tenuis</i> var. <i>borealis</i>	---	---	---	---	---	---	---	---	---	---	---	---	6.5/III	2.5/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Carex nebrascensis</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	50.0/V	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Calliergon giganteum</i>	---	---	---	---	---	---	---	---	---	---	2.7/II	---	---	---	12.5/II	6.9/II	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Carex simulata</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	63.8/V	---	---	---	---	9.4/IV	---	3.3/II	---	---	---	---	---		
<i>Epilobium palustre</i>	---	---	---	---	---	---	---	0.3/II	---	---	---	---	---	---	---	0.5/IV	---	---	---	---	0.4/III	0.4/III	0.2/II	0.4/III	0.2/II	---	---	---		
<i>Eleocharis flavescens</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	52.5/V	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Mimulus guttatus</i>	---	---	---	---	---	---	---	---	3.7/IV	---	---	---	---	---	0.3/III	---	12.5/IV	---	---	---	0.1/II	---	---	---	---	---	---	---		
<i>Eleocharis quinqueflora</i>	---	---	---	---	---	---	---	---	2.6/II	---	---	1.8/II	6.7/II	10.3/IV	5.0/III	---	1.3/II	37.6/V	18.9/V	3.8/III	---	2.9/II	---	---	2.5/III	---	---	---		
<i>Drepanocladus aduncus</i>	---	---	---	1.8/II	---	---	---	---	4.7/II	---	8.4/II	3.2/II	---	1.9/II	0.3/II	2.6/II	---	11.9/II	---	2.5/II	---	10.7/II	4.4/II	2.1/II	---	---	---	---		
<i>Scorpidium scorpioides</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	5.6/II	5.0/II	---	---	5.2/II	---	1.3/II	---	---	---	---	---	---	---	---	---	
<i>Muhlenbergia filiformis</i>	---	---	---	---	---	---	---	1.9/II	---	---	---	3.1/II	---	0.6/II	2.5/II	---	2.5/II	---	10.7/IV	---	1.4/II	2.6/II	---	---	2.8/II	---	---	---		
<i>Spiranthes romanzoffiana</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	0.3/II	---	---	---	---	0.7/IV	---	---	---	---	---	0.3/III	---	---	---		
<i>Triglochin maritimum</i> var. <i>elatum</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	1.5/III	0.4/III	---	2.5/II	1.9/II	4.4/III	1.8/III	---	---	---	---	---	---	---	---	---	
<i>Carex viridula</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1.3/II	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
<i>Eleocharis rostellata</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
<i>Salix boothii</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	15.6/V	---	---	---	---	---	---	---	---	
<i>Salix pseudomonticola</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	10.3/IV	---	---	---	---	---	---	---	---	
<i>Juncus balticus</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	7.3/IV	---	2.7/II	---	---	---	---	---	---	
<i>Equisetum laevigatum</i>	---	---	---	---	---	---	---	0.6/II	---	---	---	---	---	---	---	---	---	---	---	---	0.5/IV	---	---	---	---	---	---	---	---	
<i>Salix planifolia</i>	---	---	---	---	---	---	---	---	---	0.2/II	---	0.8/II	---	---	---	---	---	---	---	---	6.3/II	32.6/V	5.8/IV	0.5/II	2.5/IV	---	---	---		
<i>Salix wolfii</i>	---	---	---	---	---	---	---	1.3/II	---	---	---	1.2/II	---	---	---	---	---	---	---	---	---	6.0/IV	39.1/V	0.5/II	2.9/II	---	---	---		
<i>Pentaphylloides floribunda</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2.5/IV	---	6.8/III	0.9/II	4.1/II	---	---	---	---	
<i>Picea (engelmannii, glauca)</i>	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	36.0/V	2.1/II	---	---	---	---	
<i>Equisetum arvense</i>	---	---	---	---	---	---	---	---	---	---	---	1.4/II	---	---	---	---	---	---	---	---	0.3/III	---	---	28.2/V	2.					

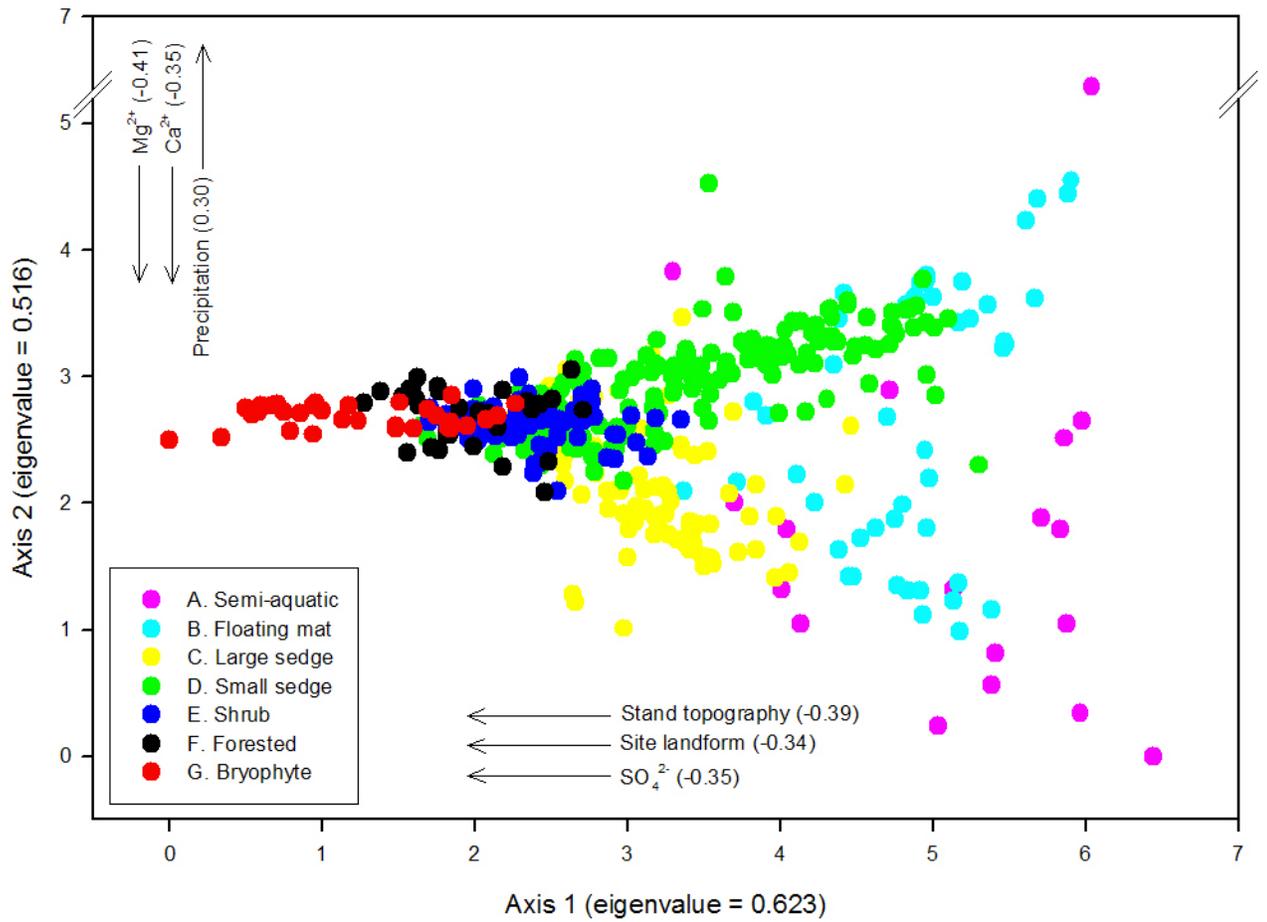


Fig. 12 DCA ordination performed using all species. Plot shows stand scores for axes 1 and 2. Stand symbols denote physiognomic groups shown in Table 4. Selected variables and Spearman's rank correlation coefficients are shown with arrows for each axis. See Table 6 for correlation coefficients of all variables.

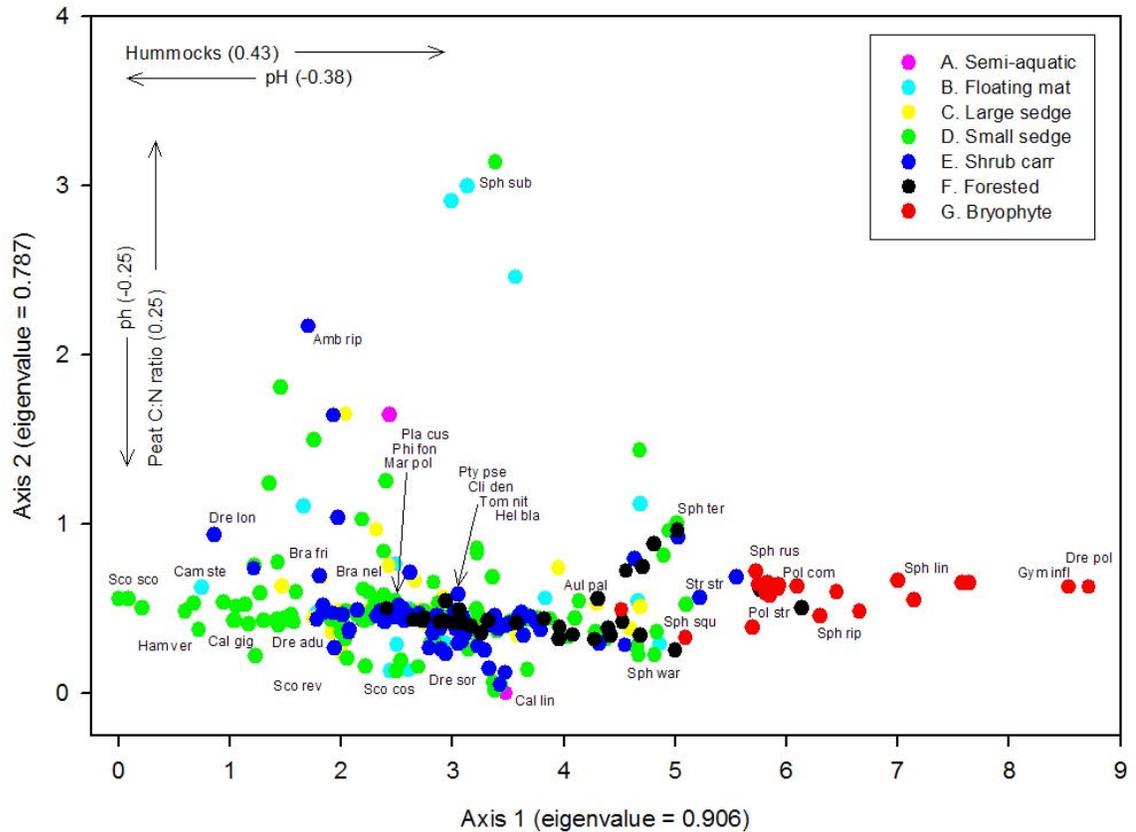


Fig. 13 DCA ordination performed using bryophytes. Plot shows stand scores and species centroids for axes 1 and 2. Stand symbols denote physiognomic groups shown in Table 4. Selected variables and Spearman's rank correlation coefficients are shown with arrows for each axis. See Table 6 for correlation coefficients of all variables. Species abbreviations are as follows: Amb rip = *Amblystegium riparium*, Amb var = *Amblystegium varium*, Aul pal = *Aulacomnium palustre*, Bra fri = *Brachythecium frigidum*, Bra nel = *Brachythecium nelsonii*, Cal cor = *Calliergon cordifolium*, Cal gig = *Calliergon giganteum*, Cal lin = *Calliergonella lindbergii*, Cam ste = *Campylium stellatum*, Cli den = *Climacium dendroides*, Dre adu = *Drepanocladus aduncus*, Dre lon = *Drepanocladus longifolius*, Dre pol = *Drepanocladus polygamus*, Dre sor = *Drepanocladus sordidus*, Gym inf = *Gymnocolea inflata*, Ham ver = *Hamatocaulis vernicosus*, Hel bla = *Helodium blandowii*, Mar pol = *Marchantia polymorpha*, Pal fal = *Palustriella falcatum*, Phi fon = *Philonotis fontana*, Pla cus = *Plagiomnium cuspidatum*, Pol com = *Polytrichum commune*, Pol str = *Polytrichum strictum*, Pty pse = *Ptychostomum pseudotriquetrum*, Sco cos = *Scorpidium cossonii*, Sco rev = *Scorpidium revolvens*, Sco sco = *Scorpidium scorpioides*, Sph lin = *Sphagnum lindbergii*, Sph rip = *Sphagnum riparium*, Sph rus = *Sphagnum russowii*, Sph squ = *Sphagnum squarrosum*, Sph sub = *Sphagnum subsecundum*, Sph ter = *Sphagnum teres*, Sph war = *Sphagnum warnstorffii*, Str str = *Straminergon stramineum*, Tom nit = *Tomentypnum nitens*

Table 6 Spearman's rank correlation coefficients of environmental variables with DCA sample scores on axes 1 and 2. DCA ordinations were performed using all species, vascular plants, and bryophytes. Variable abbreviations are given in Table 1. Highest three correlations in each column in bold and italics. Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$.

Variables	All species ($n = 476$ stands)		Vascular plants ($n = 476$ stands)		Bryophytes ($n = 387$ stands)	
	Axis 1 (EV = 0.623)	Axis 2 (EV = 0.516)	Axis 1 (EV = 0.667)	Axis 2 (EV = 0.579)	Axis 1 (EV = 0.906)	Axis 2 (EV = 0.787)
	PPT	0.24 ***	<i>0.30</i> ***	0.25 ***	0.28 ***	0.08
Snow	0.22 ***	0.28 ***	0.24 ***	0.27 ***	0.11 *	0.16 **
Elev	-0.22 ***	0.22 ***	-0.18 ***	0.25 ***	0.18 **	0.14 **
pH	0.04	-0.19 ***	-0.03	-0.24 ***	<i>-0.38</i> ***	<i>-0.28</i> ***
Temp	0.24 ***	0.21 ***	0.24 ***	0.20 ***	-0.12 *	-0.01
EC	-0.13 **	-0.29 ***	-0.16 **	-0.30 ***	-0.13 *	-0.12 *
Ca ²⁺	-0.17 **	<i>-0.35</i> ***	-0.23 ***	<i>-0.35</i> ***	-0.14 **	-0.21 ***
Mg ²⁺	-0.20 ***	<i>-0.41</i> ***	-0.26 ***	<i>-0.40</i> ***	-0.16 **	<i>-0.21</i> ***
Na ⁺	-0.07	-0.16 **	-0.09	-0.20 ***	-0.17 **	-0.13 **
K ⁺	0.01	0.05	0.04	0.02	-0.05	0.00
HCO ₃ ⁻	-0.05	-0.29 ***	-0.12 *	<i>-0.32</i> ***	<i>-0.28</i> ***	-0.21 ***
Cl ⁻	-0.08	-0.09 *	-0.09 *	-0.11 *	-0.08	0.00
SO ₄ ²⁻	<i>-0.35</i> ***	-0.20 ***	<i>-0.34</i> ***	-0.18 ***	0.08	0.03
Landform	<i>-0.34</i> ***	0.05	<i>-0.30</i> ***	0.02	-0.01	-0.11 *
StandTopo	<i>-0.39</i> ***	0.22 ***	<i>-0.35</i> ***	0.18 ***	0.01	-0.17 **
Hum	-0.32 ***	0.26 ***	-0.23 ***	0.29 ***	<i>0.44</i> ***	-0.03
Car	0.00	-0.05	-0.02	-0.03	0.16 **	0.12 *
Nit	0.09 *	-0.20 ***	0.03	-0.19 ***	-0.14 **	-0.14 **
C:N	-0.10 *	0.21 ***	-0.05	0.21 ***	0.27 ***	<i>0.24</i> ***
Peat	0.19 ***	-0.01	0.17 **	0.02	-0.03	0.07

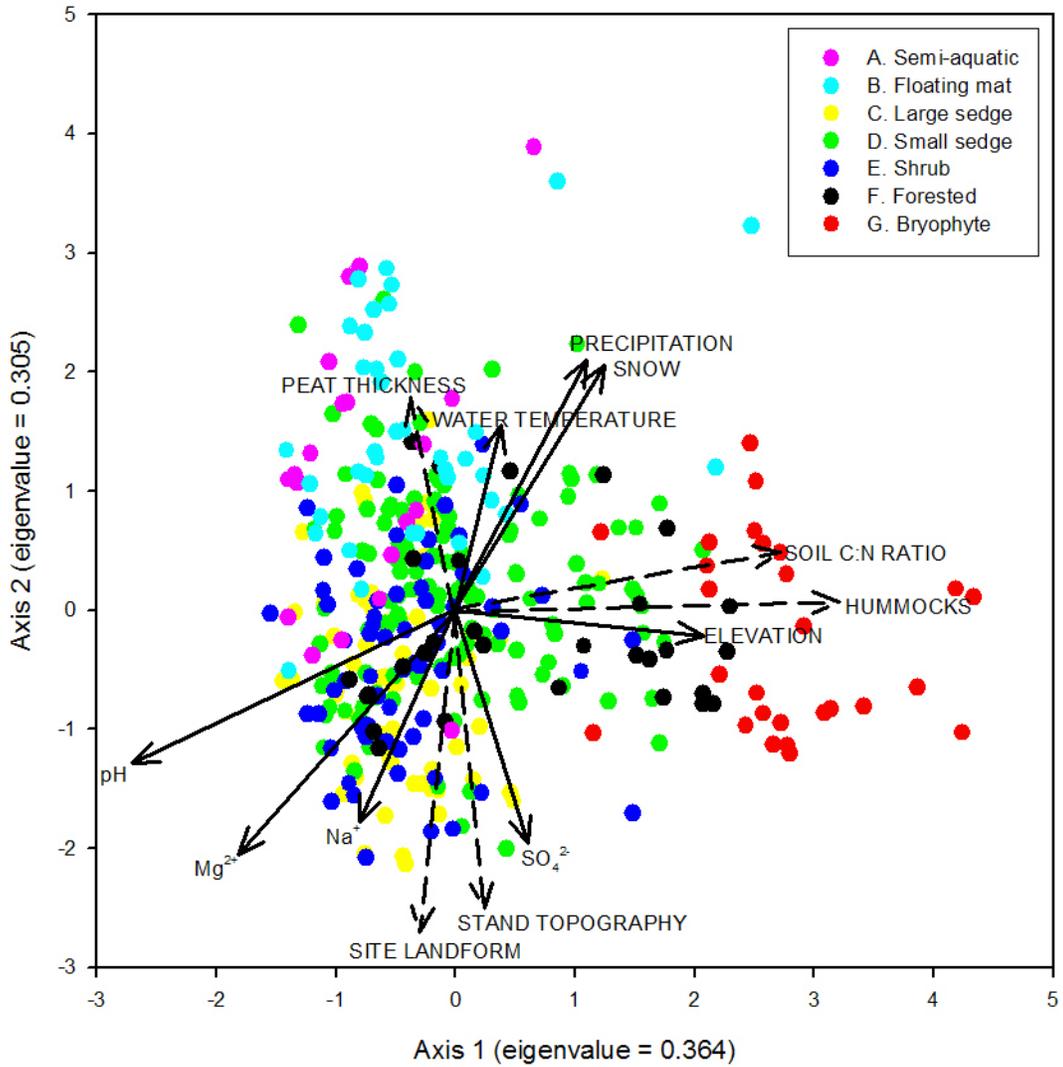


Fig. 14 CCA biplot of stand scores and environmental variables. Stand scores plotted are linear combinations of the environmental variables (LC scores). Stand symbols denote physiognomic groups shown in Table 4. Solid arrows represent regional gradients and dashed arrows represent local gradients. See Table 7 for inter-set correlations and canonical coefficients for all variables.

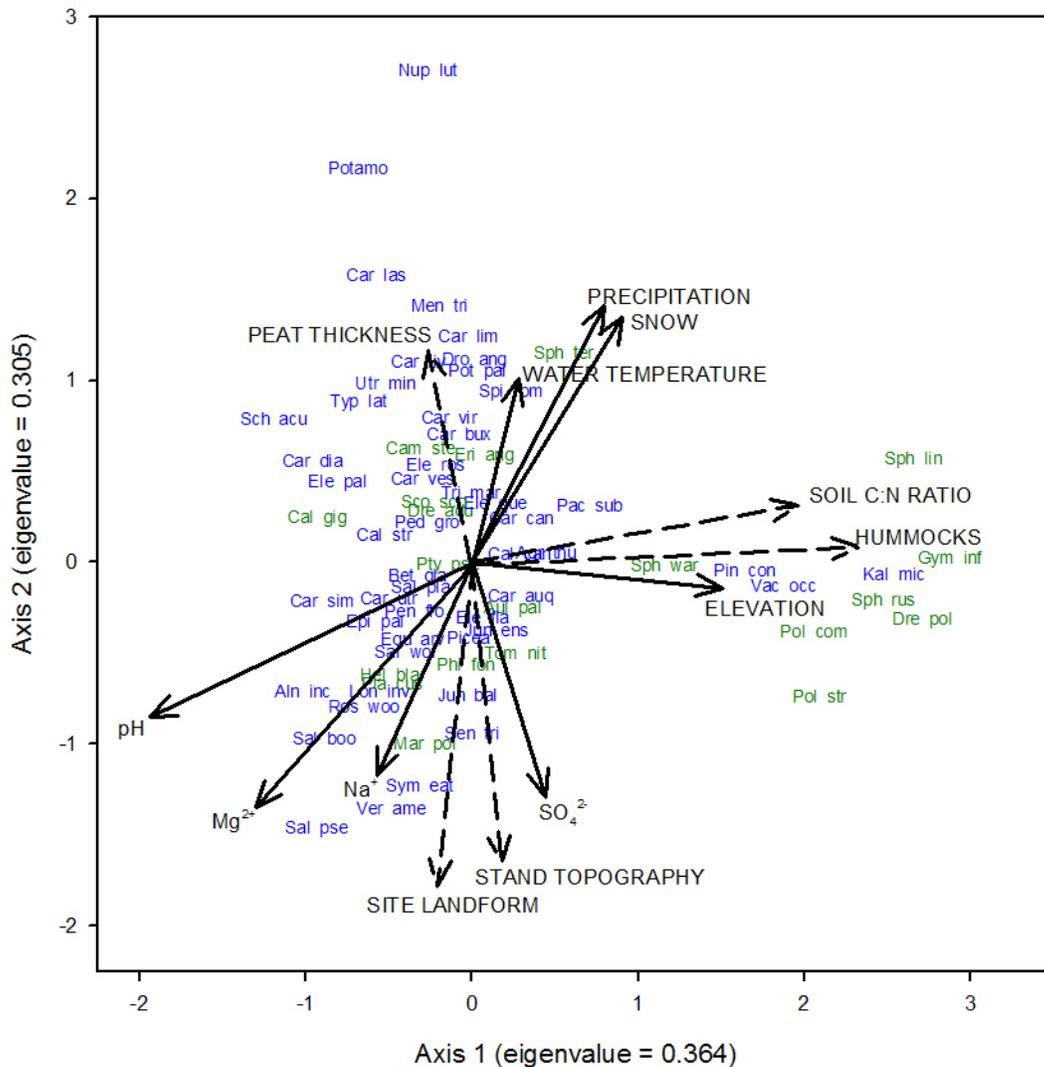


Fig. 15 CCA biplot of selected species centroids and environmental variables. Solid arrows represent regional gradients and dashed arrows represent local gradients. See Table 7 for inter-set correlations and canonical coefficients for all variables. Vascular species are in blue, bryophytes in green. Species abbreviations are the same as Fig. 13 for bryophytes and as follows for vascular plants: Agr thu = *Agrostis thurberiana*, Aln inc = *Alnus incana* var. *occidentalis*, Bet gla = *Betula glandulosa*, Cal can = *Calamagrostis canadensis*, Car auq = *Carex aquatilis*, Car bux = *Carex buxbaumii*, Car can = *Carex canescens*, Car dia = *Carex diandra*, Car las = *Carex lasiocarpa*, Car lim = *Carex limosa*, Car liv = *Carex livida*, Car sim = *Carex simulata*, Car utr = *Carex utriculata*, Car ves = *Carex vesicaria*, Car vir = *Carex viridula*, Dro ang = *Drosera anglica*, Ele fla = *Eleocharis flavescens* var. *thermalis*, Ele pal = *Eleocharis palustris*, Ele que = *Eleocharis quinqueflora*, Ele ros = *Eleocharis rostellata*, Epi pal = *Epilobium palustre*, Equ arv = *Equisetum arvense*, Eri ang = *Eriophorum angustifolium*, Jun bal = *Juncus balticus*, Jun ens = *Juncus ensifolius*, Kal mic = *Kalmia microphylla*, Lon inv = *Lonicera involucrata*, Men tri = *Menyanthes trifoliata*, Nup lut = *Nuphar lutea* ssp. *polysepala*, Pac sub = *Packera subnuda*, Ped gro = *Pedicularis groenlandica*, Pen flo = *Pentaphylloides floribunda*, Picea = *Picea* (*engelmannii*, *glauca*), Pin con = *Pinus contorta* var. *latifolia*, Potamo = *Potamogeton* sp., Ros woo = *Rosa woodsii*, Sal pla = *Salix planifolia*, Sal pse = *Salix pseudomonticola*, Sal wol = *Salix wolfii*, Sch acu = *Schoenoplectus acutus* var. *occidentalis*, Sen tri = *Senecio triangularis*, Spi rom = *Spiranthes romanoffiana*, Sym eat = *Symphytotrichum eatonii*, Tri mar = *Triglochin maritimum* var. *elatum*, Vac occ = *Vaccinium occidentale*, Ver ame = *Veronica americana*, Pot pal = *Potentilla palustris*, Typ lat = *Typha latifolia*, Utr min = *Utricularia minor*

Table 7 Intra-set correlations and canonical coefficients for environmental variables and CCA axes 1 and 2. Variable abbreviations are given in Table 1.

Variables	Intra-set correlations		Canonical coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
PPT	0.26	0.50	0.01	0.14
Snow	0.29	0.49	-0.05	0.21
Elev	0.49	-0.05	0.19	-0.46
pH	-0.65	-0.31	-0.21	-0.04
Temp	0.09	0.38	-0.01	0.24
Mg ²⁺	-0.44	-0.49	-0.11	-0.33
Na ⁺	-0.18	-0.32	-0.11	0.04
SO ₄ ²⁻	0.15	-0.47	0.20	-0.19
Landform	-0.07	-0.68	-0.07	-0.34
StandTopo	0.03	-0.61	0.14	-0.20
Hum	0.78	0.01	0.60	-0.14
C:N	0.64	0.12	0.34	0.11
Peat	-0.04	0.41	-0.08	0.23

Table 8 Test of significance and %TVE of individual environmental variables based on different subsets of the species data: all species, vascular plants, and bryophytes. *P* = significance probability of the constrained axis in CCA using the individual variable as the only constraining variable; calculated by Monte Carlo permutation test with 199 permutations (H_0 : influence of variable on the vegetation not significantly different from random, $P \leq 0.01$). EV = eigenvalue of the constrained axis. TVE = total variation explained, calculated as a sum of all constrained eigenvalues in a model using all environmental variables as constraining variables. %TVE = fraction of TVE associated with each variable. Asterisk (*) = variables included in the forward selection of each subset, used in Table 9.

Variable	All Species			Vascular plants			Bryophytes		
	<i>P</i>	EV	%TVE	<i>P</i>	EV	%TVE	<i>P</i>	EV	%TVE
A. Climate									
*PPT	0.005	0.162	9.3	0.005	0.159	10.2	0.005	0.197	7.9
*Snow	0.005	0.160	9.2	0.005	0.169	10.8	0.005	0.154	6.2
B. Elevation									
*Elev	0.005	0.169	9.8	0.005	0.174	11.1	0.005	0.184	7.4
C. Water chemistry									
*pH	0.005	0.219	12.6	0.005	0.169	10.8	0.005	0.436	17.6
*Temp	0.005	0.117	6.8	0.005	0.119	7.6	0.005	0.122	4.9
EC	0.005	0.158	9.1	0.005	0.162	10.4	0.005	0.186	7.5
Ca ²⁺	0.005	0.174	10.0	0.005	0.175	11.2	0.005	0.206	8.3
*Mg ²⁺	0.005	0.202	11.7	0.005	0.211	13.5	0.005	0.214	8.6
*Na ⁺	0.005	0.111	6.4	0.005	0.116	7.4	0.005	0.132	5.3
K ⁺	n.s.			n.s.			0.005	0.103	4.1
HCO ₃ ⁻	0.005	0.166	9.6	0.005	0.161	10.3	0.005	0.226	9.1
Cl ⁻	0.005	0.058	3.3	0.005	0.064	4.1	n.s.		
*SO ₄ ²⁻	0.005	0.143	8.3	0.005	0.129	8.3	0.005	0.229	9.2
D. Site landform									
*Landform	0.005	0.191	11.0	0.005	0.183	11.7	0.005	0.201	8.1
E. Stand topography									
*StndTopo	0.005	0.202	11.7	0.005	0.199	12.7	0.005	0.205	8.3
*Hum	0.005	0.265	15.3	0.005	0.253	16.2	0.005	0.337	13.6
F. Soil characteristics									
*Car	0.005	0.080	4.6	0.005	0.075	4.8	0.005	0.119	4.8
*Nit	0.005	0.112	6.5	0.005	0.101	6.5	0.005	0.182	7.3
*C:N	0.005	0.221	12.8	0.005	0.136	8.7	0.005	0.490	19.7
*Peat	0.005	0.101	5.8	0.005	0.096	6.1	0.005	0.130	5.2
TVE (all variables)		1.733			1.563			2.484	

Table 9 Variation within the species data (all species) explained by variable subsets. A = climate, B = elevation, C = groundwater chemistry, D = site landforms, E = stand topography and microtopography, F = soil characteristics. Variables included in each subset are those selected by forward selection, see Table 8. See Fig. 6 for an explanation of the components of variation.

Datasets		Variance (sum of EV and %TVE)											
Y	Z	Y		Z		Y Z		Y∩Z		Z Y		Y∪Z	
		EV	%	EV	%	EV	%	EV	%	EV	%	EV	%
Regional variables													
A	BCDEF	0.217	13.8	1.469	93.1	0.110	7.0	0.107	6.8	1.361	86.2	1.578	100.0
B	ACDEF	0.169	10.7	1.446	91.6	0.130	8.2	0.039	2.5	1.409	89.3	1.578	100.0
C	ABDEF	0.642	40.7	1.250	79.2	0.328	20.8	0.314	19.9	0.936	59.3	1.578	100.0
Local variables													
D	ABCEF	0.191	12.1	1.524	96.6	0.054	3.4	0.137	8.7	1.387	87.9	1.578	100.0
E	ABCDF	0.475	30.1	1.281	81.2	0.297	18.8	0.178	11.3	1.103	69.9	1.578	100.0
F	ABCDE	0.458	29.0	1.325	84.0	0.253	16.0	0.205	13.0	1.121	71.0	1.579	100.1
Regional vs. local													
ABC	DEF	0.886	56.1	0.935	59.3	0.643	40.7	0.243	15.4	0.692	43.9	1.578	100.0

Table 10 Vascular plants and bryophytes in YNP fens and their distribution along the poor–rich gradient in boreal and Rocky Mountain fens. Boreal species from Chee & Vitt (1989). Rocky Mountain species from Johnson & Steingraeber (2003). Asterisk (*) = boreal species also considered extreme rich fen indicators in Rocky Mountain.

	Poor fens	→	Rich fens	→	Extreme rich fens	YNP pH range
Common species of boreal fens						
Vascular plants						
<i>Scheuchzeria palustris</i>	-----					4.4 - 5.9
<i>Carex limosa</i>	-----					4.4 - 7.5
<i>Menyanthes trifoliata</i>	-----					4.4 - 7.6
<i>Eriophorum angustifolium</i>	-----					3.5 - 8.0
<i>Carex utriculata</i>	-----					3.4 - 8.0
<i>Carex lasiocarpa</i>	-----					4.4 - 8.0
<i>Potentilla palustris</i>		-----				4.4 - 8.0
<i>Epilobium palustre</i>		-----				3.4 - 8.0
<i>Carex flava</i>		-----				6.7 - 7.4
<i>Tofieldia glutinosa</i>			-----			5.5 - 7.6
<i>Parnassia palustris</i>				-----		6.1 - 8.0
<i>Carex diandra</i>				-----		6.2 - 7.6
* <i>Triglochin maritimum</i>				-----		4.6 - 7.6
* <i>Triglochin palustris</i>				-----		4.2 - 7.6
* <i>Carex microglochin</i>					-----	6.3 - 6.8
<i>Muhlenbergia glomerata</i>					-----	5.5 - 6.6
<i>Platanthera hyperborea</i>					-----	6.5
Bryophytes						
<i>Gymnocolea inflata</i>	-----					3.2 - 5.0
<i>Sphagnum lindbergii</i>	-----					3.4 - 5.2
<i>Sphagnum riparium</i>	-----					3.5 - 5.8
<i>Sphagnum fuscum</i>	-----					4.4 - 4.6
<i>Straminergon stramineum</i>	-----					4.3 - 6.6
<i>Tomentypnum nitens</i>		-----				4.8 - 7.6
<i>Sphagnum warnstorffii</i>		-----				4.2 - 6.9
<i>Sphagnum teres</i>			-----			3.3 - 6.7
<i>Ptychostomum pseudotriquetrum</i>			-----			3.4 - 8.0
<i>Calliergon giganteum</i>				-----		5.8 - 8.0
<i>Campylium stellatum</i>				-----		5.7 - 7.6
<i>Meesia triquetra</i>					-----	5.7 - 6.1
* <i>Scorpidium scorpioides</i>					-----	5.2 - 7.6
Additional extreme rich fen indicators for the Rocky Mountains						
Vascular plants and bryophytes						
<i>Eriophorum gracile</i>						4.0 - 6.2
<i>Carex viridula</i>						6.0 - 7.6
<i>Salix candida</i>			full range unknown			6.6 - 8.0
<i>Thalictrum alpinum</i>						7.1 - 7.4
<i>Carex scirpoidea</i>						not found
<i>Kobresia myosuroides</i>						not found
<i>Kobresia simpliciuscula</i>						not found
<i>Salix myrtilifolia</i>						not found
<i>Trichophorum pumilum</i>						not found
<i>Calliergon trifarium</i>						not found
<i>Scorpidium turgescens</i>						not found

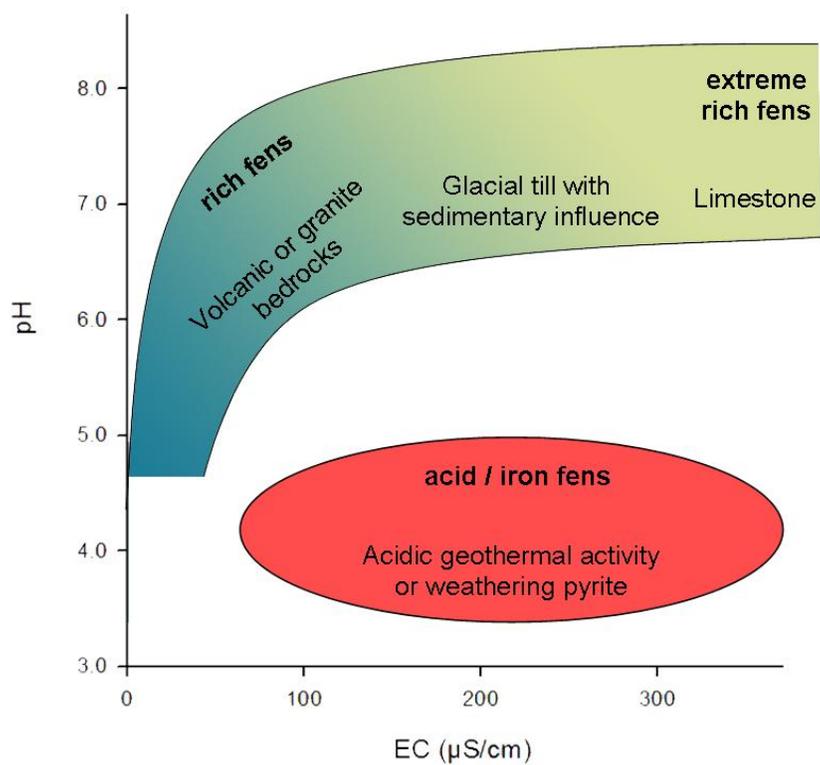


Fig. 16 Range of pH and EC for Rocky Mountain fens, determined by bedrock geology.

APPENDIX A: Key to the Plant Communities of YNP Fens

Appendix A: Key to plant communities of Yellowstone National Park fens

NOTE: Vegetation within fens is often a mosaic of hummocks and hollows, shrub margins and open sedge expanses. This classification strives to capture the range of plant communities found within YNP fens. For instance, hummocks are classified separately from hollows and water tracks. The spectrum of diversity, however, is difficult to fully capture and there are likely patches of vegetation that are not adequately described in this classification.

1. Stand dominated by herbs or bryophytes; if present, shrubs cover < 25% AND trees cover < 10% of the stand.....2
1. Stand with $\geq 25\%$ cover of shrubs OR $\geq 10\%$ cover of trees.....26
 2. Vegetation aquatic and dominated by the floating leaves of *Nuphar lutea* ssp. *polysepala*. Several other aquatic communities are possible in pools, ponds, and lakes within YNP fens, but *Nuphar lutea* ssp. *polysepala* is the most common and is the only aquatic community described in this classification.....
 -***Nuphar lutea* ssp. *polysepala* – *Potamogeton* spp. plant community (A.2)**
 2. Vegetation not aquatic, though may occur in > 20 cm of standing water.....3
3. *Schoenoplectus acutus* var. *occidentalis* abundant ($\geq 25\%$ cover) or appears to dominate the stand with continuous cover, possibly over a layer of *Carex* species.....
 -***Schoenoplectus acutus* var. *occidentalis* – *Carex utriculata* plant community (A.3)**
3. *Schoenoplectus acutus* var. *occidentalis* not abundant (< 25% cover).....4
 4. *Typha latifolia* abundant ($\geq 25\%$ cover).....
 -***Typha latifolia* – *Carex utriculata* plant community (A.4)**
 4. *Typha latifolia* not abundant (< 25% cover).....5
5. *Calamagrostis canadensis* dominates or co-dominates the herbaceous layer.....
 -***Calamagrostis canadensis* – *Plagiomnium cuspidatum* plant community (D.1)**
5. *Calamagrostis canadensis* does not dominate or co-dominate the herbaceous layer.....6
 6. Stand primarily composed of densely matted liverworts (*Gymnocolea inflata*), possibly with other bryophyte species intermixed; *Carex aquatilis* and/or *Eriophorum* species often present and may reach up to 30% cover; stand located on the edge of acidic pools in a fen influenced by geothermal activity.....
 -***Gymnocolea inflata* – *Drepanocladus polygamus* plant community (G.1)**
 6. Stand not primarily composed of densely matted liverworts; stand often with $\geq 25\%$ cover of herbaceous species, possibly over a dense layer of moss.....7

7. Individual cover of at least one species of *Eleocharis* \geq the individual cover of any other species of *Cyperaceae*; in some cases *Eleocharis* species may co-dominate with species of *Cyperaceae*, *Poaceae*, *Juncaceae*, or other herbaceous species.....8
7. Species of *Eleocharis* may be present, but no one species has individual cover \geq the individual cover of other species of *Cyperaceae*.....13
8. *Eleocharis palustris* abundant (\geq 25% cover); stand typically located in a shallow pond or other depressional area that experiences seasonal standing water.....
.....***Eleocharis palustris* – *Utricularia minor* plant community (A.1)**
8. *Eleocharis palustris* not abundant (< 25% cover).....9
9. *Eleocharis flavescens* var. *thermalis* is abundant (\geq 25% cover); stand small and located immediately surrounding an upwelling spring, possibly influenced by geothermal activity.....
.....***Eleocharis flavescens* var. *thermalis* – *Mimulus guttatus* plant community (D.8)**
9. *Eleocharis flavescens* var. *thermalis* is not abundant (< 25% cover).....10
10. *Eleocharis rostellata* abundant (\geq 25% cover).....
.....***Eleocharis rostellata* – *Utricularia minor* plant community (D.11)**
10. *Eleocharis rostellata* not abundant (< 25% cover).....11
11. Either *Eleocharis tenuis* var. *borealis* OR *Carex livida* well represented (cover > 10%); *Eleocharis quinqueflora* may have greater cover, but either one of these two species is a prominent component of the herbaceous layer.....
.....***Carex livida* – *Drosera anglica* plant community (D.05)**
11. Cover of both *Eleocharis tenuis* var. *borealis* AND *Carex livida* \leq 10%.....12
12. Stand located in a low area, such a hollow between hummocks, a water track, or other area where water is present at the soil surface; stand may contain a distinct bryophyte layer dominated by species tolerant of saturated or submerged conditions, such as *Drepanocladus* species or *Scorpidium* species; *Eleocharis quinqueflora* is the dominant graminoid or co-dominates with *Carex aquatilis*; stand generally not diverse but may contain up to 20% cover of *Drosera anglica*, *Triglochin maritimum* var. *elatum*, *Triglochin palustris*, or *Utricularia minor*.....
.....***Eleocharis quinqueflora* – *Carex aquatilis* plant community (D.9)**
12. Stand located on a hummock or other raised area and contains a distinct layer of bryophytes, most often dominated by *Aulacomnium palustre*, *Tomentypnum nitens*, or *Sphagnum warnstorffii*; *Eleocharis quinqueflora* is a prominent component of the herbaceous layer, but may not dominate; *Muhlenbergia filiformis* and/or *Agrostis thurberiana* commonly present and may be more abundant than *Eleocharis*

- quinqueflora*; herbaceous layer often diverse and may contain up to 20% cover of *Packera subnuda*, *Pedicularis groenlandica*, *Triglochin maritimum* var. *elatum*, *Tofieldia glutinosa* ssp. *montana*, or *Viola macloskeyi* ssp. *pallens*.....
.....***Eleocharis quinqueflora* – *Muhlenbergia filiformis* plant community (D.10)**
- 13.** *Carex utriculata* or *Carex aquatilis* dominates the herbaceous layer, or the two species co-dominate.....14
- 13.** Stand may contain *Carex utriculata* and/or *Carex aquatilis*, but one or more other species is more abundant than both *Carex utriculata* and *Carex aquatilis*.....18
- 14.** *Philonotis fontana* is a significant component of the bryophyte layer, typically \geq 25% cover; species richness high (generally $>$ 20 species) and stand includes \geq 5% cover of one or more of the following species: *Symphotrichum eatonii*, *Epilobium ciliatum*, *Mimulus guttatus*, *Senecio triangularis*; several other species of *Cyperaceae*, *Poaceae*, *Juncaceae* may be intermixed with *Carex utriculata* and *Carex aquatilis*; stand associated with a spring mound, seeping slope, or other spring-fed system.....***Philonotis fontana* – *Carex utriculata* plant community (C.3)**
- 14.** *Philonotis fontana* is not a significant component of the bryophyte layer; *Symphotrichum eatonii*, *Epilobium ciliatum*, *Mimulus guttatus*, *Senecio triangularis* are generally absent or with $<$ 5% cover.....15
- 15.** Cover of *Carex utriculata* $>$ cover of *Carex aquatilis*.....
.....***Carex utriculata* – *Galium trifidum* plant community (C.2)**
- 15.** Cover of *Carex utriculata* \leq cover of *Carex aquatilis*.....16
- 16.** Bryophyte layer generally \geq 75% cover and dominated by *Sphagnum* species (except *Sphagnum warnstorffii*) or *Polytrichum* species, and may contain small patches of the matted liverwort *Gymnocolea inflata*; site pH $<$ 5.0 and may show signs of acid geothermal activity. Couplet may be difficult to determine without knowledge of *Sphagnum* species or a pH meter.....
.....***Carex aquatilis* – *Sphagnum* spp. plant community (G.2)**
- 16.** Stand not as above; bryophyte layer dominated by a range of different species, including *Sphagnum warnstorffii*; site pH generally $>$ 5.0.....17
- 17.** *Carex aquatilis* dominates or co-dominates stand with \geq 25% cover; stand may be co-dominated by *Carex utriculata*, *Carex vesicaria*, *Carex diandra*, or *Calamagrostis stricta*; bryophyte layer dominated by species tolerant of saturated conditions, such as *Drepanocladus* species, *Plagiomnium cuspidatum*, or *Ptychostomum pseudotriquetrum*; stand with low species richness (generally $<$ 10 species) and herbaceous dicots not well represented.....***Carex aquatilis* – *Carex utriculata* plant community (D.2)**

17. <i>Carex aquatilis</i> generally with < 25% cover; stand may be co-dominated by <i>Agrostis thurberiana</i> , <i>Carex canescens</i> , <i>Carex illota</i> , <i>Deschampsia caespitosa</i> , or <i>Muhlenbergia filiformis</i> ; bryophyte layer dominated by <i>Aulacomnium palustre</i> , <i>Tomentypnum nitens</i> , or <i>Sphagnum warnstorffii</i> , but also may contain <i>Drepanocladus</i> species, <i>Plagiomnium cuspidatum</i> , or <i>Ptychostomum pseudotriquetrum</i> ; stand with higher species richness than the last (15–20 species) and up to 20% cover of the following herbaceous dicots: <i>Pedicularis groenlandica</i> , <i>Packera subnuda</i> , <i>Symphyotrichum foliaceum</i> , <i>Caltha leptosepala</i> , <i>Sedum rhodanthum</i> , or <i>Gentianopsis detonsa</i> var. <i>elegans</i>	
.....	<i>Carex aquatilis</i> – <i>Pedicularis groenlandica</i> plant community (D.3)
18. <i>Carex lasiocarpa</i> abundant (\geq 25% cover) or the most dominant graminoid.....	
.....	<i>Carex lasiocarpa</i> – <i>Potentilla palustris</i> plant community (B.1)
18. <i>Carex lasiocarpa</i> not abundant (< 25% cover).....	19
19. <i>Carex limosa</i> dominates or co-dominates the herbaceous layer; <i>Menyanthes trifoliata</i> generally present and may co-dominate.....	
.....	<i>Carex limosa</i> – <i>Menyanthes trifoliata</i> plant community (B.2)
19. <i>Carex limosa</i> does not dominate or co-dominates the herbaceous layer.....	20
20. <i>Carex vesicaria</i> abundant (\geq 25% cover).....	
.....	<i>Carex vesicaria</i> – <i>Carex aquatilis</i> plant community (C.1)
20. <i>Carex vesicaria</i> not abundant (< 25% cover).....	21
21. <i>Carex simulata</i> abundant (\geq 25% cover).....	
.....	<i>Carex simulata</i> – <i>Epilobium palustre</i> plant community (D.7)
21. <i>Carex simulata</i> not abundant (< 25% cover).....	22
22. <i>Carex nebrascensis</i> abundant (\geq 25% cover).....	
.....	<i>Carex nebrascensis</i> – <i>Ptychostomum pseudotriquetrum</i> plant community (D.6)
22. <i>Carex nebrascensis</i> not abundant (< 25% cover).....	23
23. <i>Carex buxbaumii</i> abundant (\geq 25% cover).....	
.....	<i>Carex buxbaumii</i> – <i>Campyllum stellatum</i> plant community (D.4)
23. <i>Carex buxbaumii</i> not abundant (< 25% cover).....	24
24. <i>Carex livida</i> abundant (\geq 25% cover).....	
.....	<i>Carex livida</i> – <i>Drosera anglica</i> plant community (D.05)
24. <i>Carex livida</i> not abundant (< 25% cover).....	25

25. *Eriophorum* species abundant ($\geq 25\%$ cover); *Carex aquatilis* typically present with at least 10% cover.....***Carex aquatilis* – *Carex utriculata* plant community (D.2)**
25. Not as described. There are many small patch communities that may not be adequately described in this classification. Please re-read the couplets and read the plant community descriptions to see if the community could possibly fit within a described community, otherwise the stand is an.....**Unidentified plant community**
26. Stand with $< 10\%$ tree cover.....27
26. Stand with $\geq 10\%$ tree cover, typically *Pinus contorta* var. *latifolia* or *Picea (engelmannii, glauca)*.....31
27. Cover of *Salix* species \geq than cover of Ericaceous shrubs, including *Kalmia microphylla*, *Ledum glandulosum*, or *Vaccinium occidentale*.....28
27. Cover of *Salix* species $<$ than cover of Ericaceous shrubs; stunted individuals of *Pinus contorta* var. *latifolia* may be present with low cover; stand located on a hummock or the fen margin adjacent to a forested area.....30
28. Individual cover of *Salix boothii*, *Salix pseudomonticola*, *Salix bebbiana*, or *Salix geyeriana* \geq the individual cover of *Salix planifolia* or *Salix wolfii*.....
.....***Salix boothii* – *Salix pseudomonticola* plant community (E.1)**
28. Individual cover of *Salix boothii*, *Salix pseudomonticola*, *Salix bebbiana*, or *Salix geyeriana* $<$ the individual cover of *Salix planifolia* or *Salix wolfii*.....29
29. Cover of *Salix planifolia* \geq cover of *Salix wolfii*.....
.....***Salix planifolia* – *Carex aquatilis* plant community (E.2)**
29. Cover of *Salix planifolia* $<$ cover of *Salix wolfii*.....
.....***Salix wolfii* – *Pentaphylloides floribunda* plant community (E.3)**
30. Bryophyte layer dominated by *Aulacomnium palustre* and/or *Sphagnum warnstorffii*; site pH > 5.0 and there is no sign of acidic geothermal activity.....
.....***Pinus contorta* var. *latifolia* – *Aulacomnium palustre* – *Sphagnum warnstorffii* plant community (F.2)**
30. Bryophyte layer generally $\geq 75\%$ cover and dominated by *Sphagnum russowii*, other *Sphagnum* species (except *Sphagnum warnstorffii*), or *Polytrichum* species; site pH < 5.0 and may show signs of acid geothermal activity. Couplet may be difficult to determine in the field without knowledge of *Sphagnum* species or a pH meter.....
.....***Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var. *latifolia* plant community (G.3)**

31. Tree canopy dominated by *Picea (engelmannii, glauca)*.....
.....***Picea (engelmannii, glauca)* – *Equisetum arvensis* plant community (F.1)**
31. Tree canopy dominated by *Pinus contorta* var. *latifolia*.....32
32. Bryophyte layer dominated by *Aulacomnium palustre* and/or *Sphagnum warnstorffii*; site pH > 5.0 and there is no sign of acidic geothermal activity.....
.....***Pinus contorta* var. *latifolia* – *Aulacomnium palustre* – *Sphagnum warnstorffii* plant community (F.2)**
32. Bryophyte layer generally >75% cover and dominated by *Sphagnum russowii*, other *Sphagnum* species (except *Sphagnum warnstorffii*), or *Polytrichum* species; site pH < 5.0 and may show signs of acid geothermal activity. Couplet may be difficult to determine in the field without knowledge of *Sphagnum* species or a pH meter.....
.....***Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var. *latifolia* plant community (G.3)**

APPENDIX B: Plant Community Descriptions

A. AQUATIC AND SEMI-AQUATIC COMMUNITIES

A.1: *Eleocharis palustris* – *Utricularia minor* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community occurs most often in shallow standing water in basin and gently sloping fens. Stands occur in rich fens where pH values are circumneutral, ranging from 5.5–7.6, and ion concentrations are variable. This community was found once within a fen influenced by neutral, high chloride geothermal activity (near Roaring Mountain) where EC was 1250 $\mu\text{S}/\text{cm}$, but all other stand had EC < 200 $\mu\text{S}/\text{cm}$. Peat thickness was generally < 100 cm. Average soil carbon was among the lowest for all plant communities (28.6%). Stands were surveyed throughout the park between 1950–2410 m (6400–7920 ft) elevation and received between 500–1500 mm of precipitation a year.

VEGETATION DESCRIPTION

Eleocharis palustris is the only constant in this plant community and can form dense stands (up to 80% cover). Species richness is low, on average only five species were recorded per relevé and all were vascular plants. *Utricularia minor* and *Potamogeton* species occur occasionally, but no other species were found in more than one sampled stand.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a stand of *Eleocharis palustris* with a thin organic horizon in his thermally influenced wetland type for central YNP, possibly similar to the one thermally influenced stand sampled in this study. Chadde *et al.* (1988) describe an equivalent *Eleocharis palustris* association for the northern range, though the description includes stands on mineral soil.

Rocky Mountains: *Eleocharis palustris* is a component of *Schoenoplectus lacustris* (= *acutus*) var. *acutus* stands at High Creek Fen in Colorado (Cooper 1996), but is not described as a separate community. *Eleocharis palustris* occurs in mineral soil wetlands throughout Colorado (Carsey *et al.* 2003).

Globally: *Eleocharis palustris* is a common wetland species throughout North America (Hultén 1964), but is not a major species in peatlands worldwide.

US NVC: The YNP plant community fits within *Eleocharis palustris* Herbaceous Vegetation (CEGL001833), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 5$): 49, 63, 145, 389, 481

A.2: *Nuphar lutea* ssp. *polysepala* – *Potamogeton* spp. plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Nuphar lutea* ssp. *polysepala* are common throughout YNP in shallow lakes and ponds with both organic and mineral bottom sediments. Stands were surveyed in the central volcanic plateau and in the southwestern Falls River Basin, though stands were encountered far more frequently than they were surveyed. Groundwater pH ranged from 4.4–6.4 and EC ranged from 10–93 $\mu\text{S}/\text{cm}$, though these ranges would likely be greater with more surveyed stands. Sampled elevations ranged from 1960–2450 m (6440–8040 ft) and mean annual precipitation ranged from 500–1250 mm/year. [See photos C and O in Appendix D.]

VEGETATION DESCRIPTION

This plant community is dominated by floating aquatic vegetation. Species richness is low, with only four species on average per relevé. *Nuphar lutea* ssp. *polysepala* is the most abundant species, though cover rarely exceeds 40%. *Potamogeton* species and *Utricularia minor* are both constant associates, and the rare *Schoenoplectus subterminalis* can occur in stands in Bechler Meadows. Other aquatic or emergent species may include *Menyanthes trifoliata*, *Schoenoplectus acutus* var. *occidentalis*, or *Sparganium emersum*. No bryophytes were found within relevés of this plant community.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Baker (1976) describes an equivalent community at Buckbean Fen, south of Lake Yellowstone. Mattson (1984) appears to include this community within the *Carex rostrata* (= *utriculata*) phase of his *Carex rostrata* – *Carex rostrata* habitat type for central YNP.

Rocky Mountains: Equivalent communities are described by Cooper (1990) for Rocky Mountain National Park and Cooper & Andrus (1994) for the Wind River Range in Wyoming.

Globally: A similar community occurs in Washington state (Kunze 1994). Otherwise, *Nuphar lutea* ssp. *polysepala* is not mentioned as a major component of peatlands worldwide, though *Nuphar* species are well represented throughout the northern hemisphere (Hultén 1970).

US NVC: The YNP plant community fits within *Nuphar lutea* ssp. *polysepala* Herbaceous Vegetation (CEGL002001), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 3$): 487, 493, 522.

A.3: *Schoenoplectus acutus* var. *occidentalis* – *Carex utriculata* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This community forms dense, tall stands in shallow standing water, primarily in rich basin fens. Water chemistry values were generally high in all surveyed stands; pH ranged from 5.5–7.6 and EC ranged from 107–387 $\mu\text{S}/\text{cm}$. Mean Ca^{2+} concentrations were 25 mg/L, the highest among plant communities. Peat thickness ranged from 60–240+ cm and mean soil carbon was 30.8%. Stands were sampled throughout the park at low to mid elevations, between 1950–2260 m (6380–7420 ft), where mean annual precipitation ranged from 500–1250 mm/year. [See photo L in Appendix D.]

VEGETATION DESCRIPTION

Stands are characterized by moderate to dense cover of *Schoenoplectus acutus* var. *occidentalis* (20–90% cover), which can exceed 2 m in height. Species richness is low; relevés contained only four species on average. *Carex utriculata* is a common associate, usually with low cover. *Potamogeton* species and *Utricularia minor* both occur occasionally. Stands of *Typha latifolia* can occur adjacent to this community and low cover of *Typha latifolia* can intermix with *Schoenoplectus acutus* var. *occidentalis*. No bryophytes occur with regularity.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a similar *Scirpus* (= *Schoenoplectus*) *acutus* association from the northern range.

Rocky Mountains: Stands of *Schoenoplectus acutus* var. *occidentalis* (referred to as *Scirpus acutus* or *Schoenoplectus lacustris* var. *acutus*) are described from Pine Butte Fen in north central Montana (Lesica 1986), Swamp Lake Fen in northern Wyoming (Fertig & Jones 1992; Heidel & Laursen 2003b), and High Creek Fen in South Park, Colorado (Cooper 1996). The three previously described sites are rich to extreme rich fens with high pH and high ionic concentrations, which matches the setting in YNP.

Globally: A similar community occurs in peatlands in Washington state (Kunze 1994). Otherwise, *Schoenoplectus acutus* is not a major species in peatlands worldwide, though it is common in mineral soil wetlands throughout North America (Hultén 1964).

US NVC: The YNP plant community fits within *Schoenoplectus acutus* Herbaceous Vegetation (CEGL001840), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 7$): 20, 27, 64, 229, 270, 501, 513.

A.4: *Typha latifolia* – *Carex utriculata* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This community occurs in the shallow standing water of basin fens throughout the park at low to mid elevations, 2100–2290 m (6900–7500 ft). In addition to shallow ponds, *Typha latifolia* stands can also occur within the wettest portions of spring complexes. Groundwater pH ranged from 5.9–7.5 and EC ranged from 81–387 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–240+ cm. Only one soil sample was taken within this community and had 21.0% carbon. Mean annual precipitation ranged from 500–1500 mm/year.

VEGETATION DESCRIPTION

Typha latifolia dominates this community with cover ranging between 40–80%. Low cover of *Carex utriculata* is very common. *Carex aquatilis*, *Calamagrostis stricta*, and *Utricularia minor* were all found in half of stands. In basin settings, stands contain few other species besides *Typha latifolia*. *Schoenoplectus acutus* var. *occidentalis* may occur in adjacent stands and may intergrade. In spring complexes, however, stand richness is higher and may include low cover of spring-fed species such as *Philonotis fontana* and *Mimulus guttatus*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a similar *Typha latifolia* association from the northern range.

Rocky Mountains: *Typha latifolia* is described from Swamp Lake Fen in northern Wyoming (Fertig & Jones 1992; Heidel & Laursen 2003b), but is not mentioned in other previous studies of Rocky Mountain fens. Though not common in peatlands, *Typha latifolia* is a widespread wetland community in Colorado (Carsey *et al.* 2003).

Globally: A similar community occurs in peatlands in Washington state (Kunze 1994). Otherwise, *Typha latifolia* is not a major species in peatlands worldwide, though it is common throughout North America (Hultén 1970).

US NVC: The YNP plant community fits within *Typha* (*latifolia*, *angustifolia*) Western Herbaceous Vegetation (CEGL002010), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 6$): 65, 91, 217, 227, 413, 469.

B. FLOATING MAT COMMUNITIES

B.1: Carex lasiocarpa – Potentilla palustris plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Carex lasiocarpa* occur throughout YNP, but are most frequent in Bechler Meadows where extensive basin fens dominate the landscape. This community can form large floating mats in lakes, the best example of which are in Robinson Lake, but also occurs in fens entirely filled with peat. Nearly all surveyed stands occurred on level topography in basin fens. *Carex lasiocarpa* can tolerate a wide range of water chemistry conditions. Groundwater pH ranged from 4.4–8.0. EC and ion concentrations were low in volcanic watersheds, but stands with high EC occur in northern areas of the park (such as Swan Lake Flats) where groundwater is influenced by sedimentary deposits and glacial till. Peat thickness ranges from 60–240+ cm and half of stands have peat ≥ 2 m thick. Mean soil carbon content is among the highest for plant communities, 35.7%. Elevation of sampled stands ranged from 1950–2450 m (6380–8040 ft) and mean annual precipitation ranged from 500–1500 mm/year. [See photo A in Appendix D.]

VEGETATION DESCRIPTION

Stands are typically large and have low species richness. On average, eight species were recorded per relevé, of which six were vascular plants. *Carex lasiocarpa* dominates stands with up to 80% cover and is typically the only vascular plant with $> 10\%$ cover. *Carex utriculata* is the most common associated species, followed by *Potentilla palustris*. In addition, the following species occur with low constancy: *Menyanthes trifoliata*, *Mentha arvensis*, *Potamogeton* species, *Calamagrostis stricta*, and *Carex aquatilis*. Floating mat stands can support a dense understory of *Sphagnum subsecundum*, *Sphagnum teres*, or hummocks of *Sphagnum fuscum*. In other locations, *Ptychostomum pseudotriquetrum*, *Drepanocladus aduncus*, and/or *Drepanocladus sordidus* comprise the bryophyte layer or bryophytes are absent. In Bechler Meadows, several rare species occur within this community, including *Dulichium arundinaceum*, *Eriophorum gracile*, *Lycopodiella inundata*, *Lysimachia thyrsiflora*, and *Scheuchzeria palustris*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Robinson Lake, which is dominated by *Carex lasiocarpa*, was included in Bursik's study of northeastern Rocky Mountain peatlands, but plant communities were not described (Bursik 1990).

Rocky Mountains: Heidel & Laursen (2003b) describe a similar community from the Shoshone National Forest in Wyoming. Chadde *et al.* (1998) describe an equivalent *Carex lasiocarpa* plant community from peatlands in the northern Rocky Mountains.

Carex lasiocarpa occurs within shrub stands at Pine Butte Fen in Montana, but does not form large stands as in YNP (Lesica 1986). Cooper & Jones (2004) describe two associations dominated by *Carex lasiocarpa* from the Kootenai National Forest in Montana: *Carex lasiocarpa* / “Brown Mosses” Herbaceous Peatland and *Carex lasiocarpa* / *Sphagnum* spp. Herbaceous Peatland. The two associations are distinguished by the bryophyte layer and water chemistry values. YNP contains stands equivalent to both described associations, but all *Carex lasiocarpa* stands in YNP are included in one plant community. Cooper & Jones (2004) also describe a *Dulichium arundinaceum* Herbaceous Peatland provisional association that includes low cover of *Carex lasiocarpa* and may be similar to a few stands in YNP at Robinson Lake.

Globally: *Carex lasiocarpa* is a widespread peatland species and is a component of minerotrophic fens in Washington state (Kunze 1994), the Sierra Nevada mountains of California (Cooper & Wolf 2006), northern Minnesota (Glaser *et al.* 1981), Canada (Slack *et al.* 1980; Chee & Vitt 1989; Vitt & Chee 1990), England and Wales (Wheeler 1980a; Wheeler 1980b), the Italian Alps (Gerdol *et al.* 1994), and Scandinavia (Sjörs 1950; Økland 1990). Chee & Vitt (1989) list *Carex lasiocarpa* as a species with a wide tolerance for water chemistry values. High water tables with either seasonal or semi-permanent flooding seem to be more important for the occurrence of *Carex lasiocarpa* stands than water chemistry.

US NVC: The YNP plant community fits within *Carex lasiocarpa* Herbaceous Vegetation (CEGL001810) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 27$): 40, 46, 66, 84, 101, 207, 297, 329, 447, 467, 470, 471, 476, 480, 482, 484, 486, 488, 489, 494, 496, 505, 506, 507, 508, 520, 521.

B.2: *Carex limosa* – *Menyanthes trifoliata* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community occurs most often on the edges of pools and small lakes where the rhizomes of *Carex limosa* form a solid mat extending over the water surface. Floating mats of this plant community appear to be an important successional stage of basin fens, filling in ponds and leading the way for other sedge species to establish. *Carex limosa* may also occur away from pond margins and in these instances is often co-dominated with other species of *Cyperaceae*. In YNP, this community occurs throughout the central volcanic plateau and in Bechler Meadows, but was not found in the northern range. Elevation of sampled stands ranged from 1980–2510 m (6500–8240 ft) and mean annual precipitation ranged from 500–1250 mm/year. Groundwater pH ranged from 4.4–7.5 and EC ranged from 10–212 $\mu\text{S}/\text{cm}$. Peat thickness almost always exceeds 120 cm and is \geq

240 cm in more than half of stands. Only one soil sample was taken from this community and it contained 47.6% organic carbon, indicating very little decomposition. [See photos C and O in Appendix D.]

VEGETATION DESCRIPTION

Carex limosa is the dominant species within this community (up to 80% cover), though *Menyanthes trifoliata* is nearly always present and can co-dominate. Species richness is low; relevés contains seven species on average, of which six were vascular plants. In some stands, *Potentilla palustris* and/or *Drosera anglica* have high cover (30–50% cover). Stands removed from the water's edge may contain up to 20% cover of *Carex utriculata*, *Carex aquatilis*, *Carex livida*, and/or *Eriophorum angustifolium*. The bryophyte layer may contain high cover of *Drepanocladus longifolius*, *Hamatocaulis vernicosus*, *Scorpidium scorpioides*, *Sphagnum teres*, *Sphagnum subsecundum*, or *Sphagnum squarrosum*, depending on location.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Baker (1976) describes a *Carex diandra* – *Potentilla palustris* type from Buckbean Fen that includes *Carex limosa* and *Menyanthes trifoliata*. The presence of *Carex diandra* in Buckbean Fen is an unusual variation of this *Carex limosa* – *Menyanthes trifoliata* plant community. Mattson (1984) describes a *Carex limosa* series from central YNP with one habitat type and two phases; all elements would be included within this plant community.

Rocky Mountains: Floating mat communities of *Carex limosa* are described from a range of fens throughout the Rocky Mountains by Lesica (1986), Cooper (1990), Cooper & Andrus (1994), Chadde *et al.* (1998).

Globally: Throughout the northern hemisphere, *Carex limosa* is a widespread peatland species, occurring across the range of water chemistry conditions from true bogs to rich fens (Chee & Vitt 1989). This community is consistently found in the wettest sections of peatlands, such as hollows, flarks, pond margins, and floating mats. *Carex limosa* is described from peatlands in the Sierra Nevada mountains of California (Cooper & Wolf 2006), the Great Lakes of Minnesota (Glaser *et al.* 1981), Canada (Vitt *et al.* 1975; Slack *et al.* 1980; Chee & Vitt 1989), Scandinavia (Sjörs 1950; Økland 1990), England and Wales (Wheeler 1980a; Wheeler 1980b), and the Italian Alps (Gerdol *et al.* 1994).

US NVC: The YNP plant community fits within *Carex limosa* Herbaceous Vegetation (CEGL001811) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 20$): 44, 67, 72, 76, 121, 122, 129, 131, 133, 134, 255, 334, 340, 363, 364, 367, 429, 430, 479, 483.

C. LARGE SEDGE COMMUNITIES

***C.1: Carex vesicaria – Carex aquatilis* plant community**

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Carex vesicaria* are occasional in areas with deep standing water in either basin or gently sloping fens. *Carex vesicaria* and *Carex utriculata*, both large-stature sedges, share similar ecological requirements, though *Carex vesicaria* is less common and can be distinguished by its tufted growth form and greatly enlarged perigynia. Surveyed stands occurred in rich fens, where pH ranged from 5.3–6.6 and EC ranged from 32–74 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 70–240+ cm and mean soil carbon was 33.1%. Surveyed elevations ranged from 2400–2490 m (7860–8160 ft) and mean annual precipitation ranged from 500–1250 mm/year.

VEGETATION DESCRIPTION

Stands of this community are dominated by moderate to high cover of *Carex vesicaria* (30–90% cover). Species richness is low; on average five species were record per relevé, of which four were vascular plants. Low cover of *Carex aquatilis* is common and *Carex utriculata*, *Calamagrostis canadensis*, or *Eriophorum angustifolium* may also occur in stands. No bryophytes occur with regularity.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes an equivalent *Carex vesicaria* series from central YNP.

Rocky Mountains: Stands dominated by *Carex vesicaria* have been documented in fens in the Shoshone and Medicine Bow National Forests of Wyoming (Heidel & Laursen 2003a; Heidel & Laursen 2003b; Heidel & Jones 2006).

Globally: A similar community occurs in peatlands in Washington state (Kunze 1994) and in the Sierra Nevada mountains of California (Cooper & Wolf 2006), but is not mentioned as a major peatland species worldwide.

US NVC: The YNP plant community fits within *Carex vesicaria* Herbaceous Vegetation (CEGL002661), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 5$): 146, 294, 298, 314, 318

C.2: *Carex utriculata* – *Galium trifidum* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Carex utriculata – *Galium trifidum* is the most commonly encountered community in YNP fens and is equally common in mineral soil wetlands. *Carex utriculata* is a large sedge capable of growing in deep standing water and can occupy areas of standing water in almost any fen. Most commonly, stands occur on flat topography, though occasionally stands were found on slopes up to 10 degrees. Water chemistry is not a defining characteristic of this community; pH ranged from 4.8–8.0 and EC ranged from 10–473 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–240+ cm and mean soil carbon was 30.1%. This plant community was surveyed in all regions of the park and at all elevations, between 1880–2710 m (6160–8880 ft). Mean annual precipitation spans the entire range of surveyed sites (350–1500 mm/year). [See photos D and L in Appendix D.]

VEGETATION DESCRIPTION

Stands typically have low richness (eight species per relevé, on average, of which seven were vascular plants) and can occur either as monotypic stands of *Carex utriculata* or with low cover of *Carex aquatilis*, *Galium trifidum*, *Epilobium ciliatum*, or *Epilobium palustre*. The bryophytes *Plagiomnium cuspidatum* and *Ptychostomum pseudotriquetrum* are commonly found within the thatch at the base of *Carex utriculata* culms. Over 100 species were recorded within stands of this community, but only the seven mentioned species occur with > 20% constancy.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Baker (1976) describes an equivalent *Carex utriculata* type from Buckbean Fen. Mattson (1984) describes a *Carex rostrata* (= *utriculata*) series for central YNP with several habitat types; most elements of his series would be included in this community, except where mentioned elsewhere in this document. Chadde *et al.* (1988) describe a *Carex rostrata* (= *utriculata*) association for the northern range with two phases: a *Carex rostrata* phase and a *Carex aquatilis* phases; both fall within this community, except where *Carex aquatilis* clearly co-dominates.

Rocky Mountains: *Carex utriculata* communities are described from a range of fens throughout the Rocky Mountains by Cooper (1990), Fertig & Jones (1992), Cooper & Andrus (1994), Chadde *et al.* (1998), Heidel & Laursen (2003a), and Heidel & Laursen (2003b). Like for other dominant sedge species, Cooper & Jones (2004) describe two *Carex utriculata* associations from the Kootenai National Forest in northern Montana: *Carex utriculata* / “Brown Mosses” Herbaceous Vegetation Peatland and *Carex utriculata* / *Sphagnum* spp. Herbaceous Vegetation Peatland. The two associations are distinguished by the bryophyte layer and water chemistry values. YNP contains stands

equivalent to both the described associations, but all *Carex utriculata* stands in YNP are included in this plant community.

Globally: Similar stands of *Carex utriculata* occur in peatlands in Washington state (Kunze 1994) and the Sierra Nevada Mountains of California (Cooper & Wolf 2006). Gignac *et al.* (2004) list *Carex utriculata* as a widespread peatland species in Canada that occurs across the water chemistry spectrum and typically in shallow standing water. In Europe, stands of the true *Carex rostrata* appear to have a similar ecological niche as North American *Carex utriculata* (Wheeler 1980a; Wheeler 1980b; Gerdol *et al.* 1994).

US NVC: The YNP plant community fits within *Carex utriculata* Herbaceous Vegetation (CEGL001562), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 63$): 6, 21, 35, 48, 50, 56, 57, 60, 68, 74, 79, 83, 88, 100, 102, 112, 127, 135, 144, 147, 156, 163, 164, 168, 174, 179, 180, 182, 196, 203, 208, 210, 228, 232, 237, 247, 252, 258, 271, 289, 290, 291, 317, 321, 322, 331, 362, 386, 415, 427, 431, 433, 436, 440, 451, 456, 458, 468, 497, 515, 517, 518, 519

C.3: *Philonotis fontana* – *Carex utriculata* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This herbaceous, spring-fed community occurs on steep slopes and spring mounds, the common habitat of *Philonotis fontana* (Vitt *et al.* 1988). Slope of sampled stands ranged from 2–25° and averaged 12°, the steepest average slope of all communities. Because it occurs on slopes, peat accumulation is generally < 120 cm and mean soil carbon was only 24.9%. Groundwater pH of surveyed stands ranged from 5.6–8.0 and EC ranged from 17–447 µS/cm. Stands were surveyed throughout the park, between 1800–2480 m (6160–8120 ft) elevation and 350–1250 mm/year mean annual precipitation. **[See photos E and F in Appendix D.]**

VEGETATION DESCRIPTION

This plant community is among the most diverse in YNP fens. On average, relevés contained 22 species, of which 19 were vascular plants. Steep slopes and spring mounds experience high rates of groundwater discharge, which oxygenate the soil, increase nutrient delivery rates, and allow for high species richness. *Carex utriculata* and *Carex aquatilis* are the most frequently occurring graminoids and can dominate the herbaceous layer. Other potential graminoids include *Juncus ensifolius*, *Agrostis scabra*, *Agrostis exarata*, *Muhlenbergia filiformis*, *Poa palustris*, *Carex luzulina* var. *ablata*, *Carex interior*, *Glyceris striata*, *Carex cusickii*, and *Carex neurophora*. Several herbaceous

dicots are frequent in this plant community, including *Symphyotrichum eatonii*, *Senecio triangularis*, *Veronica americana*, *Mimulus guttatus*, and *Epilobium ciliatum*. Beneath the vascular species, a lush carpet of bryophytes (up to 80% cover) dominated by *Philonotis fontana* blankets the ground surface and collects near flowing water. *Plagiomnium cuspidatum*, *Marchantia polymorpha*, *Helodium blandowii*, *Drepanocladus aduncus*, and *Ptychostomum pseudotriquetrum* are also common.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: This plant community appears to be similar to Mattson's (1984) *Carex rostrata* (= *utriculata*) – *Juncus ensifolius* habitat type from central YNP.

Rocky Mountains: No similar communities have been described from peatlands in the Rocky Mountains.

Globally: In a survey of fens in the Sierra Nevada mountains of California, Cooper & Wolf (2006) list several communities characterized by *Philonotis fontana* that may be similar to this community, but no descriptions are given.

US NVC: There are no equivalent associations within the NVC.

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 25$): 90, 92, 93, 95, 96, 150, 151, 158, 160, 166, 169, 176, 192, 193, 195, 197, 198, 231, 243, 300, 337, 343, 383, 385, 400

D. SMALL SEDGE AND GRASS COMMUNITIES

D.1: *Calamagrostis canadensis* – *Plagiomnium cuspidatum* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community was surveyed only five times in YNP. Four were part of basin fen complexes in the park's central volcanic plateau. The fifth stand was located on the margin of a large, gently sloping fen. *Calamagrostis canadensis* is a common wetland species in YNP, but occurs more frequently in mineral soil wetlands. Groundwater pH ranged from 5.3–6.6 and EC ranged from 51–363 $\mu\text{S}/\text{cm}$ in surveyed stands. Peat depth ranged from 60–240+ cm and the only soil sample contained 34.6% carbon. Stands were located between 2350–2420 m (7720–7940 ft) elevation, where mean annual precipitation was between 500–1000 mm/year.

VEGETATION DESCRIPTION

High cover (20–80% cover) of *Calamagrostis canadensis* characterizes this plant community and *Carex aquatilis*, *Carex canescens*, *Galium trifidum*, *Geum macrophyllum* var. *perincisum*, and *Viola macloskeyi* ssp. *pallens* are frequent associates. Stands contained ten species per relevé on average, of which eight were vascular plants. *Plagiomnium cuspidatum* has high constancy within this plant community and *Ptychostomum pseudotriquetrum*, *Brachythecium nelsonii*, *Sphagnum fimbriatum*, and *Calliergon cordifolium* all contributed high cover to one or more stands.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a *Calamagrostis canadensis* series from central YNP, but all habitat types in his series occur on mineral soil. *Calamagrostis canadensis* stands in YNP's fens may instead fall within the *Calamagrostis canadensis* phase of Mattson's *Carex rostrata* (= *utriculata*) – *Carex rostrata* habitat type.

Rocky Mountains: Cooper (1990) and Chadde *et al.* (1998) recognize *Calamagrostis canadensis* stands that occur within peatland complexes.

Globally: *Calamagrostis canadensis* is a common wetlands species throughout the northern hemisphere (Hultén 1964), but is not a major peatland species.

US NVC: The closest association in the NVC is *Calamagrostis canadensis* Western Herbaceous Vegetation (CEGL001559), which is a wide ranging community most often found on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 5$): 238, 295, 296, 299, 320

D.2: *Carex aquatilis* – *Carex utriculata* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Carex aquatilis* – *Carex utriculata* occur in wet areas of sloping and basin fens throughout the park and this is the second most common plant community sampled. Because *Carex aquatilis* is a common Rocky Mountain wetland species, this community occurs in a wide range of environmental conditions and can also occur on mineral soil. Stands were sampled across the entire elevation range, between 1880–2710 m (6160–8880 ft), and across the precipitation gradient (350–1500 mm/year). The only notable exception is that no *Carex aquatilis*-dominated stands were sampled in the park's southwest corner. Stands were found with a variety of water chemistry values; pH ranged from 3.4–7.6 and EC ranged from 22–447 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–240+ cm and mean soil carbon was 29.6%. [See photo G in Appendix D.]

VEGETATION DESCRIPTION

Carex aquatilis dominates stands of this community, typically with 50% or greater cover. Stands are moderately diverse, containing ten species on average, of which eight were vascular plants. *Carex utriculata* is commonly present and can co-dominate. Other common vascular species include *Galium trifidum*, *Viola macloskeyi* ssp. *pallens*, *Calamagrostis stricta*, *Symphyotrichum foliaceum*, *Carex canescens*, and *Senecio sphaerocephalus*. Brown mosses *Plagiomnium cuspidatum*, *Ptychostomum pseudotriquetrum*, and *Drepanocladus aduncus* are common and can have high cover.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a similar *Carex aquatilis* – *Carex aquatilis* habitat type from central YNP. Chadde *et al.* (1988) describe an equivalent *Carex aquatilis* association from the northern range.

Rocky Mountains: *Carex aquatilis* communities are described from fens throughout the Rocky Mountains by Lesica (1986), Cooper (1990), Cooper & Andrus (1994), Cooper (1996), Johnson (1996), Chadde *et al.* (1998), Heidel & Laursen (2003b), Johnson & Steingraeber (2003), and Heidel & Jones (2006). Stands are found across a wide range of water chemistry values.

Globally: A similar community occurs in peatlands in Washington state (Kunze 1994), though the dominant species is *Carex sitchensis* (= *aquatilis* var *dives*). *Carex aquatilis* occurs in peatlands throughout Canada in a wide range of conditions (Slack *et al.* 1980; Chee & Vitt 1989; Gignac *et al.* 2004). Throughout western North America, *Carex aquatilis* is a common wetland species, occurring on both organic and mineral soil, and its range extends throughout the northern hemisphere (Hultén 1964).

US NVC: The YNP plant community fits within *Carex aquatilis* Herbaceous Vegetation (CEGL001802) and *Carex aquatilis*–*Carex utriculata* Herbaceous Vegetation (CEGL001803), depending on the cover of *Carex utriculata*. The NVC differentiates stands with a clear dominance of *Carex aquatilis* from those co-dominated by the two species. Both NVC associations also include stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 40$): 14, 18, 39, 43, 45, 47, 82, 89, 98, 118, 123, 128, 137, 157, 200, 202, 212, 216, 230, 235, 244, 246, 248, 251, 264, 269, 274, 279, 292, 332, 355, 357, 359, 361, 369, 387, 419, 437, 450, 457

D.3: *Carex aquatilis* – *Pedicularis groenlandica* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community occurs in drier portions of sloping fens, such as hummocks, strings, or on the margins, where the soil may be saturated but not covered in standing water. All stands were located in rich fens of volcanic watersheds, where pH ranged from 4.9–6.9 and EC ranged from 21–183 $\mu\text{S}/\text{cm}$. Peat thickness was highly variable and ranged between 40–240+ cm. Mean soil carbon was 28.8%. Stands were sampled at mid to high elevations, from 2290–2710 m (7500–8880 ft), where mean annual precipitation ranged from 500–1500 mm/year. [See photo H in Appendix D.]

VEGETATION DESCRIPTION

Drier soil conditions allow for higher species richness; sampled stands contained 19 species per relevé on average, of which 15 were vascular plants. *Carex aquatilis* is a constant species, but contributes only 10–40% cover and is frequently mixed with *Deschampsia caespitosa*, *Carex canescens*, *Agrostis thurberiana*, *Eleocharis quinqueflora*, and/or other graminoids. Herbaceous dicots are an important component of stands. *Pedicularis groenlandica*, *Packera subnuda*, *Symphyotrichum foliaceum*, and *Galium trifidum* occur with high constancy and *Caltha leptosepala* and *Senecio sphaerocephalus* are also common. Higher elevation species such as *Carex illota* and *Sedum rhodanthum* reach their maximum in this community type. The bryophyte layer is typically dense. *Aulacomnium palustre*, and *Ptychostomum pseudotriquetrum* are the most common bryophyte species, but *Tomentypnum nitens* and *Sphagnum warnstorffii* can also contribute high cover.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a similar *Carex aquatilis* – *Pedicularis groenlandica* habitat type for central YNP.

Rocky Mountains: Though *Carex aquatilis* stands are documented from numerous fens throughout the Rocky Mountains (see *Carex aquatilis* – *Carex utriculata* plant community description above), only Cooper (1990) describes a similar *Carex aquatilis* – *Pedicularis groenlandica* community. Other descriptions lack adequate detail to determine if they are synonymous.

Globally: *Carex aquatilis* occurs in peatlands throughout Canada in a wide range of conditions (Slack *et al.* 1980; Chee & Vitt 1989; Gignac *et al.* 2004). Throughout western North America, *Carex aquatilis* is a common wetland species, occurring on both organic and mineral soil, and its range extends throughout the northern hemisphere (Hultén 1964).

US NVC: The YNP plant community likely fits within *Carex aquatilis* – *Pedicularis groenlandica* Herbaceous Vegetation (CEGL001804), but there is no description available to compare with the YNP stands (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 13$): 12, 260, 285, 311, 316, 339, 438, 442, 448, 449, 452, 453, 460

D.4: *Carex buxbaumii* – *Campyllum stellatum* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community was surveyed within the central volcanic plateau of the park on level to gently sloping topography. Stands clearly dominated by *Carex buxbaumii* are infrequent, but *Carex buxbaumii* is more often a component of other plant communities. Groundwater pH in sampled stands ranged from 5.7–7.5 and EC ranged from 30–181 $\mu\text{S}/\text{cm}$. Peat thickness ranged between 60–240+ cm and mean soil carbon was 22.5%. Stands were found at mid elevations, between 2210–2380 m (7260–7800 ft), in high precipitation regions (750–1500 mm/year).

VEGETATION DESCRIPTION

Carex buxbaumii is the dominant graminoid in this plant community, with cover ranging from 20–40%. Species richness is moderate; sampled stands had 16 species per relevé on average, of which 14 were vascular plants. *Viola macloskeyi* ssp. *pallens*, *Carex utriculata* and *Carex livida* are all frequent with low cover and other possible species include *Galium trifidum*, *Deschampsia caespitosa*, *Packera subnuda*, *Juncus ensifolius*, *Pedicularis groenlandica*, and *Eriophorum angustifolium*. *Campyllum stellatum* typically dominates the bryophyte layer.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Most elements within Mattson's (1984) *Carex buxbaumii* series for central YNP would be included in this community.

Rocky Mountains: It appears that *Carex buxbaumii*-dominated stands are rare throughout the Rocky Mountains. Chadde *et al.* (1998) mention *Carex buxbaumii* as a minor community type in the northern Rocky Mountains. Cooper & Jones (2004) only sampled one plot dominated by *Carex buxbaumii* in the Kootenai National Forest of Montana and did not describe the community in their report.

Globally: *Carex buxbaumii* is widespread throughout North America, but infrequent. According to the USDA PLANTS National Database, *Carex buxbaumii* is listed as sensitive, threatened, or endangered in at least nine states (USDA 2007).

US NVC: The YNP plant community fits within *Carex buxbaumii* Herbaceous Vegetation (CEGL001806) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 6$): 38, 70, 336, 404, 410, 516

D.5: *Carex livida* – *Drosera anglica* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community is found in the central volcanic plateau and is also one of the major communities in fens of the southwestern Falls River Basin. Stands occur on saturated soil in basin or gently sloping fens. Water chemistry values are characteristic of volcanic watersheds; pH ranged from 4.4–7.6 and EC ranged from 11–277 $\mu\text{S}/\text{cm}$. Peat thickness ranged between 40–240+ cm and mean soil carbon was 30.1%. Elevations of sampled stands ranged from 1960–2450 m (6400–8040 ft), and mean annual precipitation ranged from 500–1500 mm/year. [See photo B in Appendix D.]

VEGETATION DESCRIPTION

Carex livida is typically the dominant vascular species in this community, (typically 30–60% cover) but can co-dominate with either *Eleocharis quinqueflora* or *Eleocharis tenuis* var. *borealis*. *Drosera anglica* occurs with high constancy and can contribute up to 20% cover. Sampled stands had moderate species richness, with twelve species per relevé on average, of which ten were vascular plants. Common vascular associates *Pedicularis groenlandica*, *Eriophorum angustifolium*, *Triglochin maritimum* var. *elatum* are all characteristic of this plant community. *Scorpidium scorpioides* and *Drepanocladus aduncus* are the most common bryophytes and occur in pools of shallow standing water.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a *Carex livida* phase of the *Eleocharis pauciflora* (= *quinqueflora*) – *Carex aquatilis* habitat type for central YNP, which may be similar to this plant community.

Rocky Mountains: *Carex livida* is mentioned by Chadde *et al.* (1998) as a sensitive species often occurring within *Carex lasiocarpa* stands, but a separate *Carex livida* community type is not described.

Globally: A *Carex livida* / *Sphagnum* spp. community occurs in Washington State and may be similar to some stands found in YNP (Kunze 1994). Like *Carex buxbaumii*, *Carex livida* is circumpolar in distribution, but is not a common dominant in peatlands worldwide.

US NVC: There are no equivalent associations within the NVC. The closest associations in the NVC are *Carex (livida, utriculata)* / *Sphagnum* spp. Herbaceous Vegetation (CEGL003423) and *Trichophorum caespitosum* - *Carex livida* Herbaceous Vegetation (CEGL001842). Both types are peatland communities, but *Carex (livida, utriculata)* / *Sphagnum* spp. Herbaceous Vegetation is a community from poor fens and bogs in Washington State and *Trichophorum caespitosum* - *Carex livida* Herbaceous Vegetation is known only from three sites in Idaho (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 24$): 75, 77, 80, 104, 105, 259, 263, 286, 349, 401, 407, 409, 472, 473, 475, 477, 485, 490, 491, 495, 498, 499, 509, 511

D.6: *Carex nebrascensis* – *Ptychostomum pseudotriquetrum* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Carex nebrascensis – *Ptychostomum pseudotriquetrum* is a minor plant community in YNP fens. Stands were often associated with springs, seeps, and areas of neutral, high chloride geothermal activity. Water samples from all four surveyed stands had sub-neutral pH (5.6–6.7) and moderate to extremely high EC (88–1250 $\mu\text{S}/\text{cm}$). Peat thickness ranged from 40–240+ cm and the one soil sample collected contained 22.4% carbon. Surveyed stand occurred between 2100–2360 m (6900–7740 ft) and mean annual precipitation ranged from 500–1000 mm/year.

VEGETATION DESCRIPTION

Stands of this type are clearly dominated by *Carex nebrascensis* (30–80% cover), but can have high richness. On average, relevés included 18 species, of which 14 were vascular plants. Associated species typically have low cover and include *Agrostis scabra*, *Epilobium ciliatum*, *Eleocharis quinqueflora*, *Juncus ensifolius*, *Triglochin maritimum* var. *elatum*, *Deschampsia caespitosa*, *Agrostis thurberiana*, and *Mimulus guttatus*. Common bryophytes include *Ptychostomum pseudotriquetrum* and *Philonotis fontana*, also both with low cover.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: No similar communities have been described from YNP.

Rocky Mountains: No similar communities have been described from peatlands in the Rocky Mountains, though *Carex nebrascensis* is a recognized wetland plant community in Colorado, more often occurring on mineral soil (Carsey *et al.* 2003).

Globally: *Carex nebrascensis* is not a major peatland species worldwide.

US NVC: The YNP plant community fits within *Carex nebrascensis* Herbaceous Vegetation (CEGL001813), which includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 4$): 110, 234, 382, 391

D.7: *Carex simulata* – *Epilobium palustre* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Carex simulata* – *Epilobium palustre* were encountered most often on gentle slopes in the park's northern, low elevation drainages where precipitation is low and watersheds are influenced by glacial till. Elevations ranged from 1880–2450 m (6160–8040 ft) and mean annual precipitation ranged from 350–1250 mm/year, but most sites were located below 2300 m (7500 ft) and with 750 mm/year or less precipitation. Water chemistry values indicate rich fens; pH ranged from 5.5–8.0 and EC ranged from 68–372 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–240+ cm and mean soil carbon was among the highest for plant communities, 38.1%.

VEGETATION DESCRIPTION

Carex simulata is the clear dominant species within this community and typically occurs with high cover (30–90%). Species richness is moderate; on average relevés contained twelve species, of which nine were vascular plants. *Carex utriculata*, *Carex aquatilis*, *Deschampsia caespitosa*, and *Calamagrostis stricta* are all common associates and can

contribute up to 30% cover. *Epilobium palustre* and *Galium trifidum* frequently occur with low cover. Several bryophytes can occur with high cover, such as *Calliergon giganteum*, *Plagiomnium cuspidatum*, *Drepanocladus aduncus*, and *Amblystegium riparium*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a similar *Carex simulata* association for the northern range.

Rocky Mountains: In the Rocky Mountains, *Carex simulata* communities are described primarily from rich to extreme rich fens, such as Pine Butte Fen in Montana (Lesica 1986), Swamp Lake Fen in northern Wyoming (Fertig & Jones 1992; Heidel & Laursen 2003b), High Creek Fen in Colorado (Cooper 1996), and similar extreme rich fens in South Park, Colorado (Johnson & Steingraeber 2003). Chadde *et al.* (1998) describe *Carex simulata* stands as uncommon, but do not mention water chemistry values. Heidel & Laursen (2003a) describe *Carex simulata* stands from fens in the Medicine Bow National Forest in Wyoming, but do not give water chemistry values.

Globally: Fens dominated by *Carex simulata* occur in the Sierra Nevada mountains of California (Cooper & Wolf 2006). This species is widespread throughout western North America (USDA 2007).

US NVC: The YNP plant community fits within *Carex simulata* Herbaceous Vegetation (CEGL001825) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 16$): 1, 3, 15, 19, 52, 108, 111, 161, 184, 204, 293, 327, 335, 439, 463, 502

D.8: *Eleocharis flavescens* var. *thermalis* – *Mimulus guttatus* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This minor plant community occurs directly around the mouth of warm upwelling springs in close proximity to geothermal activity, primarily neutral, high chloride thermal areas. Water temperature of sampled stands ranged from 23–45°C, pH ranged from 5.5–7.1, and EC ranged from 72–508 $\mu\text{S}/\text{cm}$. Peat thickness is difficult to gauge, as stands occurred directly within the opening of spring, but surrounding areas had peat between 60–240+ cm thick. No soil samples were taken from this plant community. Elevations of surveyed stands ranged from 220–2380 m (7280–7800 ft) and mean annual precipitation ranged from 500–1250 mm/year.

VEGETATION DESCRIPTION

Only nine species were found within this plant community across four sampled stands, with an average of five species per stand. *Eleocharis flavescens* var. *thermalis* is the dominant species and grows in circular mats around springs with 30–70% cover. Accompanying species typically include *Mimulus guttatus*, *Agrostis scabra*, *Juncus brevicaudatus*, and *Symphyotrichum eatonii*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

All levels: No similar communities have been described from YNP, the Rocky Mountains, or peatlands worldwide.

US NVC: There are no equivalent associations within the NVC.

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 4$): 226, 239, 346, 384

D.9: *Eleocharis quinqueflora* – *Carex aquatilis* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Eleocharis quinqueflora* – *Carex aquatilis* occur in small to mid-sized patches in hollows and water tracks of many different fens where the water table is just above the surface. This is the third most common plant community sampled in the park and water chemistry characteristics are highly variable. Mean pH was 6.1, but pH ranged from 4.2–7.4 and EC ranged from 17–372 $\mu\text{S}/\text{cm}$. Within stands of this community, the water table is often 1–2 cm above the ground surface, in contrast to surrounding hummocks where the water table may be at or below the ground surface. Peat thickness ranges from 40–240+ cm and mean soil carbon was 30.5%. Stands were located between 1950–2570 m (6400–8440 ft) with mean annual precipitation between 400–1500 mm/year.

VEGETATION DESCRIPTION

This plant community generally supports only moderate cover of vascular plants and bare organic muck is often exposed. On average, relevés contained eight species, of which six were vascular plants. *Eleocharis quinqueflora* is the dominant vascular species (20–70% cover) and is frequently associated with low cover of *Carex aquatilis* (< 20% cover). In addition, *Eriophorum angustifolium*, *Carex utriculata*, *Pedicularis groenlandica*, *Triglochin maritimum* var. *elatum*, *Drosera anglica*, and *Utricularia minor* are occasional, but not common. The most common bryophyte species include *Drepanocladus aduncus*, *Scorpidium scorpioides*, and *Ptychostomum pseudotriquetrum*, but all occur with < 40% constancy.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes an *Eleocharis pauciflora* (= *quinqueflora*) series for central YNP with multiple habitat types and phases; most elements of the series would be considered part of this plant community, except where mentioned elsewhere in this document.

Rocky Mountains: *Eleocharis quinqueflora* communities are described for many different fens throughout the Rocky Mountains (Cooper 1990; Fertig & Jones 1992; Cooper & Andrus 1994; Cooper 1996; Johnson 1996; Chadde *et al.* 1998; Heidel & Laursen 2003a; Heidel & Laursen 2003b; Johnson & Steingraeber 2003; Heidel & Jones 2006). Stands contain a wide range of associated species depending on water chemistry. Cooper & Jones (2004) describe an *Eleocharis quinqueflora* – *Trichophorum ceaspitosum* / “Brown Mosses” Herbaceous Vegetation Peatland association from the Kootenai National Forest in Montana which appears to have similar characteristics, but is more specific than the YNP plant community and includes *Trichophorum ceaspitosum*, which is absent from the YNP flora.

Globally: Several *Eleocharis pauciflora* (= *quinqueflora*) communities are listed for fens in the Sierra Nevada of California (Cooper & Wolf 2006). *Eleocharis quinqueflora* is a widespread species at higher elevations in western North America, but is considered rare the eastern United States (USDA 2007). *Eleocharis quinqueflora* occurs in fens in England and Wales (Wheeler 1980a; Wheeler 1980b) and maybe widespread in other European peatlands.

US NVC: The YNP plant community fits within *Eleocharis quinqueflora* Herbaceous Vegetation (CEGL001836). Some stands from YNP have characteristics similar to *Carex* spp. - *Triglochin maritima* - *Eleocharis quinqueflora* Marl Fen Herbaceous Vegetation (CEGL002268), but the description includes several species not found in YNP and is considered to be restricted to North and South Dakota (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 36$): 9, 11, 13, 26, 31, 33, 41, 94, 115, 119, 148, 153, 225, 250, 257, 262, 275, 277, 282, 284, 308, 309, 315, 325, 338, 341, 345, 351, 352, 354, 356, 398, 402, 444, 445, 503

D.10: *Eleocharis quinqueflora* – *Muhlenbergia filiformis* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community occurs on hummocks and other raised areas in gently sloping and basin fens where the soil is saturated, but not flooded. Water chemistry values indicate that this plant community occurs in rich fens of volcanic and glacial till watersheds; pH

ranged from 5.1–7.6 and EC ranged from 18–366 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 50–240+ cm and mean soil carbon was 30.8%. Surveyed stands were found between 1880–2510 m (6160–8240 ft) elevation and with 400–1250 mm/year of precipitation.

VEGETATION DESCRIPTION

This plant community is one of the most diverse herbaceous dominated communities, with 21 species per relevé on average, of which 18 were vascular plants. Stands are characterized by a dense bryophyte layer (up to 100% cover), typically raised as a hummock. The hummocks themselves are most often dominated by *Aulacomnium palustre* and/or *Tomentypnum nitens* but may also contain high cover (up to 80%) of *Sphagnum teres*, *Sphagnum warnstorffii*, *Ptychostomum pseudotriquetrum*, or *Campylium stellatum*. Above the bryophyte layer, this community contains a diverse mix of herbaceous species dominated by *Eleocharis quinqueflora* and *Muhlenbergia filiformis*. Additionally, *Pedicularis groenlandica*, *Packera subnuda*, *Carex utriculata*, *Carex echinata*, *Viola macloskeyi* ssp. *pallens*, *Carex livida*, *Tofieldia glutinosa* ssp. *montana*, *Triglochin maritimum* var. *elatum*, and *Juncus ensifolius*, are frequently interspersed.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984)'s *Senecio cymbalaroides* (= *Packera subnuda*) phase of the *Eleocharis pauciflora* (= *quinqueflora*) – *Carex aquatilis* habitat type for central YNP may be similar to this plant community.

Rocky Mountains: Fertig & Jones (1992) describe extensive marl flats dominated by *Eleocharis quinqueflora* and *Triglochin maritimum* at Swamp Lake Fen in northern Wyoming that have a hummocky topography. The hummocks at Swamp Lake may match this community.

Globally: Several *Eleocharis pauciflora* (= *quinqueflora*) communities are listed for fens in the Sierra Nevada of California (Cooper & Wolf 2006). One or more of the Sierran communities may be similar to the YNP community, but no descriptions are given.

US NVC: There are no equivalent associations within the NVC. Stands in this plant community may fall into *Eleocharis quinqueflora* Herbaceous Vegetation (CEGL001836) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 22$): 16, 34, 42, 69, 71, 106, 120, 149, 150, 154, 191, 261, 344, 350, 399, 423, 474, 478, 492, 500, 512, 524

D.11: *Eleocharis rostellata* – *Utricularia minor* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Only four stands of this plant community were sampled in the park, all within the central volcanic plateau. *Eleocharis rostellata* can form large stands where the water table is just above the ground surface. Because it was sampled in few sites, the pH range is tight, from 6.1–6.6. EC ranged from 72–763 $\mu\text{S}/\text{cm}$. Water temperatures are often high, 22–38°C, and the stands can be located near neutral, high chloride geothermal activity. Peat thickness ranged from 50–150 cm and average soil carbon is low, 18.62%. Elevations of surveyed stands ranged from 2100–2380 m (6900–7800 ft) and mean annual precipitation ranged from 500–1500 mm/year.

VEGETATION DESCRIPTION

High cover (50–90%) of *Eleocharis rostellata* is constant in this community and is easily recognized by its tendency to bend in half and root at the tip. Stands contain few other species; on average seven species were found per relevé, of which six were vascular plants. Low cover (1%) of *Symphyotrichum eatonii* is the most frequent associate. *Utricularia minor* occurred in half of sampled stands with 10–30% cover floating in shallow water. Other possible vascular species include *Agrostis scabra*, *Triglochin maritimum* var. *elatum*, *Pedicularis groenlandica*, *Eleocharis quinqueflora*, and *Carex viridula*. Bryophytes *Scorpidium scorpioides*, *Drepanocladus aduncus*, and *Calliergon giganteum* were each found in one stand.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a similar *Eleocharis rostellata* association occurring in thermally warmed waters near Mammoth Hot Springs, though the community was not on organic soil.

Rocky Mountains: Chadde *et al.* (1998) mention *Eleocharis rostellata* as an uncommon type known from Montana and YNP. Heidel & Laursen (2003b) describe small patches of *Eleocharis rostellata* from Swamp Lake Fen in Wyoming.

Globally: *Eleocharis rostellata* is described as occurring adjacent to springs and other groundwater discharge areas in fens in the Midwestern United States (Amon *et al.* 2002), but is otherwise not mentioned as a major peatland species worldwide.

US NVC: The YNP plant community fits within *Eleocharis rostellata* Herbaceous Vegetation (CEGL003428), which also includes stands on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 4$): 109, 224, 347, 416

E. SHRUB COMMUNITIES

E.1: *Salix boothii* – *Salix pseudomonticola* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community occurs exclusively in northern valleys of the park, at low elevations and with low annual precipitation. Elevations of sampled stands ranged from 1180–2070 m (6160–6800 ft) and annual precipitation ranged from 350–450 mm/year. *Salix boothii* - *Salix pseudomonticola* stands are often associated with stands of *Carex simulata* – *Epilobium palustre*, but occur on steeper slopes where woody shrubs can develop. Water chemistry values indicate rich fens in glacial till watersheds; pH ranged from 6.8–8.0 and EC ranged from 142–366 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–120 cm and mean soil carbon was 35.7%.

VEGETATION DESCRIPTION

Salix boothii is the most common shrub dominant in this community, but other *Salix* species may be present or co-dominate, including *Salix pseudomonticola*, *Salix bebbiana*, *Salix geyeriana*, or *Salix planifolia*. The shrub strata typically cover 30–50% of stands. Species richness is high, with 23 species on average per relevé, of which 21 were vascular plants. *Carex utriculata*, *Carex aquatilis*, *Carex simulata*, and *Juncus balticus* are the most frequent dominant graminoids and *Deschampsia caespitosa*, *Festuca idahoensis*, and *Glyceria striata* also occur with low cover. Several herbaceous dicots are regularly found within this plant community, including *Viola macloskeyi* ssp. *pallens*, *Galium trifidum*, *Stellaria longifolia*, and *Epilobium palustre*, along with both *Equisetum laevigatum* and *Equisetum arvense*. *Plagiomnium cuspidatum* and *Ptychostomum pseudotriquetrum* are the most common bryophytes.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a *Salix geyeriana* / *Carex rostrata* (= *utriculata*) association from the northern range that includes cover of *Salix boothii* and *Salix bebbiana*.

Rocky Mountains: No similar communities have been described from peatlands in the Rocky Mountains.

Globally: No similar communities have been described from peatlands worldwide.

US NVC: The NVC includes several associations dominated by *Salix boothii*. Stands from this YNP plant community would be separated among the associations based on understory species. The most similar association is *Salix boothii* / Mesic Forbs Shrubland (CEGL001180), which occurs often on organic soils. Other similar associations include:

Salix boothii / *Carex utriculata* Shrubland (CEGL001178), *Salix boothii* / Mesic Graminoids Shrubland (CEGL001181), and *Salix (boothii, geyeriana)* / *Carex aquatilis* Shrubland (CEGL001176), but all three often occur as riparian communities on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 8$): 2, 4, 5, 17, 159, 170, 171, 173

E.2: *Salix planifolia* – *Carex aquatilis* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Salix planifolia* – *Carex aquatilis* occur throughout YNP in a range of conditions. This plant community can be found on level to gently sloping topography, where it is subject to seasonal standing water, or on steeper slopes and fen margins, where the mid-summer water table may drop below the ground surface. Stands were found throughout the elevation and climatic gradients and in watersheds dominated by glacial till, rhyolite, and andesite. Elevations of surveyed stands ranged from 1990–2570 m (6540–8440 ft) and mean annual precipitation ranged from 400–1500 mm/year. Groundwater pH ranged from 5.2–7.6 and EC ranged from 8–408 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–240+ cm and mean soil carbon was 33.0%. **[See photo J in Appendix D.]**

VEGETATION DESCRIPTION

Vegetation in this community is characterized by 40–80% cover of shrub species, a dense herbaceous understory, and an equally dense bryophyte layer. Species richness is high, with 21 species on average per relevé, of which 17 were vascular plants. *Salix planifolia* is the dominant shrub in this community and may be accompanied by up to 20% cover of *Salix wolfii*, *Betula glandulosa*, or *Pentaphylloides floribunda*. One stand included in this community contained high cover of the rare species *Salix candida*, which indicates high calcium groundwater. *Carex aquatilis* and *Carex utriculata* are the most frequent herbaceous dominants, though *Calamagrostis stricta*, *Carex simulata*, *Carex lasiocarpa*, and *Eriophorum chamissonis* may have high cover in individual stands. Common herbaceous dicots include *Galium trifidum*, *Viola macloskeyi* ssp. *pallens*, *Pedicularis groenlandica*, *Epilobium palustre*, *Symphyotrichum foliaceum*, and *Gentianopsis detonsa* var. *elegans*. The most common dominant bryophytes include *Aulacomnium palustre*, *Ptychostomum pseudotriquetrum*, and *Plagiomnium cuspidatum*, though many other species are possible.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Baker (1976) describes a *Calamagrostis* – *Salix* – *Sedum rodanthum* type from Buckbean Fen that would be included in this community. Mattson (1984) describes a *Carex aquatilis* / *Salix phylicifolia* (= *planifolia*) habitat type from central YNP that is similar to this community. Chadde *et al.* (1988) describes a minor *Salix candida* / *Carex rostrata* (= *utriculata*) association for the northern range that includes cover of *Salix planifolia* and would be included in this broader *Salix planifolia* plant community.

Rocky Mountains: *Salix planifolia* / *Carex aquatilis* communities are described from several Colorado and Wyoming peatlands (Cooper 1990; Cooper & Andrus 1994; Johnson 1996; Heidel & Laursen 2003a, Heidel & Laursen 2003b; Johnson & Steingraeber 2003; Heidel & Jones 2006). In the calcareous fens described, stands often contain *Salix candida*. *Salix planifolia* appears to be less common farther north into Montana. Some *Salix planifolia* individuals are found at Pine Butte Fen in Montana, but it is not a dominant community (Lesica 1986). Chadde *et al.* (1998) list *Salix planifolia* / *Carex aquatilis* as an uncommon type for the northern Rocky Mountains. Cooper & Jones (2004) do not describe a *Salix planifolia* association from the Kootenai National Forest in Montana; instead it appears that *Betula glandulosa* occupies the ecological niche in northern Montana. They do, however, describe a *Salix candida* / *Carex utriculata* Shrubby Peatland association that is similar to the *Salix candida*-dominated stands included in this plant community.

Globally: *Salix planifolia* occurs in fens in Alberta, Canada, but is not a major species (Chee & Vitt 1989). Stands dominated by *Betula* species appear to be more widespread worldwide in peatlands than *Salix*-dominated stands.

US NVC: The YNP plant community fits within *Salix planifolia* / *Carex aquatilis* Shrubland (CEGL001227), though individual stands may fall into other *Salix planifolia*-dominated associations based on understory species (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 35$): 36, 53, 78, 85, 86, 97, 99, 113, 116, 125, 126, 199, 254, 256, 268, 280, 283, 324, 330, 358, 388, 403, 405, 408, 412, 414, 418, 421, 422, 426, 428, 432, 434, 443, 446

E.3: *Salix wolfii* – *Pentaphylloides floribunda* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands of *Salix wolfii* – *Pentaphylloides floribunda* are similar to the equally common *Salix planifolia* – *Carex aquatilis* plant community, but occur more frequently in northern

areas of the park where precipitation is lower and water chemistry values are higher. This plant community occurs most often in sloping fens, with stand slopes ranging from 0–20°. Measured groundwater pH ranged from 4.8–8.0 and EC ranged from 43–447 µS/cm. Peat thickness ranged from 40–240+ cm and mean soil carbon was 36.3%. Elevations of surveyed stands ranged from 1900–2710 m (6240–8880 ft) and mean annual precipitation ranged from 400–1500 mm/year. [See photos I and L in Appendix D.]

VEGETATION DESCRIPTION

This diverse shrub community is dominated by *Salix wolfii* (10–80% cover), but may contain up to 40% cover of *Pentaphylloides floribunda* or up to 20% cover of *Salix planifolia* or *Betula glandulosa*. On average, sampled relevés contained 23 species, of which 20 were vascular plants. Like other willow communities in YNP, the understory is dominated by a mix of *Carex aquatilis* and *Carex utriculata*, but also may contain *Poa palustris*, *Carex simulata*, *Deschampsia caespitosa*, *Calamagrostis canadensis*, *Bromus ciliatus*, and *Juncus balticus*. Common herbaceous dicots include *Symphyotrichum foliaceum*, *Galium trifidum*, *Viola macloskeyi* ssp. *pallens*, *Pedicularis groenlandica*, *Gentianopsis detonsa* var. *elegans*, *Fragaria virginiana*, *Geum macrophyllum* var. *perincisum*, *Angelica pinnata*, and *Epilobium palustre*. The most common bryophytes are *Plagiomnium cuspidatum*, *Aulacomnium palustre*, *Ptychostomum pseudotriquetrum*, and *Tomentypnum nitens*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a *Salix wolfii* / *Carex aquatilis* habitat type that is similar to this plant community. Mattson states this habitat type does not occur in fens, but shows soil data indicating stands had organic layers up to 50 cm thick. Chadde *et al.* (1988) describe a similar *Salix wolfii* / *Carex aquatilis* association for the northern range.

Rocky Mountains: Chadde *et al.* (1998) describe a *Salix wolfii* / *Carex aquatilis* community type from the northern Rocky Mountains, but mention that it is a minor type in Idaho and Montana.

Globally: No similar communities have been described from peatlands worldwide. *Salix wolfii* occurs primarily within the Rocky Mountain states and extending into Oregon, but is not a widespread species throughout North America (USDA 2007).

US NVC: The NVC includes several associations dominated by *Salix wolfii*. Stands from this YNP plant community would be separated among the associations based on understory species. The most similar association is *Salix wolfii* / *Swertia perennis* - *Pedicularis groenlandica* Shrubland (CEGL001242), which occurs on organic soil in sloping fens in Idaho, but that association is limited in its geographic range. Other similar

associations include: *Salix wolfii* / *Carex aquatilis* Shrubland (CEGL001234), *Salix wolfii* / *Carex utriculata* Shrubland (CEGL001237), *Salix wolfii* / *Calamagrostis canadensis* Shrubland (CEGL002064), but all three often occur on mineral soil (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 33$): 22, 23, 29, 30, 51, 54, 55, 73, 87, 114, 162, 175, 181, 201, 205, 206, 209, 211, 213, 233, 245, 249, 253, 267, 272, 323, 328, 435, 441, 454, 455, 461, 462

F. FORESTED COMMUNITIES

F.1: *Picea (engelmannii, glauca) – Equisetum arvensis* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This forested community was sampled only in the northern valleys of the Lamar and Yellowstone Rivers and only in watersheds influenced by sedimentary deposits or glacial till. Stands occur in gently sloping fens, where cold ground water springs discharge to the surface. Average water temperature is 11° C, the coldest among the classified plant communities. Water chemistry values indicate rich fens; pH ranged from 6.1–7.5 and average pH was 7.1. EC values ranged from 95–244 µS/cm. Peat thickness ranged from 40–240+ cm and average soil carbon was 35.0%. Sampled stands ranged from 1960–2280 m (6440–7480 ft) elevation and received 400–1000 mm of precipitation per year.

[See photos K and L in Appendix D.]

VEGETATION DESCRIPTION

This plant community is the most species rich within YNP fens (on average 36 species per relevé, of which 31 were vascular plants) and supports the highest canopy cover of trees (up to 50% cover). Either *Picea engelmannii*, *Picea glauca*, or hybrid stands dominate the canopy. Twenty different shrub species may be found, many of which occur primarily within this plant community, including *Alnus incana* var. *occidentalis*, *Rosa woodsii*, *Lonicera involucrata*, and *Linnaea borealis*. The herbaceous layer is a diverse mix of graminoids, herbaceous dicots, and fern allies. *Equisetum arvense* is always present and may dominate the understory. *Carex disperma* was present in most stands and is a strong indicator for this community. Rare sedge *Carex leptalea* was found exclusively in this plant community. Other frequent herbs include graminoids *Calamagrostis canadensis*, *Poa palustris*, *Bromus ciliatus*, *Carex aquatilis*, *Glyceria striata*, and *Carex utriculata* and herbaceous dicots *Viola macloskeyi* ssp. *pallens*, *Galium trifidum*, *Geum macrophyllum* var. *perincisum*, *Geranium richardsonii*, *Chamerion angustifolium*, *Streptopus amplexifolius*, *Maianthemum stellatum*, *Angelica pinnata*, *Saxifraga odontoloma*, and *Thalictrum sparsiflorum* var. *saximontanum*. The abundant bryophyte layer consistently supports *Plagiomnium cuspidatum*, *Aulacomnium palustre*, and *Helodium blandowii* and often *Marchantia polymorpha* and *Drepanocladus aduncus*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Chadde *et al.* (1988) describe a similar *Picea engelmannii* / *Calamagrostis canadensis* community type from the northern range.

Rocky Mountains: Johnson (1996) describes the treed fen component of a fen in Rocky Mountains National Park that is similar to this community. Chadde *et al.* (1998) describe two types from the northern Rocky Mountains that shares characteristics with the YNP community: *Picea engelmannii* / *Equisetum arvense* and *Picea engelmannii* / *Carex disperma*. The forested component of Swamp Lake Fen in northern Wyoming is also similar to this community (Fertig & Jones 1992; Heidel & Laursen 2003b).

Globally: No similar communities have been described from peatlands worldwide, but certain elements of this community, such as *Carex leptalea* and *Carex disperma* are circumboreal and occur in peatlands in Canada and Europe (Hultén 1964; Chee & Vitt 1989; Gignac *et al.* 2004).

US NVC: The YNP plant community fits within *Picea engelmannii* / *Equisetum arvense* Forest (CEGL005927), but individual stands may also fit the characteristics of *Picea engelmannii* / *Calamagrostis canadensis* Forest (CEGL002678) or *Picea (engelmannii) X glauca, engelmannii* / *Carex disperma* Forest (CEGL000405) (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 10$): 24, 58, 59, 61, 165, 167, 172, 177, 178, 360

F.2: *Pinus contorta* var. *latifolia* – *Aulacomnium palustre* – *Sphagnum warnstorffii* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

This plant community represents the forested component of rich fens in the central volcanic plateau with moderate to high levels of precipitation. Stands occur most often on the margins of sites, but also as hummocks within the peatland expanse. Groundwater pH ranged from 4.8–7.4 and EC ranged from 10–365 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 40–180 cm and mean soil carbon was 33.18%. Elevations of sampled stands ranged from 1950–2510 m (6400–8240 ft) and mean annual precipitation ranged from 500–1500 mm/year.

VEGETATION DESCRIPTION

In this community, *Pinus contorta* var. *latifolia* creates an open canopy (typically 20–30% cover) over a dense bryophyte layer (up to 90% cover). Species richness is high; on average, relevés contained 29 species, of which 25 were vascular plants. The dominant bryophyte species are *Aulacomnium palustre* and *Sphagnum warnstorffii*, both rich fen mosses, which grow together with varying cover. Other possible bryophytes include *Sphagnum teres*, *Sphagnum squarrosum*, and *Sphagnum riparium*. *Vaccinium occidentale* is the most common shrub dominant, and *Lonicera caerulea* and *Kalmia*

microphylla are also common. *Carex aquatilis* is a constant in the herbaceous understory and contributes up to 30% cover. Other common herbs include *Viola macloskeyi* ssp. *pallens*, *Symphyotrichum foliaceum*, *Calamagrostis canadensis*, *Carex utriculata*, *Packera subnuda*, *Spiranthes romanzoffiana*, *Eleocharis quinqueflora*, *Antennaria corymbosa*, and *Fragaria virginiana*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: Mattson (1984) describes a similar *Vaccinium occidentale* / *Carex aquatilis* habitat type from central YNP.

Rocky Mountains: Cooper & Andrus (1994) describe a similar *Vaccinium occidentale* – *Kalmia polifolia* (= *microphylla*) community with abundant *Aulacomnium palustre* from the Wind River Range in Wyoming. Chadde *et al.* (1998) describe a *Pinus contorta* / *Vaccinium occidentale* community type from the northern Rocky Mountains that shares characteristics of this YNP community. Cooper & Jones (2004) describe a *Kalmia microphylla* / *Sphagnum* spp. Dwarf-shrub Peatland provisional association from the Kootenai National Forest in Montana, but the bryophyte strata within this community is dominated by either *Sphagnum warnstorffii* or *Sphagnum russowii*, which have been separated in this classification.

Globally: A similar community occurs in bogs (which may actually be poor fens) in Washington state, though no *Sphagnum* species were specified (Kunze 1994). Depending on bryophyte composition, the Washington state community may be similar to the YNP community. Both *Aulacomnium palustre* and *Sphagnum warnstorffii* are widespread peatland species throughout the northern hemisphere, but occur with a variety of vascular species depending on location (Slack *et al.* 1980; Chee & Vitt 1989; Gignac *et al.* 1991; Amon *et al.* 2002).

US NVC: There are no equivalent associations within the NVC. The most similar associations have been described from peatlands in Alaska, including *Pinus contorta* / *Sphagnum* spp. Woodland (CEGL003201), *Pinus contorta* / *Carex aquatilis* var. *dives* Woodland (CEGL003203), *Pinus contorta* / *Vaccinium ovalifolium* Woodland (CEGL003206), or from the Pacific Northwest, including *Pinus contorta* var. *contorta* / *Ledum groenlandicum* / *Sphagnum* spp. Woodland (CEGL003337) and *Pinus contorta* / *Carex (aquatilis, angustata)* Woodland (CEGL000140). None of these associations adequately describe the YNP community (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 22$): 37, 103, 124, 152, 155, 187, 273, 276, 278, 281, 287, 342, 353, 406, 411, 417, 420, 424, 459, 464, 466, 504

G. BRYOPHYTE COMMUNITIES

G.1: *Gymnocolea inflata* – *Drepanocladus polygamus* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Mats dominated by the leafy liverwort *Gymnocolea inflata* occur on the margins of very acidic pools in acidic geothermal fens. Groundwater pH ranged from 3.2–3.5 and EC ranged from 79–428 $\mu\text{S}/\text{cm}$. Peat thickness is hard to gauge in these stands, as they extend over pools of water, but surrounding areas had peat thickness that spanned the measurable range, 40–240+ cm. No soil samples were taken from this community. Sampled stands occurred within a narrow elevation range, 2480–2490 m (8140–8180 ft), but the community likely occurs across a wider range. Mean annual precipitation ranged from 500–1000 mm/year. [See photo M in Appendix D.]

VEGETATION DESCRIPTION

All five sampled stands contained the matted leafy liverwort *Gymnocolea inflata* intermixed with *Drepanocladus polygamus*. The mats are dark brownish black in color and very distinctive. Low cover of *Carex aquatilis* was also consistent in all sampled stands. On average, relevés contained only four species, of which only one was a vascular plant. The only other species in sampled stands include *Sphagnum lindbergii*, *Amblystegium varium*, *Polytrichum commune*, and *Eriophorum angustifolium*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: No similar communities have been described from YNP.

Rocky Mountains: No similar communities have been described from peatlands in the Rocky Mountains.

Globally: *Gymnocolea inflata* most often occurs in bogs and poor fens (Chee & Vitt 1989), but a similarly acidic and highly mineralized community of *Gymnocolea inflata* is described from Alaska (Gough *et al.* 2006).

US NVC: There are no equivalent associations within the NVC.

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 5$): 302, 304, 373, 374, 379

G.2: *Sphagnum* spp. – *Carex aquatilis* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

In geothermally influenced sites, *Carex aquatilis* occurs with a suite of acid-tolerant mosses. Stands of this community can form either hummocks or dense carpets with intermittent pools of acidic water. Groundwater pH ranged from 2.9–5.2 and EC ranged from 30–426 $\mu\text{S}/\text{cm}$. SO_4^{2-} concentrations can be as high as 190 mg/L. Peat thickness ranged from 40–240+ cm and mean soil carbon was 31.2%. Elevations of sampled stands ranged from 2290–2490 m (7520–8180 ft) and mean annual precipitation ranged from 500–1000 mm/year. [See photo N in Appendix D.]

VEGETATION DESCRIPTION

This community is characterized by a dense carpet or hummocks of *Sphagnum* moss (often 80–100% cover). The most common species include *Sphagnum russowii*, *Sphagnum lindbergii*, *Sphagnum fimbriatum*, and *Sphagnum riparium*. In certain locations with extreme acidity, *Sphagnum* species are replaced by either *Polytrichum commune* or *Polytrichum strictum*. Both *Sphagnum*-dominated stands and *Polytrichum*-dominated stands are included in this community. Species richness is generally low, on average relevés contained seven species, of which five were vascular plants. *Carex aquatilis* is a constant vascular species, contributing 20–90% cover, and can be associated with *Carex canescens*, *Eriophorum chamissonis*, and *Viola macloskeyi* ssp. *pallens*. Low cover of *Pinus contorta* var. *latifolia* (< 10% cover) is common, often as small stunted individuals or seedlings. Low cover of *Kalmia microphylla* is also possible.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: No similar communities have been described for YNP.

Rocky Mountains: Cooper (1990) describes a stand dominated by *Carex aquatilis* and *Sphagnum russowii* in Rocky Mountain National Park, but this stand is not associated with geothermal or other geochemical acidity and no pH is given. Cooper *et al.* (2002) describe a *Sphagnum*-dominated, acidic iron fen in Colorado influenced by groundwater rich in sulfuric acid from weathering pyrite. Stands in iron fens may be similar to this YNP community.

Globally: A similar community occurs in bogs in Washington state (Kunze 1994), though the dominant species is *Carex sitchensis* (= *aquatilis* var. *dives*) and the *Sphagnum* species are not named. *Carex aquatilis* occurs with *Sphagnum russowii*, *Sphagnum lindbergii*, *Sphagnum fimbriatum*, and *Sphagnum riparium* in poor fens in Canada, though stand composition is different than in YNP (Slack *et al.* 1980).

US NVC: The YNP plant community fits within *Carex aquatilis* - *Sphagnum* spp. Herbaceous Vegetation (CEGL002898), which occurs in similar highly mineralized and acidic conditions in Colorado (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 12$): 7, 138, 143, 241, 242, 305, 312, 313, 375, 377, 380, 381

G.3: *Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var. *latifolia* plant community

DISTRIBUTION AND ENVIRONMENTAL SETTING

Stands with a forested or shrub component within acidic fens are classified in this plant community, which occurs either on margins or as hummocks within the peatland expanse. Most fens where this community occurred were considered acidic geothermal fens because they contain signs of geothermal activity, such as bubbling gas in water pools or barren, white patches of deposited material. But a few sites were acidic with no obvious signs of geothermal activity. In these locations, the acidity may be caused by the dominance of *Sphagnum* moss, though this was not tested. These non-geothermal sites may be as close to a poor fen as is possible in YNP. Groundwater pH ranged from 3.2–5.0 and EC ranged from 10–428 $\mu\text{S}/\text{cm}$. Peat thickness ranged from 45–240+ cm, but was generally > 120 cm. Mean soil carbon was the second highest among communities, 39.4%. Elevations of sampled stands ranged from 2290–2570 m (7500–8440 ft) and mean annual precipitation ranged from 500–1000 mm/year. [See photos M, O, and P in Appendix D.]

VEGETATION DESCRIPTION

This plant community is characterized by a dense cover of *Sphagnum* species (up to 100% cover) beneath ericaceous shrubs and an open canopy of *Pinus contorta* var. *latifolia*. Species richness is low compared to other communities that support shrub or tree species; on average relevés contained ten species, of which eight were vascular plants. *Sphagnum russowii* is the most common *Sphagnum* species in the bryophyte layer, but may be replaced by *Sphagnum riparium*, *Sphagnum fuscum*, *Sphagnum lindbergii*, or *Sphagnum capillifolium*. *Polytrichum commune* is frequently interspersed with the *Sphagnum* species. Overstory shrubs include *Kalmia microphylla*, *Vaccinium occidentale*, and *Ledum glandulosum*. *Pinus contorta* var. *latifolia* is generally represented by scattered individuals or up to 40% canopy cover. *Carex aquatilis* is the only dominant herb, often associated with low cover of *Carex canescens*, *Calamagrostis canadensis*, or *Carex utriculata*.

RELATIONSHIP TO PRIOR CLASSIFICATIONS AND STUDIES

Yellowstone National Park: No similar communities have been described from YNP.

Rocky Mountains: Chadde *et al.* (1998) describe a *Pinus contorta* / *Vaccinium occidentale* community type from the northern Rocky Mountains that shares characteristics of this YNP community, but specific moss species are not mentioned. Cooper *et al.* (2002) describe a *Sphagnum*-dominated, acidic iron fen in Colorado influenced by groundwater rich in sulfuric acid from weathering pyrite. Stands in iron fens may be similar to this YNP community. Cooper & Jones (2004) describe a *Kalmia microphylla* / *Sphagnum* spp. Dwarf-shrub Peatland provisional association from the Kootenai National Forest in Montana, but the bryophyte strata within this community is dominated by either *Sphagnum warnstorffii* or *Sphagnum russowii*, which have been separated in this classification.

Globally: A similar community occurs in bogs (which may actually be poor fens) in Washington state, though no *Sphagnum* species were specified (Kunze 1994). Similar communities also occur in the Sierra Nevada Mountains of California (Cooper & Wolf 2006) and the Italian Alps (Gerdol *et al.* 1994).

US NVC: Similar to YNP's *Pinus contorta* var. *latifolia* – *Aulacomnium palustre* – *Sphagnum warnstorffii* plant community, there are no equivalent associations within the NVC. The most similar associations have been described from peatlands in Alaska, including *Pinus contorta* / *Sphagnum* spp. Woodland (CEGL003201), *Pinus contorta* / *Carex aquatilis* var. *dives* Woodland (CEGL003203), *Pinus contorta* / *Vaccinium ovalifolium* Woodland (CEGL003206), or from the Pacific Northwest, including *Pinus contorta* var. *contorta* / *Ledum groenlandicum* / *Sphagnum* spp. Woodland (CEGL003337) and *Pinus contorta* / *Carex (aquatilis, angustata)* Woodland (CEGL000140). None of these associations adequately describe the YNP community (NatureServe 2007).

RELEVÉS INCLUDED WITHIN THIS COMMUNITY ($n = 16$): 10, 130, 132, 140, 214, 215, 240, 265, 301, 303, 310, 365, 366, 368, 376, 378

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APPENDIX C: Vascular Plant and Bryophyte Species Lists for YNP Fens

Appendix C.1: Vascular plant species list for YNP fens. Asterisk (*) = species of special concern for the state of Wyoming from Keinath *et al.* (2003). *n* = number of fens in which the species was recorded. Nomenclature follows Dorn (2001).

Scientific Name	Common Name	<i>n</i>
Alliaceae		
<i>Allium brevistylum</i> S. Wats.	shortstyle onion	3
<i>Allium schoenoprasum</i> L.	wild chive	5
Apiaceae		
<i>Angelica arguta</i> Nutt.	Lyall's angelica	6
<i>Angelica pinnata</i> S. Wats.	small-leaf angelica	29
<i>Heracleum maximum</i> Bartr.	common cowparsnip	4
<i>Ligusticum canbyi</i> Coult. & Rose	Canby's licorice-root	7
<i>Osmorhiza</i> Raf.	sweetroot	1
Asteraceae		
<i>Achillea millefolium</i> L. var. <i>lanulosa</i> (Nutt.) Piper	western yarrow	7
<i>Agoseris</i> Raf.	agoseris	1
<i>Anaphalis margaritacea</i> (L.) Benth.	common pearleverlasting	1
<i>Antennaria corymbosa</i> E. Nels.	flattop pussytoes	32
<i>Antennaria pulcherrima</i> (Hook.) Greene	showy pussytoes	4
<i>Arnica longifolia</i> D.C. Eat.	spearleaf arnica	1
<i>Arnica mollis</i> Hook.	hairy arnica	8
<i>Cirsium</i> P. Mill.	thistle	11
<i>Crepis runcinata</i> (James) Torr. & Gray	dandelion hawksbeard	12
<i>Erigeron acris</i> L. var. <i>kamtschaticus</i> (DC.) Herder	bitter fleabane	1
<i>Packera pseud aurea</i> (Rydb.) W.A. Weber & A. Löve	falsegold groundsel	27
<i>Packera subnuda</i> (DC.) Trock & Barkley	ragwort	51
<i>Senecio hydrophilus</i> Nutt.	water groundsel	1
<i>Senecio integerrimus</i> Nutt. var. <i>exaltatus</i> (Nutt.) Cronq.	Columbia ragwort	3
<i>Senecio serra</i> Hook.	butterweed groundsel	8
<i>Senecio sphaerocephalus</i> Greene	ballhead ragwort	41
<i>Senecio triangularis</i> Hook.	arrowleaf groundsel	25
<i>Solidago canadensis</i> L.	Canada goldenrod	2
<i>Symphyotrichum eatonii</i> (Gray) Nesom	Eaton's aster	27
<i>Symphyotrichum foliaceum</i> (DC.) Nesom	alpine leafybract aster	74
<i>Taraxacum officinale</i> G.H. Weber ex Wiggers	common dandelion	2
Betulaceae		
<i>Alnus incana</i> (L.) Moench var. <i>occidentalis</i> (Dippel) C.L. Hitchc.	thinleaf alder	4
<i>Betula glandulosa</i> Michx.	bog birch	39
Brassicaceae		
<i>Barbarea orthoceras</i> Ledeb.	erectpod wintercress	2
<i>Cardamine pensylvanica</i> Muhl. ex Willd.	Pennsylvania bittercress	19
<i>Erysimum cheiranthoides</i> L.	treacle wallflower	1
<i>Rorippa palustris</i> (L.) Bess.	bog yellowcress	9
Callitrichaceae		
<i>Callitriche palustris</i> L.	spring waterstarwort	1
Calochortaceae		
<i>Streptopus amplexifolius</i> (L.) DC.	claspleaf twistedstalk	3

Scientific Name	Common Name	<i>n</i>
Caprifoliaceae		
<i>Linnaea borealis</i> L.	twinflower	5
<i>Lonicera caerulea</i> L.	sweetberry honeysuckle	33
<i>Lonicera involucrata</i> Banks ex Spreng.	twinberry honeysuckle	7
Caryophyllaceae		
<i>Cerastium fontanum</i> Baumg.	mouse-ear chickweed	13
<i>Moehringia lateriflora</i> (L.) Fenzl	bluntleaf sandwort	1
<i>Stellaria borealis</i> Bigelow	boreal starwort	2
<i>Stellaria crassifolia</i> Ehrh.	thickleaved chickweed	4
<i>Stellaria longifolia</i> Muhl. ex Willd.	longleaf chickweed	23
<i>Stellaria longipes</i> Goldie	longstalk starwort	19
Chenopodiaceae		
<i>Chenopodium rubrum</i> L.	red goodefoot	1
Convallariaceae		
<i>Maianthemum stellatum</i> (L.) Link	false Solomon's seal	7
Cornaceae		
<i>Cornus canadensis</i> L.	bunchberry dogwood	1
<i>Cornus sericea</i> L.	redosier dogwood	1
Crassulaceae		
<i>Sedum rhodanthum</i> Gray	redpod stonecrop	14
Cupressaceae		
<i>Juniperus communis</i> L.	common juniper	2
Cyperaceae		
<i>Carex aquatilis</i> Wahlenb.	water sedge	134
<i>Carex aurea</i> Nutt.	golden sedge	18
<i>Carex brunnescens</i> (Pers.) Poir.	brownish sedge	2
<i>Carex buxbaumii</i> Wahlenb.	buxbaum sedge	21
<i>Carex canescens</i> L.	silvery sedge	61
<i>Carex capillaris</i> L.	hairlike sedge	5
* <i>Carex cusickii</i> Mackenzie ex Piper & Beattie	Cusick's sedge	2
* <i>Carex diandra</i> Schrank	lesser panicled sedge	4
<i>Carex disperma</i> Dewey	softleaved sedge	11
* <i>Carex echinata</i> Murr.	star sedge	20
* <i>Carex flava</i> L.	yellow sedge	2
<i>Carex gynocrates</i> Wormsk. ex Drej.	northern bog sedge	2
<i>Carex haydeniana</i> Olney	cloud sedge	2
<i>Carex illota</i> Bailey	sheep sedge	5
<i>Carex interior</i> Bailey	inland sedge	11
<i>Carex laeviculmis</i> Meinsh.	smoothstem sedge	1
<i>Carex lasiocarpa</i> Ehrh.	woolly sedge	27
<i>Carex leporinella</i> Mackenzie	sierrahare sedge	1
* <i>Carex leptalea</i> Wahlenb.	bristlestalked sedge	3
* <i>Carex limosa</i> L.	mud sedge	17
* <i>Carex livida</i> (Wahlenb.) Willd.	livid sedge	32
* <i>Carex luzulina</i> Olney var. <i>ablata</i> (Bailey) F.J. Herm.	serrate sedge	11
* <i>Carex microglochin</i> Wahlenb.	fewseeded bog sedge	3
<i>Carex microptera</i> Mackenzie var. <i>microptera</i>	ovalhead sedge	2
<i>Carex nebrascensis</i> Dewey	Nebraska sedge	7

Scientific Name	Common Name	<i>n</i>
Cyperaceae continued		
<i>Carex neurophora</i> Mackenzie	alpine nerved sedge	10
<i>Carex norvegica</i> Retz. ssp. <i>steverii</i> (Holm) E. Murr.	Steven's sedge	1
<i>Carex pellita</i> Muhl ex Willd.	woolly sedge	5
<i>Carex praegracilis</i> W. Boott	clustered field sedge	1
<i>Carex saxatilis</i> L. (unconfirmed)	rock sedge	1
<i>Carex simulata</i> Mackenzie	analogue sedge	30
<i>Carex utriculata</i> Boott	Northwest Territory sedge	132
<i>Carex vesicaria</i> L.	blister sedge	20
<i>Carex viridula</i> Michx.	green sedge	9
* <i>Dulichium arundinaceum</i> (L.) Britt.	threeway sedge	1
* <i>Eleocharis flavescens</i> (Poir.) Urban var. <i>thermalis</i> (Rydb.) Cronq.	yellow spikerush	4
<i>Eleocharis palustris</i> (L.) Roemer & J.A. Schultes	spikesedge	7
<i>Eleocharis quinqueflora</i> (F.X. Hartmann) Schwarz	fewflowered spikesedge	65
<i>Eleocharis rostellata</i> (Torr.) Torr.	beaked spikesedge	5
* <i>Eleocharis tenuis</i> (Willd.) J.A. Schultes var. <i>borealis</i> (Svens.) Gleason	elliptic spikerush	10
<i>Eriophorum angustifolium</i> Honckeney	narrowleaf cottonsedge	42
* <i>Eriophorum chamissonis</i> C.A. Mey.	russet cottensedge	20
* <i>Eriophorum gracile</i> W.D.J. Koch	slender cottonsedge	8
* <i>Eriophorum viridicarinarum</i> (Engelm.) Fern.	thinleaf cottonsedge	6
<i>Schoenoplectus acutus</i> (Muhl. ex Bigelow) A.& D. Löve var. <i>occidentalis</i> (S. Wats.) S.G. Sm.	tule	10
* <i>Schoenoplectus subterminalis</i> (Torr.) Soják	swaying bulrush	2
Droseraceae		
* <i>Drosera anglica</i> Huds.	English sundew	23
Equisetaceae		
<i>Equisetum arvense</i> L.	field horsetail	35
<i>Equisetum laevigatum</i> A. Braun	smooth horsetail	15
Ericaceae		
<i>Gaultheria humifusa</i> (Graham) Rydb.	western wintergreen	7
<i>Kalmia microphylla</i> (Hook.) Heller	alpine laurel	24
<i>Ledum glandulosum</i> Nutt.	western Labrador tea	13
<i>Vaccinium occidentale</i> Gray	bog blueberry	36
<i>Vaccinium scoparium</i> Leib. ex Coville	grouse whortleberry	5
Fabaceae		
<i>Lupinus polyphyllus</i> Lindl. var. <i>prunophilus</i> (M.E. Jones) L. Phillips	hairy bigleaf lupine	2
<i>Trifolium hybridum</i> L.	alsike clover	3
<i>Trifolium longipes</i> Nutt. ssp. <i>reflexum</i> (A. Nels.) J. Gillett	droopflower clover	3
Gentianaceae		
<i>Gentianopsis detonsa</i> (Rottb.) Ma var. <i>elegans</i> (A. Nels.) N. Holmgren	Rocky Mountain fringed gentian	52
<i>Swertia perennis</i> L.	alpine bog swertia	10
Geraniaceae		
<i>Geranium richardsonii</i> Fisch. & Trautv.	Richardson geranium	12
Grossulariaceae		
<i>Ribes hudsonianum</i> Richards.	northern black currant	1
<i>Ribes lacustre</i> (Pers.) Poir.	prickly currant	1
Hippuridaceae		
<i>Hippuris vulgaris</i> L.	maretail	5

Scientific Name	Common Name	<i>n</i>
Iridaceae		
* <i>Sisyrinchium idahoense</i> Bickn.	Idaho blue-eyed grass	5
Isoetaceae		
<i>Isoetes</i> L.	quillwort	1
Juncaceae		
<i>Juncus balticus</i> Willd.	Baltic rush	21
<i>Juncus brevicaudatus</i> (Engelm.) Fern.	narrowpanicle rush	26
<i>Juncus drummondii</i> E. Mey.	Drummond rush	3
<i>Juncus ensifolius</i> Wikstr.	swardleaf rush	44
* <i>Juncus filiformis</i> L.	thread rush	2
<i>Juncus longistylis</i> Torr.	longstyle rush	1
<i>Juncus nevadensis</i> S. Wats.	Sierra rush	1
<i>Juncus regelii</i> Buch.	regel rush	1
<i>Luzula multiflora</i> (Ehrh.) Lej.	common woodrush	1
<i>Luzula parviflora</i> (Ehrh.) Desv.	millet woodrush	22
Juncaginaceae		
<i>Triglochin maritimum</i> L. var. <i>elatum</i> (Nutt.) Gray	shore arrowgrass	29
<i>Triglochin palustris</i> L.	marsh arrowgrass	20
Lamiaceae		
<i>Mentha arvensis</i> L.	field mint	14
<i>Prunella vulgaris</i> L.	common selfheal	1
<i>Scutellaria galericulata</i> L.	marsh skullcap	5
Lemnaceae		
<i>Lemna</i> L.	duckweed	1
Lentibulariaceae		
* <i>Utricularia minor</i> L.	lesser bladderwort	33
Lycopodiaceae		
<i>Lycopodiella inundata</i> (L.) Holub	inundated clubmoss	1
Melanthiaceae		
<i>Zigadenus elegans</i> Pursh	mountain deathcamas	1
Menyanthaceae		
<i>Menyanthes trifoliata</i> L.	common bogbean	21
Nymphaeaceae		
<i>Nuphar lutea</i> (L.) Sm. ssp. <i>polysepala</i> (Engelm.) E.O. Beal	rocky mountain cowliily	5
Onagraceae		
<i>Chamerion angustifolium</i> (L.) Holub	fireweed	4
<i>Epilobium anagallidifolium</i> Lam.	pimpernel willowherb	7
<i>Epilobium ciliatum</i> Raf.	hairy willowherb	44
<i>Epilobium clavatum</i> Trel.	clubfruit willowherb	7
<i>Epilobium halleanum</i> Hausskn.	Halls willowherb	3
<i>Epilobium hornemannii</i> Reichenb.	Hornemann's willowherb	10
<i>Epilobium lactiflorum</i> Hausskn.	milkflower willowherb	1
<i>Epilobium palustre</i> L.	marsh willowherb	54
Ophioglossaceae		
<i>Botrychium multifidum</i> (Gmel.) Trev.	broadleaf grapefern	1
Orchidaceae		
<i>Listera cordata</i> (L.) R. Br. ex Ait. f.	heartleaf twayblade	4
<i>Platanthera dilatata</i> (Pursh) Lindl. ex Beck	white bogorchid	46
<i>Platanthera huronensis</i> (Nutt.) Lindl.	bog orchid	14

Scientific Name	Common Name	<i>n</i>
Orchidaceae continued		
<i>Platanthera hyperborea</i> (L.) Lindl.	northern bogorchid	1
<i>Platanthera obtusata</i> (Banks ex Pursh) Lindl.	northern small bogorchid	1
<i>Platanthera stricta</i> Lindl.	slender bogorchid	4
<i>Spiranthes romanzoffiana</i> Cham.	hooded ladiestresses	34
Parnassiaceae		
<i>Parnassia fimbriata</i> Koenig	rocky mountain parnassia	3
<i>Parnassia palustris</i> L. var. <i>montanensis</i> (Fern. & Rydb. ex Rydb.) C.L. Hitchc.	marsh grass of Parnassus	17
Pinaceae		
<i>Abies lasiocarpa</i> (Hook.) Nutt.	subalpine fir	6
<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	16
<i>Picea glauca</i> (Moench) Voss	white spruce	7
<i>Pinus albicaulis</i> Engelm.	whitebark pine	1
<i>Pinus contorta</i> Dougl. ex Loud. var. <i>latifolia</i> Engelm. ex S. Wats.	lodgepole pine	45
<i>Pinus flexilis</i> James	limber pine	1
Poaceae		
<i>Agrostis exarata</i> Trin.	spike bentgrass	16
<i>Agrostis idahoensis</i> Nash	Idaho redtop	2
<i>Agrostis scabra</i> Willd.	ticklegrass	58
<i>Agrostis stolonifera</i> L.	carpet bentgrass	1
<i>Agrostis thurberiana</i> A.S. Hitchc.	Thurber's bentgrass	32
<i>Alopecurus aequalis</i> Sobol.	shortawn foxtail	2
<i>Bromus ciliatus</i> L.	fringed brome	27
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	bluejoint reedgrass	46
<i>Calamagrostis stricta</i> (Timm) Koel.	slimstem reedgrass	48
<i>Danthonia intermedia</i> Vasey	timber oatgrass	4
<i>Deschampsia caespitosa</i> (L.) Beauv.	tufted hairgrass	66
<i>Elymus albicans</i> (Scribn. & J.G. Sm.) A. Löve var. <i>griffithsii</i> (Scribn. & Sm.) ex Piper) Dorn	Montana wheatgrass	1
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners var. <i>trachycaulus</i>	slender wheatgrass	3
<i>Festuca idahoensis</i> Elmer	Idaho fescue	1
<i>Glyceria striata</i> (Lam.) A.S. Hitchc.	fowl mannagrass	23
<i>Hierochloa odorata</i> (L.) Beauv.	northern sweetgrass	2
<i>Hordeum brachyantherum</i> Nevski	meadow barely	2
<i>Muhlenbergia andina</i> (Nutt.) A.S. Hitchc.	foxtail muhly	2
<i>Muhlenbergia filiformis</i> (Thurb. ex S. Wats.) Rydb.	pullup muhly	56
* <i>Muhlenbergia glomerata</i> (Willd.) Trin.	bristly muhly	2
<i>Phleum alpinum</i> L.	alpine timothy	22
<i>Phleum pratense</i> L.	timothy	11
<i>Poa interior</i> Rydb.	inland bluegrass	15
<i>Poa juncifolia</i> Scribn. var. <i>juncifolia</i>	big bluegrass	1
<i>Poa leptocoma</i> Trin.	bog bluegrass	2
<i>Poa palustris</i> L.	fowl bluegrass	30
<i>Poa reflexa</i> Vasey & Scribn. ex Vasey	nodding bluegrass	1
<i>Torreyochloa pallida</i> (Torr.) Church var. <i>pauciflora</i> (J. Presl) J.I. Davis	pale false mannagrass	1
<i>Trisetum wolfii</i> Vasey	wolf trisetum	9
Polemoniaceae		
<i>Polemonium occidentale</i> Greene	western polemonium	13

Scientific Name	Common Name	<i>n</i>
Polygonaceae		
<i>Polygonum amphibium</i> L. var. <i>stipulaceum</i> Coleman	water smartweed	3
<i>Polygonum bistortoides</i> Pursh	American bistort	1
<i>Polygonum viviparum</i> L.	viviparous bistort	1
<i>Rumex aquaticus</i> L. var. <i>fenestratus</i> (Greene) Dorn	western dock	10
Portulacaceae		
<i>Montia chamissoi</i> (Ledeb. ex Spreng.) Greene	water indianlettuce	2
Potamogetonaceae		
<i>Potamogeton</i> L.	pondweed	15
<i>Stuckenia filiformis</i> (Pers) Boerner	fineleaf pondweed	1
Primulaceae		
<i>Dodecatheon pulchellum</i> (Raf.) Merr.	southern shootingstar	8
* <i>Lysimachia thyrsoflora</i> L.	water loosestrife	2
Pyrolaceae		
<i>Moneses uniflora</i> (L.) Gray	single delight	1
<i>Orthilia secunda</i> (L.) House	sidebells wintergreen	2
<i>Pyrola asarifolia</i> Michx.	liverleaf wintergreen	12
<i>Pyrola chlorantha</i> Sw.	greenflowered wintergreen	1
Ranunculaceae		
<i>Aconitum columbianum</i> Nutt.	Columbia monkshood	6
<i>Actaea rubra</i> (Ait.) Willd.	red baneberry	2
<i>Caltha leptosepala</i> DC.	elkslip marshmarigold	14
<i>Delphinium occidentale</i> (S. Wats.) S. Wats.	larkspur	1
<i>Ranunculus alismifolius</i> Geyer ex Benth. var. <i>davisii</i> L. Benson	Davis' buttercup	3
<i>Ranunculus cymbalaria</i> Pursh	shore buttercup	2
<i>Ranunculus gmelinii</i> DC.	buttercup	4
<i>Ranunculus macounii</i> Britt.	macoun buttercup	1
<i>Ranunculus sceleratus</i> L. var. <i>multifidus</i> Nutt.	cursed buttercup	1
<i>Ranunculus uncinatus</i> D. Don ex G. Don	hooked buttercup	1
<i>Thalictrum alpinum</i> L.	alpine meadowrue	3
<i>Thalictrum sparsiflorum</i> Turcz. ex Fisch. & C.A. Mey. var. <i>saximontanum</i> Boivin	fewflower meadowrue	5
<i>Trollius albiflorus</i> (Gray) Rydb.	American globeflower	7
Rhamnaceae		
<i>Rhamnus alnifolia</i> L'Hér.	alderleaf buckthorn	3
Rosaceae		
<i>Fragaria virginiana</i> Duchesne	Virginia strawberry	38
<i>Geum macrophyllum</i> Willd. var. <i>perincisum</i> (Rydb.) Raup	largeleaf avens	44
<i>Pentaphylloides floribunda</i> (Pursh) A. Löve	shrubby cinquefoil	31
<i>Potentilla anserina</i> L.	silverweed cinquefoil	1
<i>Potentilla diversifolia</i> Lehm. var. <i>diversifolia</i>	varileaf cinquefoil	2
<i>Potentilla gracilis</i> Dougl. ex Hook.	slender cinquefoil	4
<i>Potentilla palustris</i> (L.) Scop.	purple marshlocks	40
<i>Rosa woodsii</i> Lindl.	woods rose	6
* <i>Rubus acaulis</i> Michx.	dwarf raspberry	6
<i>Spiraea splendens</i> Baumann ex K. Koch	rose meadowsweet	2
Rubiaceae		
<i>Galium boreale</i> L.	northern bedstraw	4
<i>Galium trifidum</i> L.	threepetal bedstraw	98
<i>Galium triflorum</i> Michx.	sweetscented bedstraw	1

Scientific Name	Common Name	<i>n</i>
Salicaceae		
<i>Salix bebbiana</i> Sarg.	Bebb willow	7
<i>Salix boothii</i> Dorn	blueberry willow	9
* <i>Salix candida</i> Flueggé ex Willd.	sageleaf willow	5
<i>Salix drummondiana</i> Barratt ex Hook.	Drummond's willow	4
<i>Salix geyeriana</i> Anderss.	Geyer willow	8
<i>Salix planifolia</i> Pursh	diamondleaf willow	77
<i>Salix pseudomonticola</i> Ball	false mountain willow	4
<i>Salix wolfii</i> Bebb	wolf willow	60
Saxifragaceae		
<i>Mitella pentandra</i> Hook.	fivestamen miterwort	7
<i>Saxifraga odontoloma</i> Piper	brook saxifrage	3
Scheuchzeriaceae		
* <i>Scheuchzeria palustris</i> L.	rannoch-rush	6
Scrophulariaceae		
<i>Castilleja miniata</i> Dougl. ex Hook.	scarlet indian paintbrush	8
<i>Mimulus guttatus</i> DC.	common monkeyflower	20
<i>Mimulus moschatus</i> Dougl. ex Lindl.	musk monkeyflower	6
<i>Pedicularis groenlandica</i> Retz.	elephanthead lousewort	80
<i>Veronica americana</i> Schwein. ex Benth.	American speedwell	17
<i>Veronica scutellata</i> L.	marsh speedwell	3
<i>Veronica serpyllifolia</i> L. ssp. <i>humifusa</i> (Dickson) Syme	brightblue speedwell	2
<i>Veronica wormskjoldii</i> Roemer & J.A. Schultes	American alpine speedwell	6
Sparganiaceae		
<i>Sparganium emersum</i> Rehmman	narrowleaf bur-reed	4
<i>Sparganium natans</i> L.	small bur-reed	1
Tofieldiaceae		
<i>Tofieldia glutinosa</i> (Michx.) Pers. ssp. <i>montana</i> C.L. Hitchc.	tall tofieldia	13
Typhaceae		
<i>Typha latifolia</i> L.	common cattail	10
Valerianaceae		
<i>Valeriana edulis</i> Nutt. ex Torr. & Gray	edible valerian	9
Violaceae		
<i>Viola macloskeyi</i> Lloyd ssp. <i>pallens</i> (Banks ex Ging) M.S. Baker	smooth white violet	98
<i>Viola sororia</i> Willd. var. <i>affinis</i> (Le Conte) McKinney	sand violet	2

Appendix C.2: Bryophyte species list for YNP fens. Asterisk (*) = possible new species for the state of Wyoming, based on Eckel (1996). Confirmation of new species is pending. Double asterisk (**) = confirmed new species for the state of Wyoming from R. E. Andrus, personal communication. *n* = number of fens in which the species was recorded. Nomenclature follows Weber & Wittmann (2005) for non-*Sphagnum* species and McQueen & Andrus (2007) for *Sphagnum* species.

Scientific Name	Common Name	<i>n</i>
Amblystegiaceae		
* <i>Amblystegium riparium</i> (Hedw.) Schimp. in B.S.G.	streamside amblystegium moss	29
<i>Amblystegium serpens</i> (Hedw.) Schimp. in B.S.G. var. <i>juratzkanum</i> (Schimp.) Rau & Herv.	Juratzk's amblystegium moss	1
<i>Amblystegium varium</i> (Hedw.) Lindb.	amblystegium moss	3
<i>Calliergon cordifolium</i> (Hedw.) Kindb.	calliergon moss	7
<i>Calliergon giganteum</i> (Schimp.) Kindb.	giant calliergon moss	9
<i>Calliergon richardsonii</i> (Mitt.) Kindb. in Warnst.	Richardson's calliergon moss	2
<i>Calliergonella cuspidata</i> (Hedw.) Loeske	calliergonella moss	4
<i>Calliergonella lindbergii</i> (Mitt.) Hedenäs	calliergonella moss	15
<i>Campylium stellatum</i> (Hedw.) C. Jens.	star campylium moss	23
<i>Cratoneuron filicinum</i> (Hedw.) Spruce	cratoneuron moss	2
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	drepanocladus moss	65
* <i>Drepanocladus longifolius</i> (Mitt.) Paris	drepanocladus moss	17
* <i>Drepanocladus polygamus</i> (Bruch & Schimper) Hedenäs	drepanocladus moss	2
* <i>Drepanocladus sordidus</i> (Mueller Hal.) Hedenäs	drepanocladus moss	8
* <i>Hamatocaulis vernicosus</i> (Mitt.) Hedenäs	hamatocaulis moss	9
* <i>Palustriella falcatum</i> (S. E. Bridel) L. Hedenäs	palustriella moss	5
<i>Pseudocalliergon turgescens</i> (T. Jens.) Loeske	pseudocalliergon moss	1
* <i>Scorpidium cossonii</i> (Schimp.) Hedenäs	Cosson's scorpidium moss	4
<i>Scorpidium revolvens</i> (Sw.) Hedenäs	scorpidium moss	6
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	scorpidium moss	16
<i>Straminergon stramineum</i> (Brid.) Hedenäs	straminergon moss	18
Aulacomniaceae		
<i>Aulacomnium androgynum</i> (Hedw.) Schwaegr.	aulacomnium moss	1
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	aulacomnium moss	86
Bartramiaceae		
<i>Philonotis fontana</i> (Hedw.) Brid.	philonotis moss	38
Brachytheciaceae		
<i>Brachythecium erythrorrhizon</i> Br. & Sch.	brachythecium moss	2
<i>Brachythecium frigidum</i> (Mueller Hal.) Besch.	cold brachythecium moss	8
<i>Brachythecium nelsonii</i> Grout	Nelson's brachythecium moss	10
<i>Tomentypnum nitens</i> (Hedw.) Loeske	tomentypnum moss	33
Bryaceae		
<i>Ptychostomum pseudotriquetrum</i> (Hedw.) Spence & Ramsay	ptychostomum moss	83
Cephaloziaceae		
<i>Cephalozia connivens</i> (Dicks.) Lindb.	Liverwort	1
<i>Cladopodiella fluitans</i> (Nees) Buch	Liverwort	1
Cladoniaceae		
<i>Cladonia ecmocyna</i> Leighton	cup lichen	1
Climaciaceae		
<i>Climacium dendroides</i> (Hedw.) Web. & Mohr	tree climacium moss	9

Scientific Name	Common Name	<i>n</i>
Dicranaceae		
<i>Dicranum scoparium</i> Hedw.	dicranum moss	2
<i>Dicranum tauricum</i> Sapeh.	dicranum moss	1
Ditrichaceae		
* <i>Ditrichum gracile</i> (Mitt.) Kuntze	slender ditrichum moss	1
Helodiaceae		
<i>Helodium blandowii</i> (Web. & Mohr) Warnst.	Blandow's helodium moss	30
Hypnaceae		
<i>Platydictya jungermannioides</i> (Brid.) Crum	Jungermann's platydictya moss	2
Jungermanniaceae		
<i>Gymnocolea inflata</i> (Huds.) Dumort.	liverwort	3
<i>Nardia compressa</i> (Hook.) S. F. Gray	liverwort	1
Marchantiaceae		
<i>Marchantia polymorpha</i> L.	thalloid liverwort	30
Meesiaceae		
* <i>Meesia triquetra</i> (Richt.) Ångstr.	meesia moss	3
Mniaceae		
<i>Plagiomnium cuspidatum</i> (Hedw.) Kop.	toothed plagiomnium moss	81
Polytrichaceae		
<i>Polytrichum commune</i> Hedw.	polytrichum moss	10
<i>Polytrichum strictum</i> Menzies ex Brid.	polytrichum moss	6
Sphagnaceae		
<i>Sphagnum angustifolium</i> (C. Jens. ex Russ.) C. Jens. in Tolf	sphagnum moss	1
** <i>Sphagnum capillifolium</i> (Ehrh.) Hedw.	sphagnum moss	2
** <i>Sphagnum fimbriatum</i> Wils. in Wils. & Hook. f. in Hook. f.	sphagnum moss	3
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	sphagnum moss	2
** <i>Sphagnum lindbergii</i> Schimp. in Lindb.	Lindberg's sphagnum moss	2
<i>Sphagnum platyphyllum</i> (Lindb. ex Braithw.) Sull. ex Warnst.	sphagnum moss	2
** <i>Sphagnum riparium</i> Ångstr.	streamside sphagnum moss	4
<i>Sphagnum russowii</i> Warnst.	Russow's sphagnum moss	14
<i>Sphagnum squarrosum</i> Crome	sphagnum moss	4
<i>Sphagnum subsecundum</i> Nees in Sturm	sphagnum moss	3
<i>Sphagnum teres</i> (Schimp.) Ångstr. in Hartm.	sphagnum moss	25
<i>Sphagnum warnstorffii</i> Russ.	sphagnum moss	19
Tetraphidaceae		
<i>Tetraphis pellucida</i> Hedw.	tetraphis moss	1

APPENDIX C REFERENCES

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APPENDIX D: Photos of Selected YNP Fens



A. *Carex lasiocarpa* – *Potentilla palustris* plant community in a basin fen in Bechler Meadows. Site # 157, Golden Waves Fen.



B. *Carex livida* – *Drosera anglica* plant community in Bechler Meadows. Site #162, Great Grey Owl Fen.



C. Two stands of vegetation in a basin fen: floating mat stand of *Carex limosa* – *Menyanthes trifoliata* and semi-aquatic stand of *Nuphar lutea* ssp. *polysepala* – *Potamogeton* spp. in central YNP. Site # 30, Cygnet Lake Trail Fen.



D. Large sedge community *Carex utriculata* – *Galium trifidum* in a basin fen in Swan Lake Flats. Site #56, Little Swan Lake.



E. Spring mound fen dominated by *Philonotis fontana* – *Carex utriculata*. Site #22, Indian Creek Spring Mound.



F. Steeply sloping fen dominated by *Philonotis fontana* – *Carex utriculata*. Site #24, Madison Seep Slope.



G. Gently sloping fen dominated by *Carex aquatilis* – *Carex urticulata*. Site #68, Grizzly Lake Trailhead Fen.



H. High elevation stand of *Carex aquatilis* – *Pedicularis groenlandica* in the Gallatin Mountains. Site #143, Top of the World Fen.



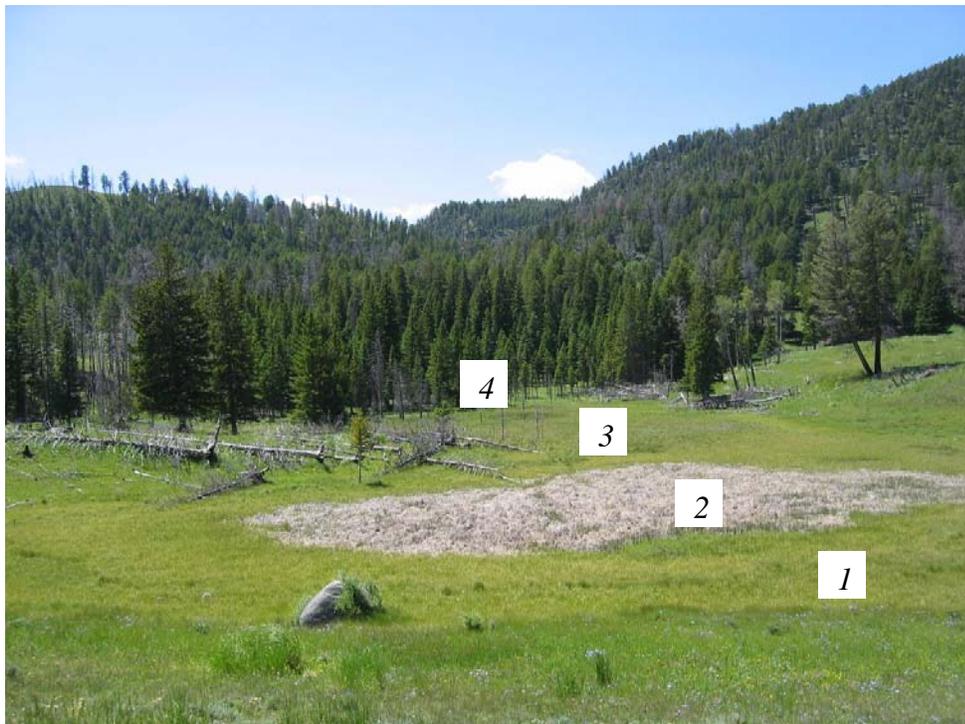
I. Shrub stand of *Salix wolfii* – *Pentaphylloides floribunda* in a gently sloping fen in northern YNP. Site #14, Pleasant Valley.



J. Stand of *Salix planifolia* – *Carex aquatilis* with high cover of *Salix candida* in a basin fen. Site #25, Swan Lake.



K. Forested stand of *Picea (engelmannii, glauca)* – *Equisetum arvensis* in northern YNP. Site #15, Elk Creek Lower Fen.



L. Gently sloping fen with multiple communities in northern YNP. 1 = *Carex utriculata* – *Galium trifidum*, 2 = *Schoenoplectus acutus* var. *occidentalis* – *Carex utriculata*, 3 = *Salix wolfii* – *Pentaphylloides floribunda*, and 4 = *Picea (engelmannii, glauca)* – *Equisetum arvensis*. Site #7, Floating Island Lake Fen.



M. Acidic geothermal fen with high sulfur content. Black mats are *Gymnocolea inflata* – *Drepanocladus polygamus* and forested margin is *Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var *latifolia*. Site #88, Bog Creek White Pools Fen.



N. Large, acidic geothermal fen in central YNP. Main vegetation is *Sphagnum* spp. – *Carex aquatilis*, here dominated by *Sphagnum lindbergii*. Site #113, Sulphur Creek Thermal Fen.



O. Floating mat vegetation in a basin fen. Multiple communities present: *Nuphar lutea* ssp. *polysepala* – *Potamogeton* spp. in lake, *Carex limosa* – *Menyanthes trifoliata* as main matrix, and *Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var *latifolia* on hummocks. Site #32, Sulphur Hills Floating Mat.



P. Close-up of vegetation in *Sphagnum russowii* – *Kalmia microphylla* – *Pinus contorta* var *latifolia*. Site #111, Peaceful Fen.