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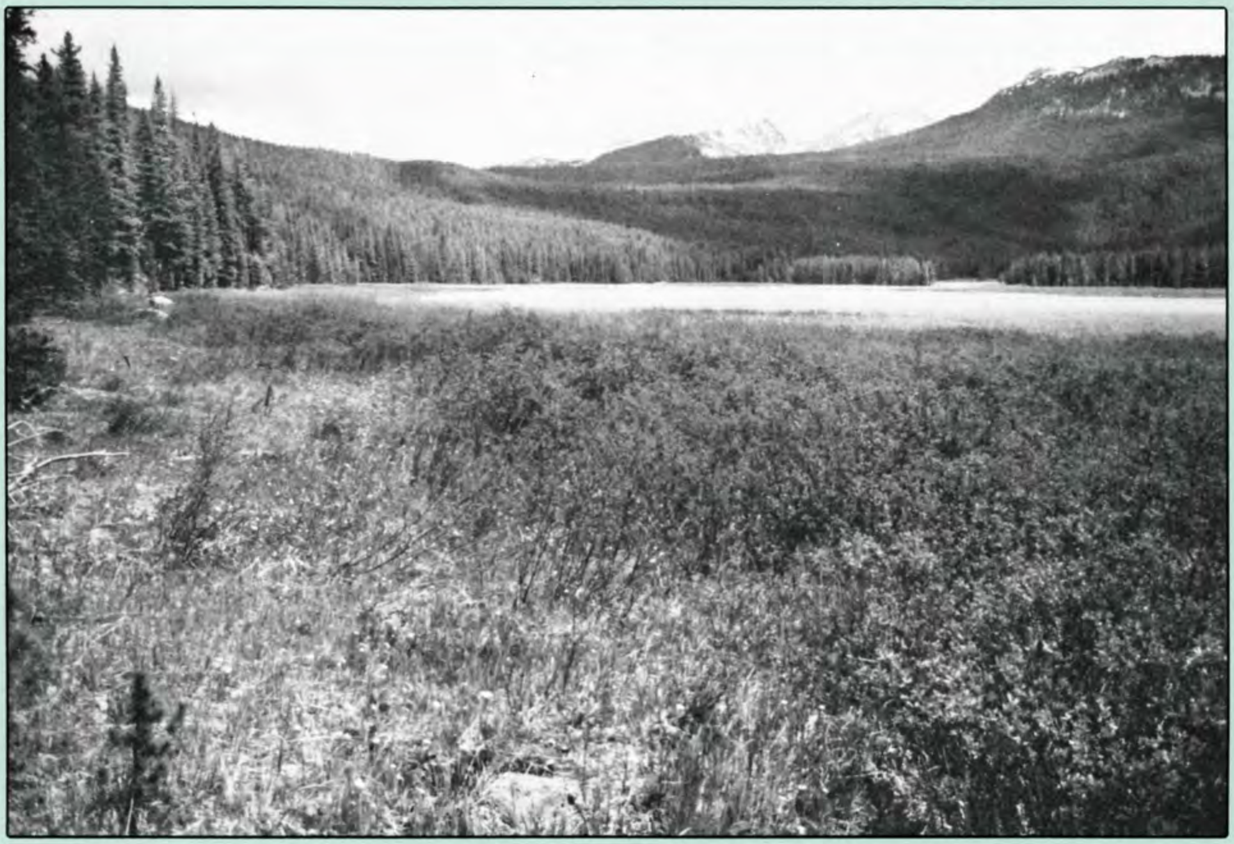

Fish and Wildlife Service

U.S. Department of the Interior

Biological Report

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ABSTRACT.—This report describes in detail the result of 1987–88 studies of hydrology, water chemistry, soils, and vegetation in the Big Meadows–Green Mountain Trail Pond wetland complex, which is at an elevation of 2,865 m in the Rocky Mountain National Park in north-central Colorado. Five water sources affect the complex and each water source somewhat differently structures the hydrological character, vegetation, and water chemistry of various portions of the wetland complex. Twelve plant communities that make up the wetland complex are described and characterized relative to hydrology, soils, and water chemistry measurements taken throughout the complex. The water table is highest in May and lowest in fall and early winter. The growing season usually lasts only 3 months (late May to late August), and water tables fluctuate drastically among years depending on the depth of the snowpack. Thus, plants and soils have developed under a hydrological regime involving large annual variability. Soil saturation during July seemingly is the critical variable for peat formation in the study area. Sites with a water table within 20–30 cm of the surface in July usually support peat soils. Oxidation–reduction potential measurements indicate that for any soil depth, the soils stay reduced for up to 3 weeks after a water table drop below that depth.

Headwater wetland ecosystems in the Rocky Mountains are some of the most pristine, yet poorly studied, ecosystems in the American West. Because many of these wetlands are large and occupy valley bottom positions behind glacial end moraines, they are a focal point for the movement of surface waters and groundwaters from higher elevations in the entire watershed. They are also the focus for sediment and nutrients moving from higher to lower portions of the watershed. Thus, they may have a critical function in regulating the movement and form of these substances.

High mountain wetlands are fundamentally different than wetlands occurring at lower elevations that were never glaciated (Cooper and Lee 1987). They occupy confined valleys widened by glaciers and buried by glacial outwash deposits. Wetlands at lower mountain elevations typically occupy (1) streamsides in narrow valleys where the soils are largely alluvial and structured by the energy of moving water or (2) intermountain basins where groundwater is the principal source of saturation. Wetlands within the zone of Pleistocene glaciation have cold soils, often accumulate peat, and are greatly influenced by a huge flush of weakly minerotrophic snowmelt water in early summer.

Wetlands occupy an estimated 0.5 to 2% of the Colorado landscape. They can only occur on slopes where there is a constant source of groundwater discharge, and along creek banks. Glacial moraines deposited during the Pleistocene have modified this runoff scenario, roughening the topography and impeding drainage. Large mountain wetland complexes have developed in nearly level valley bottoms where the kinetic energy of falling water is dissipated (Moore and Bellamy 1974). In these sites, fine-textured soils are deposited and water remains longer than on slopes.

Wetlands in the Rocky Mountains have been the focus of only a handful of ecological studies, many of which had limited scope. These studies have been summarized and reviewed elsewhere (Cooper 1986). The Big Meadows area of Rocky Mountain National Park was selected for this study because it supports many different ecosystem types, and it was the site for an earlier wetland vegetation study, a valuable background source (Bierley 1972).

My goals were to (1) develop an understanding of the distribution of plant species and soils in relation to the spatial and temporal distribution of surface- and groundwaters, (2) determine the factors controlling the distribution of peat in the wetland, and (3) characterize the chemistry of the groundwaters and surface waters in the wetland and adjacent Tonahutu Creek.

The Setting

The study area is west of the Continental Divide at the headwaters of the Colorado River (Fig. 1). Two sites were studied, Big Meadows in the Tonahutu Creek valley and Green Mountain Trail Pond (Fig. 2). Big Meadows is a 63-ha wetland that occupies the broad and relatively level bottom of the Tonahutu Creek valley (Figs. 3 and 4). Tonahutu Creek flows along the eastern edge of the wetland (Fig. 5). Green Mountain Trail Pond (Fig. 6) is a small, moraine-dammed pond in the west lateral moraine of the Tonahutu Creek valley glacier. It was formed during the last major stage of the Pleistocene (at least 12,000 years B.P.). The pond and associated wetland are about 0.5 ha in size.

The Tonahutu Creek basin is about 8,800 ha, with elevations ranging up to 3,975 m on Sprague Mountain. The elevation of both study areas is about 2,865 m.

Geology

The geologic setting is a glacially carved basin on the western side of the Front Range. Metamorphic and igneous rocks of Precambrian age dominate the basin and no sedimentary rocks occur. The rocks are generally poor in lime. The area was glaciated several times during the Pleistocene. Big Meadows contains gray-blue lake deposits, exposed along Tonahutu Creek (Meierding 1977), indicating that the valley was a moraine dammed lake that emptied when the moraine was breached by the creek in the early Holocene.

A seismic reflection study was performed in 1987 to determine the depth to bedrock in Big Meadows to define the bottom of the hydrogeologic setting. A portable energy source called a "buffalo gun" was used for the survey; the results indicate that no high-density interfaces occur until about 46 m below the surface of Big Meadows (Shuter 1988). This reflection surface is probably bedrock and indicates that after deglaciation a large volume of till and outwash was deposited in Big Meadows, filling the lake basin. Some of this deposit may have resulted from the moraine-damming of the valley and the impoundment of Tonahutu Creek. Thus, the relatively U-shaped valley has been filled to produce a flat-bottomed surface.

Climate and Weather

In a typical year, annual precipitation in much of southwestern Colorado shows two peaks, winter and a late summer monsoon. Northwestern Colorado stations, however, show only the winter peak. Winter precipitation is received as snow, which accumulates in the Tonahutu Creek basin and melts during May and June, flushing the basin with much of the year's total precipitation in just a few weeks.

A National Climate Center weather station (Grand Lake 1NW) is 5.6 km southwest of the study area (Fig. 1) and has a 49-year record of temperature and precipitation. This station is at an elevation of 2,646 m, about 220 m lower than the study area. The average annual precipitation from 1940 to 1988 was 49.5 cm. However, annual precipitation for Grand Lake varies greatly. Figure 7 indicates that the 6 wettest years since 1940 were 1957, 1961, 1969, 1983, 1984, and 1986. The driest years were 1944 and 1946; these 2 years were much drier than any other year in this period. Total precipitation in Grand Lake for 1987 was 36 cm, the lowest since 1946, when less than 20 cm of precipation was received. Total precipitation for 1988 was 44.5 cm, 90% of the average. Between 1947 and 1982, annual precipitation was consistent, with an occasional high year (e.g., 1957). However, 1983 through 1986 were remarkable for being 4 consecutive wet years, including the 3 wettest years (1983, 1984, and 1986) in the record. This was followed by 2 below-average years (1987 and 1988).

In much of western Colorado, June, on the average, is the driest summer month; however, the driest months at the Grand Lake station are October and November. A precipitation high occurs in late summer, but precipitation is rather evenly spread over the entire year. At high elevations in the Colorado River watershed a significant increase in winter precipitation occurs. Snowpack recorded in the late winter of 1988 in Big Meadows contained an average of 38–45 cm of water. This snowpack had accumulated since late December 1987; thus it represents only 5 months of precipitation. Rainfall during May–September provides an average of 20–25 cm of precipitation at Grand Lake (Fig. 8).

Precipitation measured in Big Meadows during June, July, and August of 1988 was similar to the total for these months recorded in Grand Lake. Summing the total water equivalent in snowpack for Big Meadows from December 1987 to March 1988 (38–45 cm) and the total precipitation received in Grand Lake from April 1988 to September 1988 (21.8 cm), the approximate annual total received at

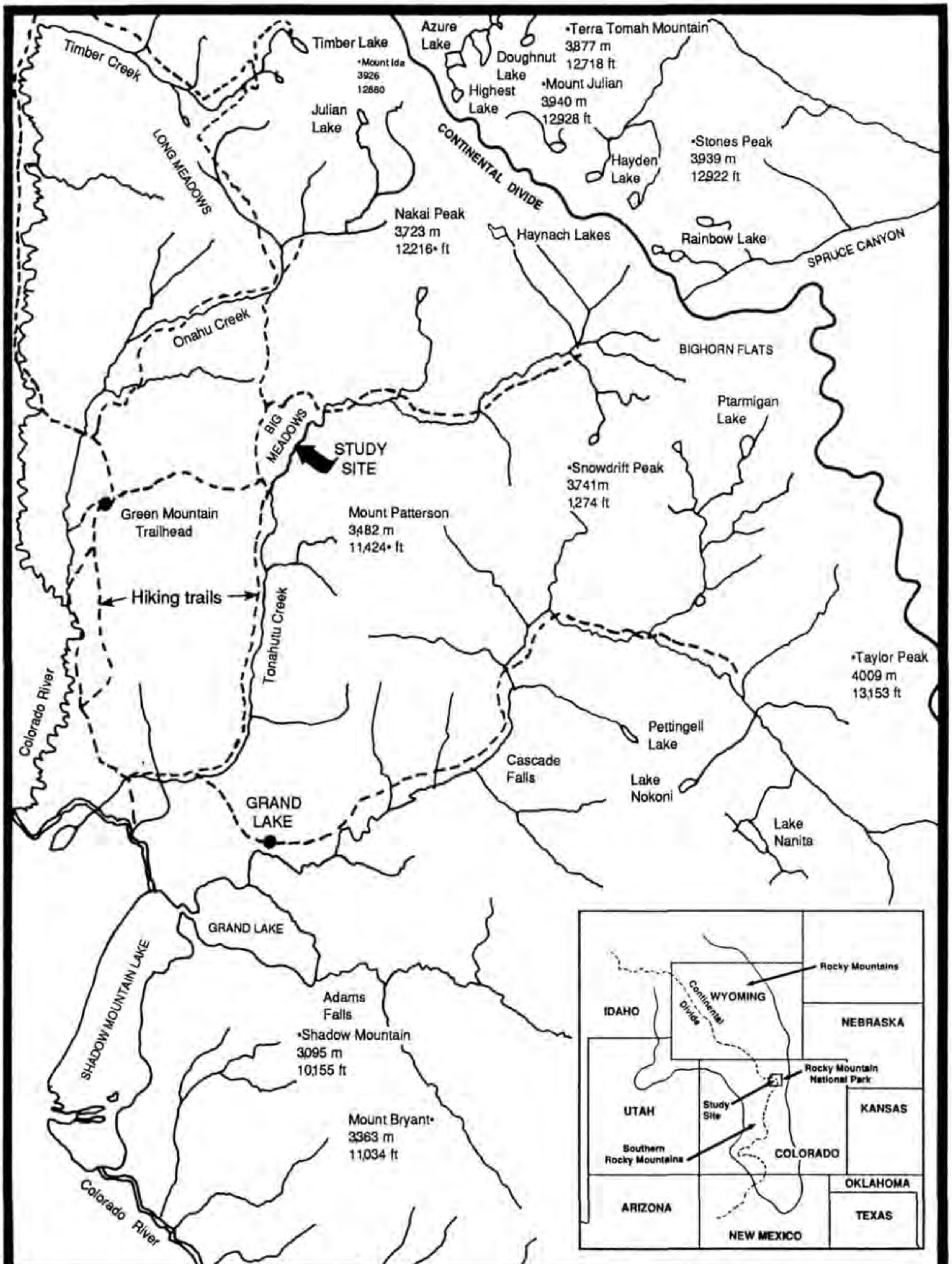


Fig. 1. Rocky Mountain National Park and the Big Meadows study area in the southwest corner of the park.

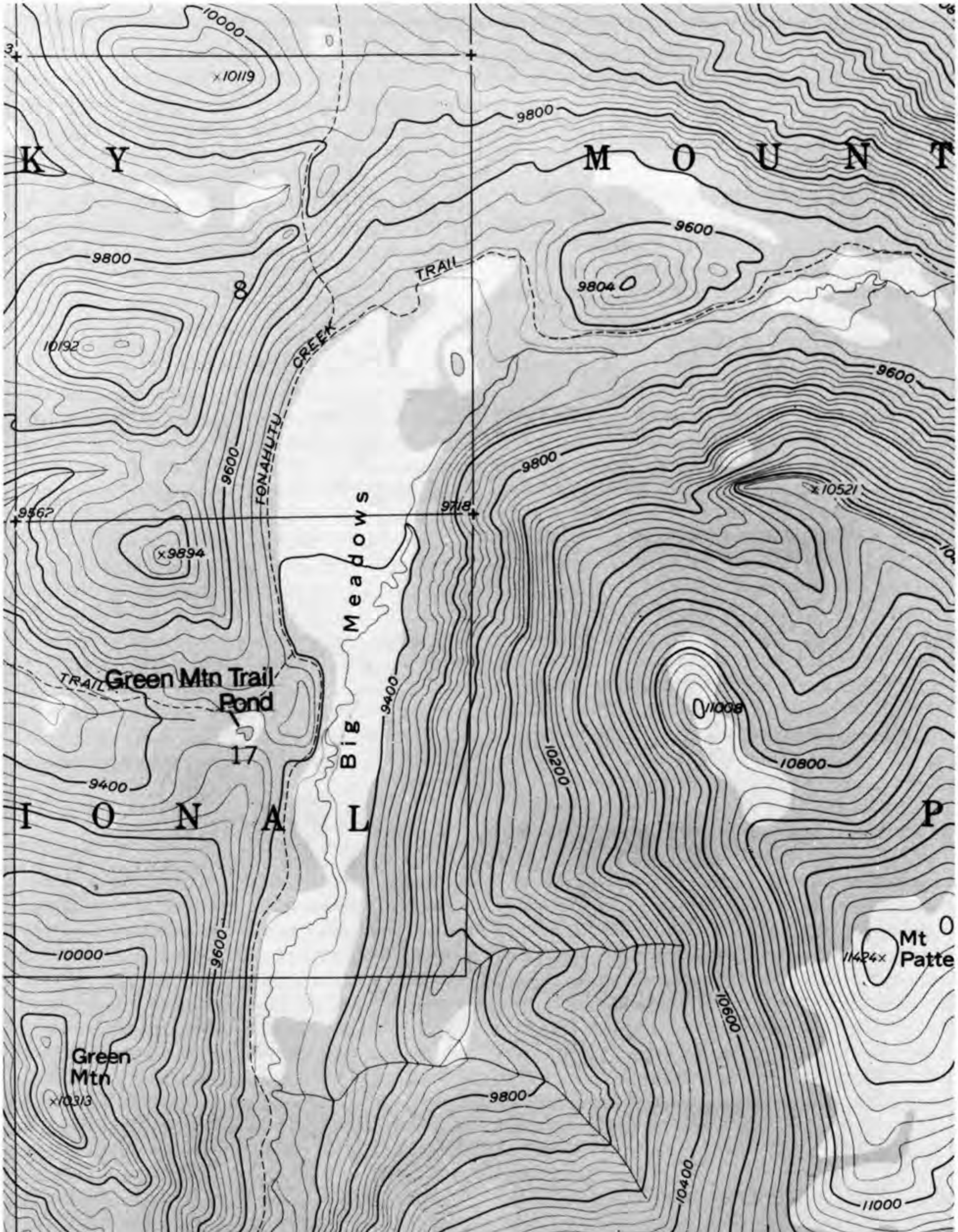


Fig. 2. Topographic map of the study area including Big Meadows and Green Mountain Trail Pond (scale 1:24,000).

Fig. 3. View looking south from the top of Mount Ida. Big Meadows is the large wetland in the *center* distance. Shadow Mountain and Granby reservoirs are at the *top* of the photograph. In the *upper right-hand corner* is the Colorado River valley. Julian Lake is in the *right foreground* and an unnamed subalpine wetland is in the *left foreground*. (Photograph courtesy of J. Benedict)

Big Meadows for water year 1988 was 66.8 cm (a water year is from 1 September to 1 September). As previously stated, the precipitation received at Grand Lake for 1988 was 90% of the 49-year average. Thus, the average for Big Meadows would be about 74 cm.

Precipitation during summer months occurs as brief afternoon showers that typically result in 0.1 to 0.3 cm of rainfall. Larger events occasionally occur. For example, during summer 1988, 15 days had at least 0.5 cm of rain (Fig. 9). Direct precipitation in the study area is small in comparison with the total amount of water received as runoff from the surrounding highlands.

Mean temperatures for Grand Lake are 24° C in July and 1° C in January. Temperatures in Big Meadows are probably somewhat cooler, and freezing temperatures can occur almost nightly during summer, because of cold air drainage and entrapment in the broad and flat wetland area. The effect of this growing-season frost on plants in the wetland is unknown.

Fig. 4. View looking north across the central portion of Big Meadows in midsummer, 1988. The dominant plant species in the wetland is *Carex aquatilis*. The dominant tree species are lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*).

Vegetation

Bierly (1972) described the vegetation of the Big Meadows study area.[1] He collected data on the presence or absence of plant species in 41 homogenous stands throughout the wetland. Indicator species were used to evaluate plant species distribution along drainage gradients. Bierly concluded that plant species were distributed continuously and normally across the drainage regime. He collected limited quantitative hydrologic data for the stands along water table and drainage gradients, but he suggested that the soil moisture regime was the overriding influence on distribution of plant species. His study did not include nutrient gradients within this report's study area.

Bierly (1972) described seven meadow and fen physiognomic vegetation types in Big Meadows. Arranged from driest to wettest, these vegetation types were dry grass meadow, dry shrub meadow, mesic grass meadow, mesic shrub fen, mesic sedge fen, wet shrub fen, and wet sedge fen. These vegetation types are compared with the community types described in this report.

Methods

Hydrology

I monitored the groundwater table in Big Meadows during 1987 and 1988 in 49 fully slotted wells. Most wells were arranged along four transects that spanned the entire width of the area. An additional 10 wells were installed

[1]Bierly misidentified several species in his study. The correct names for the most important misidentifications are as follows: *Salix brachycarpa* should be *S. planifolia*, *Penstemon whippleanus* should be *P. confertus* ssp. *procerus*, *Carex arapahoensis* should be *C. festivella*, *Luzula spicatum* should be *L. campestris*, *Antennaria parvifolia* should be *A. corymbosa*, and *Eriophorum gracile* should be *E. angustifolium*.

Fig. 5. Tonahutu Creek flows along the eastern side of Big Meadows. This view (looking north) was in October 1987, when the creek was very low. A recently constructed beaver dam is visible in the *center* of the photograph.

and monitored at the Green Mountain Trail Pond. The location of all wells and transects of wells used in this study is shown in Fig. 10.

The well casing was made of polyvinylchloride (PVC) pipe with an inside diameter of 6.35 cm. I made vertical slots in the pipe with a circular saw; the slots were about 10 cm long and 0.1 cm wide. Wells in peaty substrate were hand-augered with a standard bucket auger with a diameter just slightly larger than the well casing. The wells, which were up to 165 cm deep, were installed through the entire peat column down to the underlying alluvium and glacial outwash or till. In cobbly alluvial soils the use of an auger was impossible, and wells were installed into hand-dug holes up to 185 cm deep. The well casing was placed into the hole and carefully backfilled with the native soil. To prevent seepage of water into the well casing, I sealed the wells at the soil surface with clay extracted from some holes. Most wells were easily developed by pumping until clean water indicated that groundwater was flowing into the well. All wells seemed to work properly and water would regain the same elevation after pumping at any time during the summer. I collected data on the elevation of the water table at each station weekly throughout the snow-free season.

I installed piezometers at a number of different stations to measure hydraulic head. Piezometers were constructed of PVC pipe with an inside diameter of 1 cm and were installed using the method described by Rutter (1955) and Siegel and Glaser (1987). A metal rod that fit snugly inside the PVC pipe was used to give it rigidity and to keep the pipe from being plugged with peat as it was forced through the peat body and into the underlying alluvium. The metal rod was removed when the pipe was in place. I measured the elevation of water in piezometers at the same time as the groundwater monitoring wells.

I monitored the elevation of surface water in Tonahutu Creek with staff gauges at several stations along the creek bank. The stations were at the end of groundwater well transects that crossed Big Meadows. Readings were taken weekly in the middle of the day. To determine the total

Fig. 6. The edge of Green Mountain Trail Pond is about 2 m deep. Water lily (*Nuphar luteum* ssp. *polysepalum*) occupies the open water while buckbean (*Menyanthes trifoliata*) occurs on the pond edge in the *foreground. Carex utriculata* dominates the wetland on the far side of the pond, and *Pinus contorta* occurs on small islands in the pond. July 1988.

diurnal amplitude of surface water elevation change during spring runoff in June, I took readings several times each sampling day. I had problems with the surface water portion of the study because beavers gnawed off the wooden stakes used as staff gauges.

I developed a new method to assess the wetness of a station to handle the continuous measurements of depth to water table. A cumulative index was developed by tabulating the total centimeters of water table above 1 m (100 cm) below the soil surface for each day. For example, a station with a daily water table of 90 cm for July would have an index of 310 centimeter-days (10 cm × 31 days); a station with a water table 10 cm below the soil surface for July would have an index of 2,790 centimeter-days (90 cm × 31 days); and a station with standing water 10 cm above the soil surface for July would have an index of 3,410 centimeter-days (110 cm × 31 days). This centimeter-days index for wells for each month seems to give a more accurate picture of water table than the average depth to water table for the month. I used 1 m as the base level because most upland and wetland plants in the Rocky Mountains have all their roots within 1 m of the soil surface, and soil saturation due to capillary rise probably will not occur when water is >1 m from the soil surface. Thus, the centimeter-days index is a measure of how much of the rooting zone is saturated.

Land Surveying

I surveyed the study area to determine the elevation of wells in relation to each other and to the ground surface. All elevations are based on an arbitrary 30.48-m elevation point at the southwestern corner of Big Meadows.

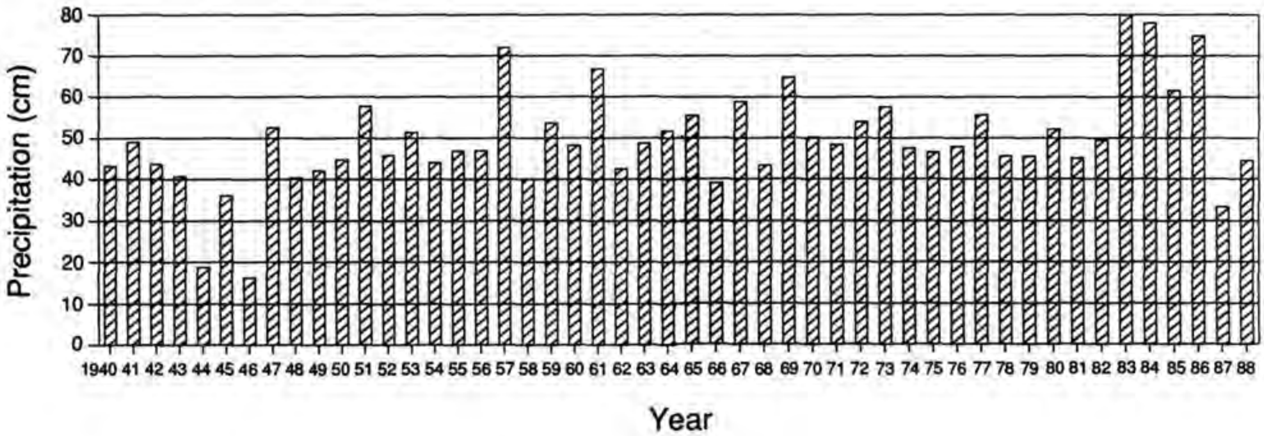


Fig. 7. Total annual precipitation for Grand Lake 1 NW station, 1940–1988.

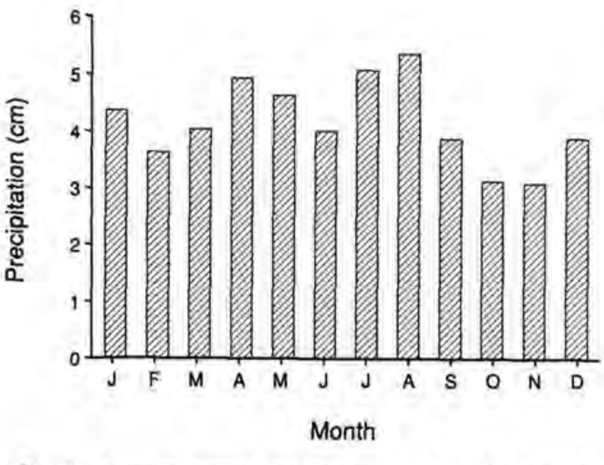


Fig. 8. Average monthly precipitation for Grand Lake 1 NW station, 1940–1988.

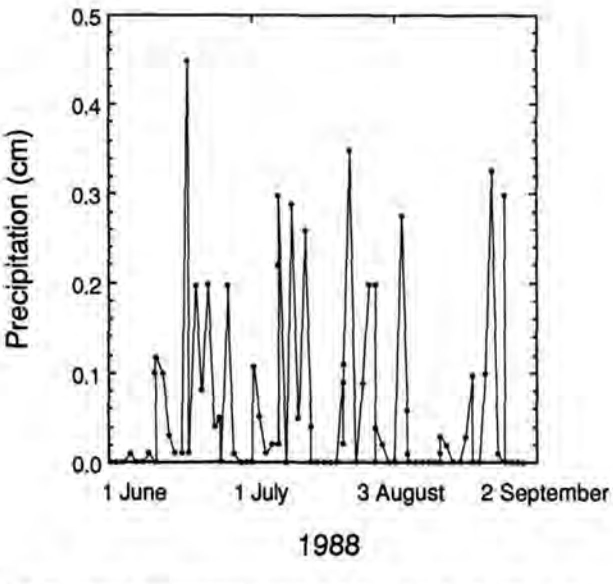


Fig. 9. Daily precipitation (cm) for Grand Lake 1 NW station, June–September 1988.

Shuter (1988) constructed water table elevation maps with the SURFACE II GRAPHICS SYSTEM. These maps were constructed only for 1987 to show the water table gradients in Big Meadows.

Vegetation

I determined where to place the groundwater wells by the vegetation composition along the transects. Wells were placed in stands of homogenous vegetation. The transect locations and well sites were selected to represent the entire range of variation in the vegetation and water table in the study area. The vegetation in the study area varies from ponds and pools, to fens and willow carrs, grasslands, shrublands, and conifer forests. Most stations were placed along transects to monitor the water table characteristics of the wetland. Hence, a large number of stations occur in the relatively homogenous sedge-dominated peatland that forms the western side of Big Meadows.

Vegetation was studied by using the releve method of Braun-Blanquet (Westhoff and Maarel 1978). A releve is

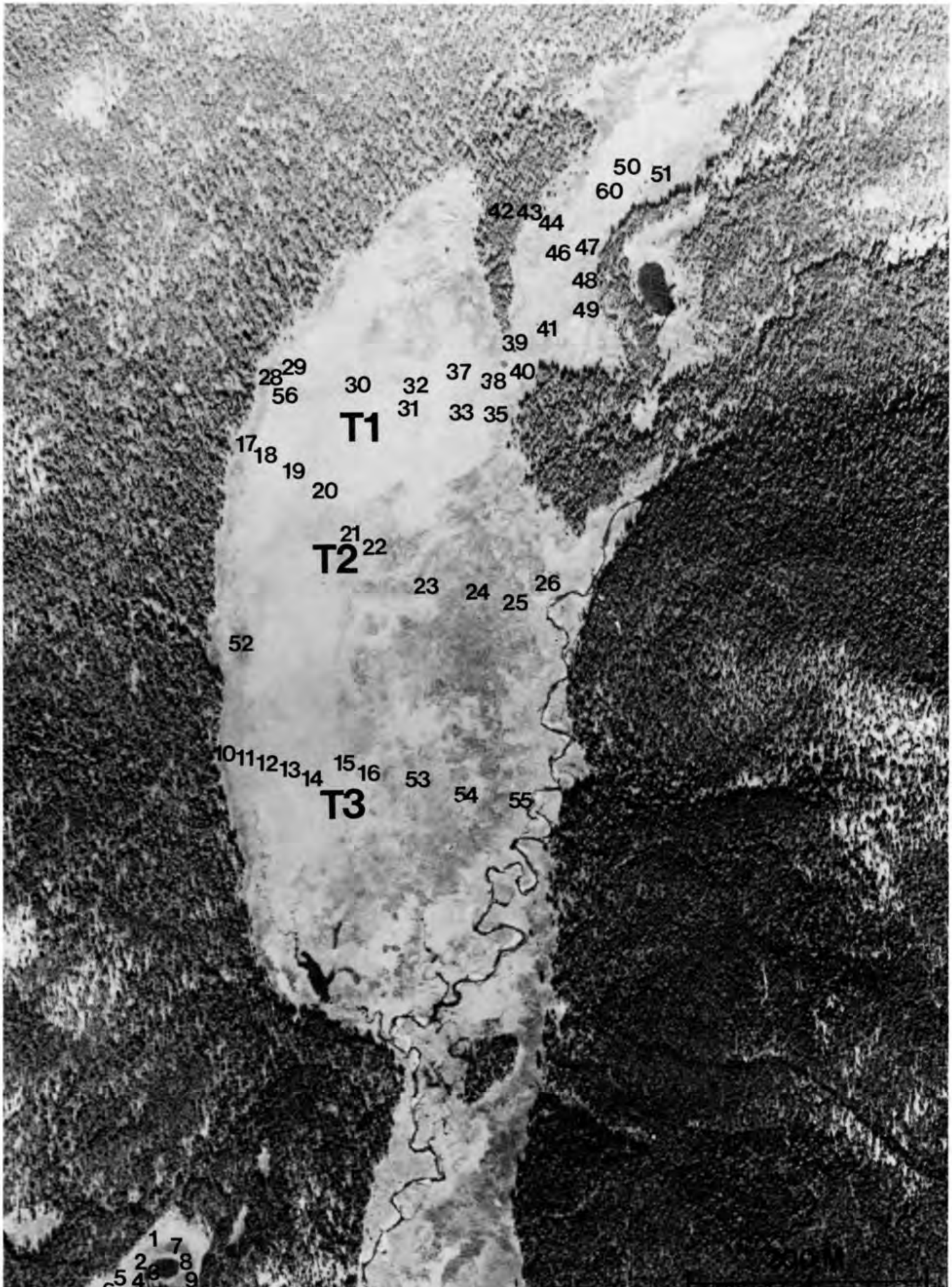


Fig. 10. Aerial photo showing sampling stations and transects at Big Meadows and Green Mountain Trail Pond. Green Mountain Trail Pond is in the *lower left*.

a sample stand used for field analysis. The Braun-Blanquet approach uses floristic criteria to classify vegetation. On the northern side of each groundwater well a releve of about 10 m^2 was taken. During the peak of each growing season, I listed all plant species within the stand and recorded canopy coverage of each species. Where microtopographic relief >10 cm occurred, the releve was doubled in size and included only that portion of the microrelief pattern that coincided with the elevation of the groundwater well. For example, in a hummocky site a groundwater well placed through the top of a hummock would be correlated only with the vegetation of hummock tops. The vegetation in the lower troughs between hummocks was ignored. Mosses are known to be specific indicators of environmental conditions, but are not abundant in the wetlands. The mosses that did occur were collected, but final identification of some species has not been completed.

I obtained a random plot within each releve by throwing a 0.2-m^2 quadrat over my shoulder. I clipped the vegetation within this plot at the end of the growing season to determine standing crop. The plant samples were first air-dried for 3 months in a heated office building. Three samples of each species were weighed, dried in an oven at 105° C for 24 h, and weighed again to determine percentage of weight loss. The samples for each species were then weighed on a balance to the nearest 0.1 g, and the percent weight loss that would have occurred had all samples been oven-dried was subtracted from the weight. Most species lost 3-5% of their weight during oven drying.

I used the Multivariate Statistics Package of Kovach (1986) to construct polythetic hierarchical dendrograms. Vascular plant nomenclature follows Weber (1987), and bryophyte nomenclature follows Weber (1973).

Soils

During summer 1988, I hand-dug pits to examine the soil at each station. The pits were described according to standard methods (Buol et al. 1980; Soil Survey Staff 1975). Soils were classified according to Soil Taxonomy (Soil Survey Staff 1975).

At 10 stations I measured oxidation-reduction potential with bright platinum-tipped probes inserted into the soil at 7, 15, 30, and, in some instances, 45 cm. Measurements to the nearest millivolt (mV) were made weekly during the growing season with a Corning model M105 pH-millivolt meter and Corning Calomel reference electrode. Three probes at each depth at each station were used for replication, and the data presented are means for the three measurements. To correct for the Calomel reference probe, 244 mV were added to the means.

Soil temperature was measured at 7, 15, and 30 cm with Cole-Parmer Type J thermocouples and a digital thermometer. Measurements were made weekly during the snow-free season, and monthly during the snow-covered season.

Chemical and textural analyses were performed on soil samples at the soils laboratory at Colorado State University in Fort Collins. Conductance and pH were taken from a 1:1 paste of soil and distilled water. Percent organic matter was determined with a modified Walkley–Black method. If organic matter was > 7% the sample was ashed at 550° C in a furnace to determine weight loss on ignition. Extractable Ca++ (extracted with ammonium chloride) and Fe (extracted with ammonium bicarbonate-DTPA) were analyzed using inductively coupled plasma atomic emission spectometry.

Soil texture was determined with the hydrometer method. Cation exchange capacity (CEC) was measured by using 0.5 normal Mg Cl^2 as the exchanging solution and the measurement of the displaced solutions by using atomic absorption spectometry. Base saturation was calculated from exchangeable cations from an ammonium chloride extract and CEC. Soil texture, CEC, and base saturation were measured as an aid in soil classification.

Radiocarbon Dating

I extracted peat cores from Big Meadows and the Green Mountain Trail Pond using a 5-cm diameter modified Livingston corer (Wright et al. 1984). All peat samples were radiocarbon dated by Teledyne Isotopes in Westwood, N.J.

Water Chemistry

I collected water samples for nutrient and metals analysis. Wells were bailed out twice or until as clean as possible and allowed to refill before samples were collected. I collected water samples from Tonahutu Creek above and below Big Meadows, springs on the western side of the wetland, the northern tributary, surface water in the wetland, and water from wells and piezometers. Water collected from piezometers was obtained from the alluvium beneath the peat.

Water samples were analyzed (by using Inductively Coupled Plasma Analysis) directly for the following ions: Ca++, Mg++, Na++, Fe, Al, Cu, and Zn. Total organic carbon was analyzed with an Astro analyzer using persulfate digestion and ultraviolet (UV) detector. Dissolved organic carbon was filtered and then analyzed as described for total organic carbon. Carbonate and bicarbonate were determined using a titration method with H_2SO_4, phenolphthalein, and bromcresol green-methol blue.

Results

Water

Surface Water Hydrology

Three surface water sources drain into Big Meadows (Fig. 11): (1) Tonahutu Creek flows along the eastern side of the meadows; (2) an unnamed spring-fed stream empties into the northern end of Big Meadows and flows as sheet water across the meadow (this tributary is called the northern tributary throughout this report); and (3) springs flow from the base of the mountains on the western side of Big Meadows.

Tonahutu Creek has become incised into its alluvial floodplain of coarse gravels. Its banks are undercut and sloughing into the creek in several areas, which indicates that it is actively meandering. Bank-full discharge for Tonahutu Creek is 1.38 m^3s^{-1}; however, the peak discharge received at that station during 1987 was 1.13 m^3s^{-1} (Shuter 1988).

Tonahutu Creek reaches its maximum discharge during early June, and peak daily flow decreases gradually during the remainder of the summer. The creek does not seem to regularly flood into the main part of Big Meadows. During peak discharge it expands its width onto gravel bars and other portions of the recently abandoned channel.

Flow in the northern tributary has not been measured, but it seems to carry at least 0.1 m^3s^{-1} in the early summer, and gradually decreases its flow in late summer until the creek eventually dries up. This water sheet-flows on the surface of Big Meadows during early summer, creating flooding conditions on the entire northern and western portions of Big Meadows, where peat soils occur.

Springs on the western side of Big Meadows flow only in early and midsummer. This water is seemingly discharged from an upland aquifer of colluvium and glacial till that blankets the upper mountain slopes. This water saturates the wetland along the western side of Big Meadows.

A ditch, or the eroded remnants of an old hiking trail (Bierley 1972), occurs in the center of Big Meadows (Fig. 12). This ditch carries surface water from north to south and intercepts the sheet flow of surface water from the northern tributary. The ditch carries 0.015–0.025 m^3s^{-1}, which represents a large percentage of the spring and all of the summer surface water input from the northern tributary. Hence, the ditch has modified the surface water flow and the mid- to late summer groundwater levels in the southern and western portions of Big Meadows. The ditch is presently being blocked off to restore the natural flow of water from north to south across Big Meadows.

Table 1. *Mean conductivity ($\mu mhos/cm^2$) in Tonahutu Creek at northern end of wetland* (N = *number of samples).*

Date	*N*	Conductivity
14 June	4	13
13 July	2	14
3 August	2	13
11 October	3	13
8 November	3	15

Water Chemistry in Tonahutu Creek

Tonahutu Creek is fed largely by snowmelt runoff and colluvial, alluvial, and bedrock aquifers. As shown in Table 1, this water is of extremely low electrical conductance throughout the year. The water also has low concentrations of Ca++ (mean of 1.18 mg/L on 14 June 1988, and 1.41 mg/L on 8 November 1988) and other ions.

Concentrations of HCO_3^-, the leading anion in the water, were low during the entire summer (ranging from 4.3 to 7.2mg/L), with an overall slight decrease in concentration late in the summer.

Total organic carbon in Tonahutu Creek is highest in the early summer, decreasing into fall, and most carbon in the water is dissolved, not suspended. Total organic carbon in the creek water increases up to 10% between the northern and southern ends of Big Meadows, a distance of about 1 km.

Concentrations of iron and the sum of cations in Tonahutu Creek increase greatly as the creek crosses Big Meadows, particularly in late summer and fall (D. J. Cooper, unpublished data). These increases result from groundwater discharge from Big Meadows into the creek. At present, it is unknown how the modification of water chemistry by wetlands influences the aquatic habitat of Tonahutu Creek and its suitability for invertebrates and fish.

Ground Water Hydrology

Shuter (1988) prepared maps of the water table from 1987 water table data. Figure 13 shows the water table on 11 July, which is the peak of the growing season. The major water gradients shown on this map are (1) the flow of water from north to south down the elevation gradient, (2) flow from seeps along the western edge of the wetland, and (3) a groundwater mound oriented north–south in the east-central portion of the wetland area. This groundwater mound (which may be recharged by Tonahutu Creek in the northeastern portion of Big Meadows) is in alluvial soil material between the peat body and Tonahutu Creek.

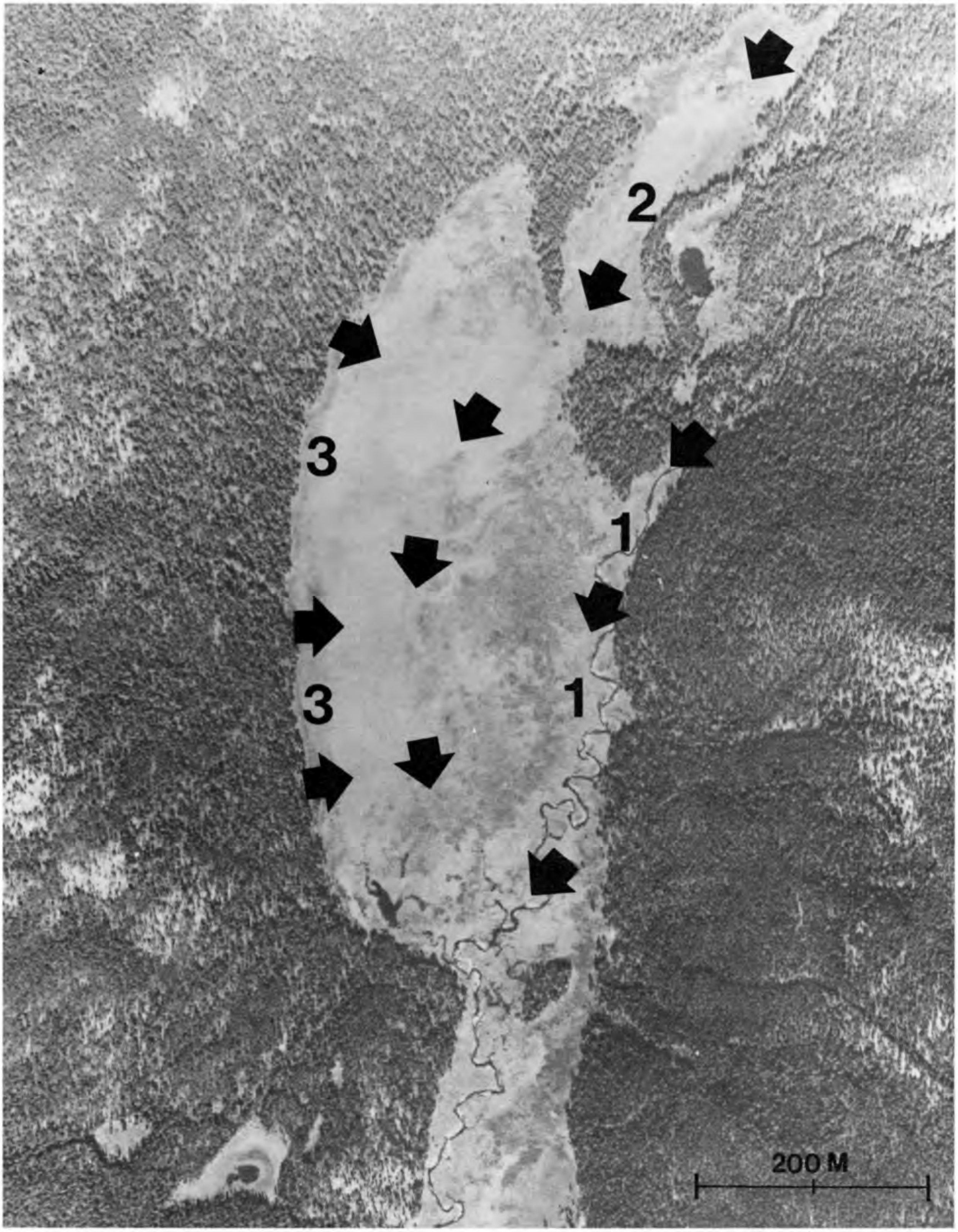


Fig. 11. Aerial photo showing the three major surface water sources in Big Meadows (1 is Tonahutu Creek, 2 is an unnamed tributary that enters Big Meadows on the north, and 3's are seeps from the western edge).

Fig. 12. View looking north up the ditch that occurs in the center of Big Meadows. The plant dominating the vegetation is *Carex aquatilis*. The high peak in the distance is Mount Ida, 3,901 m in elevation.

The principal gradient of groundwater movement from north to south is evident throughout the summer, as is a west to east gradient of groundwater entering Big Meadows from the west.

Groundwater mounds are important in the evolution of patterned mires in northern Minnesota (Siegel 1983), but little is known about them in the Rocky Mountain region.

Groundwater profiles were constructed to illustrate the elevation of the ground surface and the elevation of the groundwater surface along the transects for different dates during summer 1988. These profiles are valuable for two general purposes: to illustrate differences in water table characteristics along a transect at different times during the same year, and to compare the water table at the same date in different years.

Transect 2 (stations 17, 18, 19, 20, 21, 22, 23, 24, and 25) is oriented along the contour of the wetland and illustrates (Fig. 14) that the ground surface of the wetland is somewhat concave (particularly on the western side), rising to the mountain slopes on the west and the alluvial floodplain of Tonahutu Creek on the east. The western 250 m along this transect have peat soils. Both the ground surface and the water table in the peatland are distinctly concave. Surface flooding from the northern tributary occurs on the peat in early and midsummer.

The water table in the eastern side of the transect is higher than the water table in the peatland, even though it is well below the soil surface throughout the season. The westernmost two stations (17 and 18) on this transect are especially consistent in water table elevation in early summer because of the flow of groundwater from springs on the western wetland edge. Station 22, on the eastern edge of the peat body, also maintains a constant water table. Stations 20 and, especially, 21 are flooded for many weeks.

The drop in water table between early June and mid-July 1988 (Fig. 14) is small for peatland stations but substantial for stations in the alluvium. The drop in water table between mid-July and 1 September for all stations is substantial, but it is most dramatic for the stations in the peat body, where a drop of 30–40 cm occurred. This change coincides with the drying up of the northern tributary and reduced flow from springs on the west, which has resulted from the depletion of the colluvial and bedrock aquifers that supply these waters. The groundwater elevation is higher in the mineral soil on the eastern portion of this transect throughout the seasons, indicating that a gradient of groundwater flow to both the peatland and Tonahutu Creek occurs from this area.

Differences in the elevation of the water table along transect 2 on 1 July 1987 and 1 July 1988 are shown in Fig. 15, illustrating that the major gradients are the same for the 2 years. However, a difference in the elevation of the water table is noticeable for almost all stations, with water levels being higher in 1988. As mentioned earlier, the Grand Lake weather station recorded 10 cm greater precipitation during 1988 than 1987. The greater total snowpack in the Tonahutu Creek watershed during 1988 probably caused this difference.

The late July comparison (Fig. 16) between 1987 and 1988 reveals a much greater difference between years. For example, station 19 had a water table more than 30 cm lower in 1987 than in 1988. Most other stations also had a significantly lower water table in 1987 than in 1988. However, the difference between 1987 and 1988 varies between stations, indicating the complexity of the groundwater hydrologic regime.

Hydrographs were constructed for individual wells to illustrate the types of water table regimes in the study area. Station 10 (Fig. 17) is on the western edge of the study area and has a water table near the ground surface for much of June and early July, but its water table drops sharply by mid-August. This drop is probably associated with the depletion of the colluvial aquifer on this slope and the drying up of springs that support the water table. The major differences between 1987 and 1988 were that the water table was about 10 cm lower for the same dates in 1987 than in 1988, and the aquifer was depleted earlier in 1987.

Station 13 (Fig. 18) is in the center of the peatland expanse. Its hydrologic regime is characterized by flooding with slowly moving water from the northern tributary in June and July, with a sharp drop in the water table beginning in late July and continuing until early September. The upper peat horizons dried out in late summer. The hydrographs show that the water table was deeper throughout the summer of 1987 than in 1988 and that the water table drop occurred several weeks earlier in 1987. In mid-July during both years, a rise in water table was experienced because of a heavy rainfall.

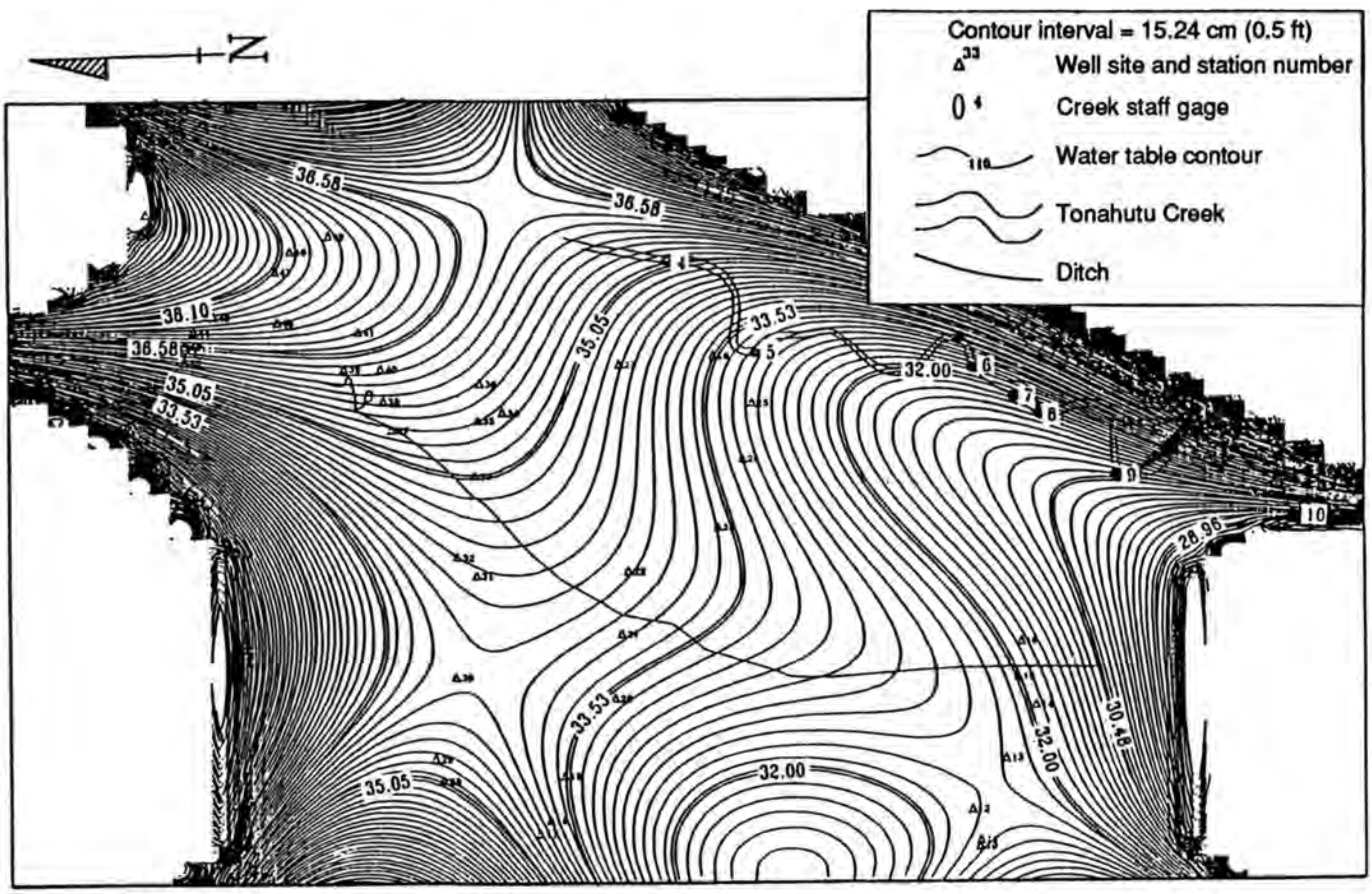


Fig. 13. Water table map of Big Meadows for 11 July 1987 (from Shuter 1988). The contour interval is 15.24 cm. The major flow directions are north to south throughout the wetland, although a west to east component occurs on the western wetland edge.

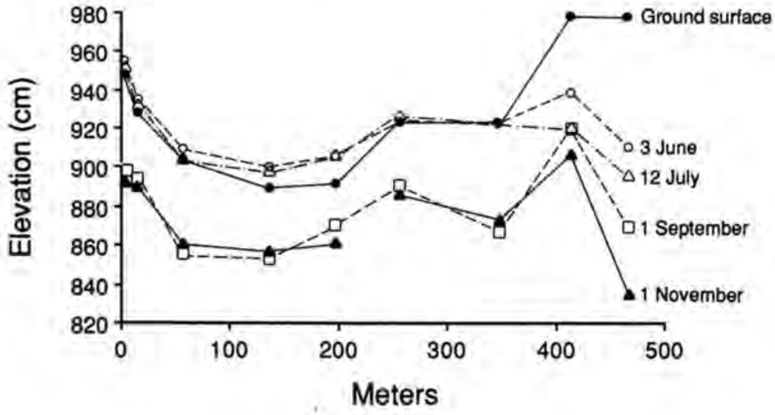


Fig. 14. Water table profile along transect 2 on different dates during 1988. West is on the left side of the figure and east is on the right side. Data points shown are the stations along transect 2, stations (*from left to right*) 17 through 25. This figure shows that the water table is highest in June and July, but drops considerably by September and remains low through early winter.

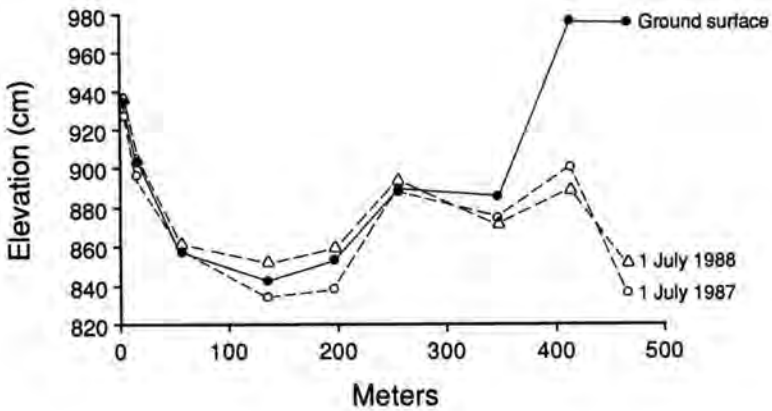


Fig. 15. Comparison of the water table elevation along transect 2 on 1 July 1987 and 1 July 1988. The water tables are similar for the 2 years.

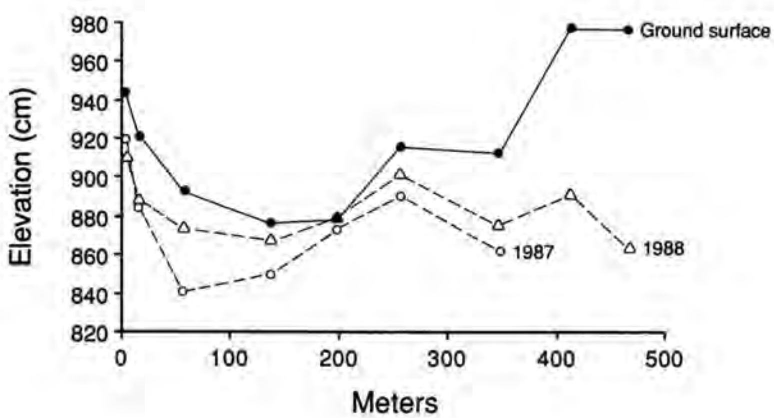


Fig. 16. Comparison of the water table elevation along transect 2 in late July 1987 and late July 1988. A greater difference in the water tables on this date can be seen than that shown for 1 July shown in Fig. 15, especially on the western side of Big Meadows.

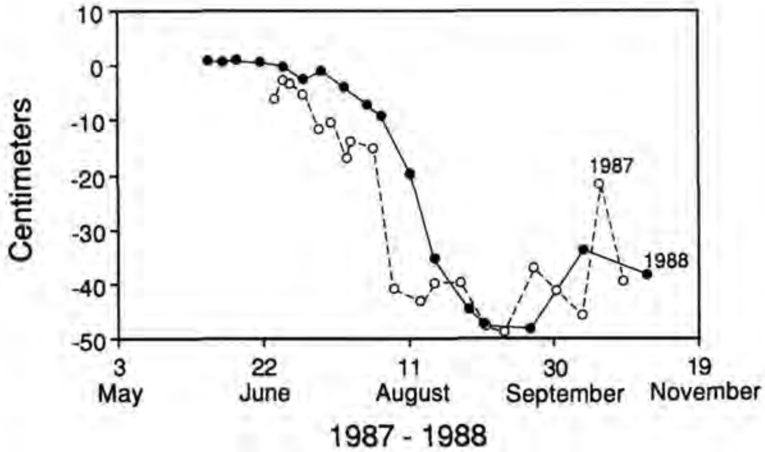


Fig. 17. Water table elevation at station 10 during 1987 and 1988. The water table is much lower during the main portion of the growing season (July and August) in 1987 than in 1988.

Station 36 is on the eastern edge of transect 1 in a coniferous forest stand. The water table (Fig. 19) is close to the soil surface in early June and drops steadily and continuously through the seasons. Slight increases in the water table in mid-July and early August are in response to rainy periods. This hydrograph indicates that forests in Colorado can occur on soils that are completely saturated in early summer.

Station 44 (Fig. 20) is in the northern portion of Big Meadows in a stand dominated by willow (*Salix planifolia*) and Canada reed grass (*Calamagrostis canadensis*). The water table in this stand is close to the surface for several weeks in early June and drops sharply by late July.

Stations 46 (Fig. 21) and 51 (Fig. 22) are both in the water track formed by the sheet flow of water from the northern tributary across the northern portion of Big Meadows. The hydrographs for these two stations declined in a similar way in early August 1987 and late August 1988 as sheet flow of the northern tributary dried up. When surface water dried up the water table dropped ≥ 30 cm in several weeks, indicating that the water table in this portion of the wetland is supported largely by this source.

The hydraulic head at the base of the peat column was measured in piezometers at stations 46, 52, 13, 26, and 32 during summer 1988 to determine if Big Meadows is a groundwater discharge or recharge area and if any temporal patterns existed for groundwater recharge and discharge. If the head at any depth in the soil was higher than the water table it indicated a groundwater discharge at that soil depth.

Figure 23 (station 46) illustrates the water table and hydraulic head at depths of 137 cm and 45 cm in the peat in the northern portion of the peatland. The hydraulic head at 137 cm was higher than the water table early in the summer, but dropped to below the water table by mid-July. The water table at 45 cm was below the water table during the entire sample period. This indicates that groundwater discharge occurs from the alluvium underlying the peat into the peat, but the pressure on this water is reduced by midsummer, and the pressure on the water in the peat body seemingly causes the peat itself to be a recharge zone. Stations 13 and 52 were groundwater discharge sites for the entire study period. Station 28 (near the wetland mar-

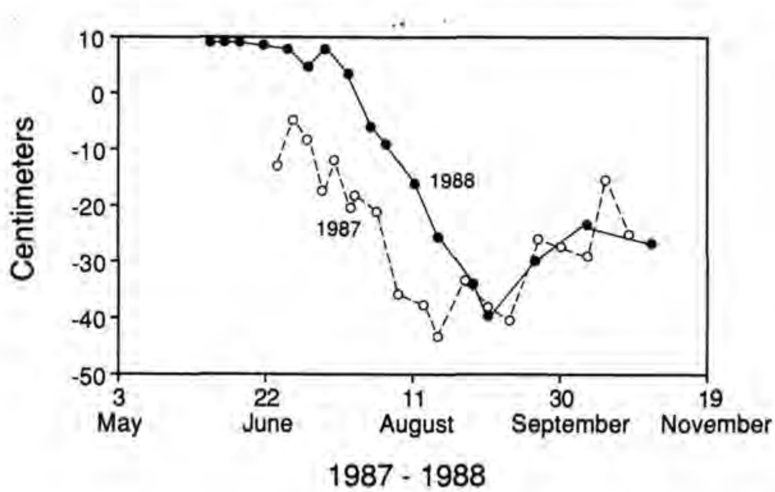


Fig. 18. Water table elevation at station 13 during 1987 and 1988. The water table is much lower during the main portion of the growing season (July and August) in 1987 than in 1988.

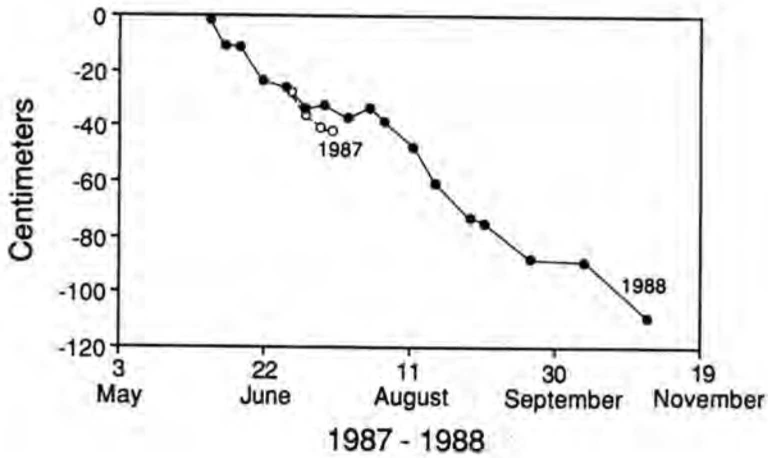


Fig. 19. Water table elevation at station 36 during 1987 and 1988. The water table is much lower during the main portion of the growing season (July and August) in 1987 than in 1988.

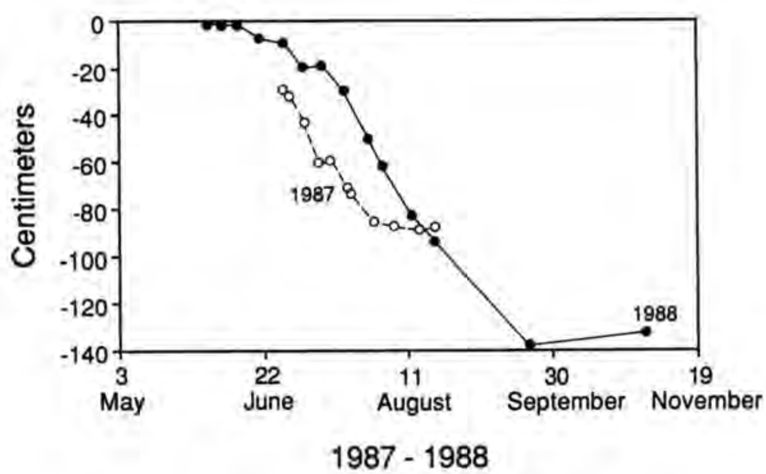


Fig. 20. Water table elevation at station 44 during 1987 and 1988. The water table is much lower during the main portion of the growing season (July and August) in 1987 than in 1988.

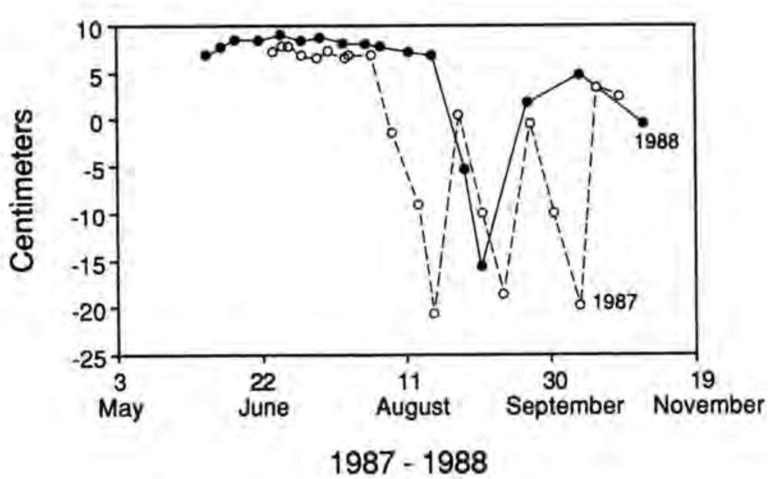


Fig. 21. Water table elevation at station 46 during 1987 and 1988. The water table is high in both years, but in 1987 drops sharply in early August, while in 1988 it does not drop until September.

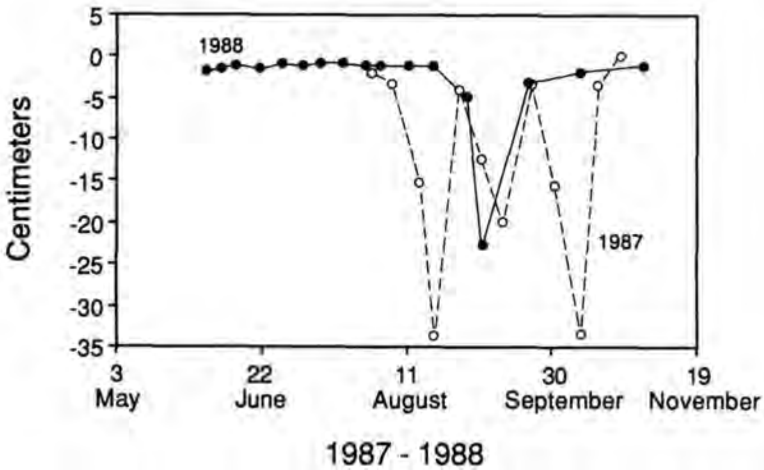


Fig. 22. Water table elevation at station 51 during 1987 and 1988. This station shows similar water table characteristics to station 46 (Fig. 21), but is even more stable.

gin) is in a groundwater recharge area for summer 1988. Preliminary data indicate that most of the peatland area in Big Meadows is a groundwater discharge zone in the early summer and in some areas is a discharge zone all summer. The positive pressure of water moving vertically up through the peat column keeps the lower peat horizons saturated and makes what surface water is delivered to this area from the northern tributary and precipitation more effective in saturating the soil surface.

Summer precipitation at Big Meadows and in the Tonahutu Creek basin above Big Meadows can have a significant effect on the water table in several portions of Big Meadows. The daily summer precipitation record from Grand Lake (Fig. 9) correlates closely with the largest summer increase in the elevation of groundwater in Big Meadows in mid-July 1988. The rainy period came at a time when water tables were beginning to fall. In mid-June 1988, the largest 1-day rainfall of the summer produced more than 1 cm of precipitation, yet its effects are not detectable in the hydrographs. Thus, the effect of precipitation on groundwater is much greater once the aquifers are somewhat depleted and the water table has dropped; then the effect of aquifer replenishment can be seen. This indicates that the seasonal pattern of precipitation may be very important to the maintenance of high water tables, and thus wetlands, in mountain areas. Where long, dry summers occur, the potential for peat oxidation may be greater than in areas heavily influenced by late summer monsoons, such as in southern Colorado. A regional comparison of mountain peatlands in the Sierra Nevadas of California (which are characterized by long, dry summers) and other areas, such as the southern Rocky Mountains (that have abundant late summer monsoon rains) would help clarify these relations.

Groundwater Chemistry and the Mineral Soil Water Limit

The mineral soil water limit (geogenous water or groundwater that has been in contact with mineral soil) as described by Sjors (1948, 1983), Malmer (1962), Damman (1986), and others, is of critical importance in understanding the source of minerals available to plants living in a peatland. When the mineral soil water limit is below the

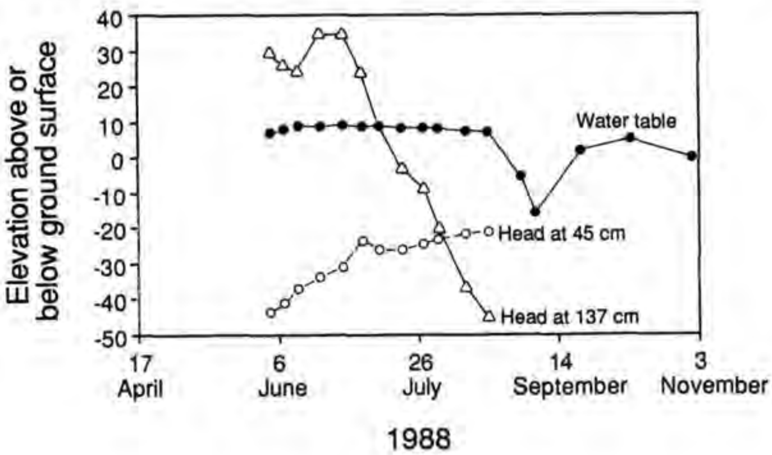


Fig. 23. Hydraulic head in piezometers at 45 and 137 cm deep in the peat and the water table elevation at station 46 during 1988. The head at 137 cm is higher than the water table in early summer, indicating a groundwater discharge site at that time, which reverses and becomes a groundwater recharge site in mid- to late summer.

depth to which plant roots penetrate, plants must derive their mineral nutrition solely from precipitation. This is the case with ombrotrophic peatlands (bogs). When the mineral soil water limit is within the root zone of a peat-forming ecosystem, it is a fen. The well-known differentiation between rich fens and poor fens (DuReitz 1954; Sjors 1983; Malmer 1986) is based on the characteristics of the mineral soil water and its concentration with ions such as Ca++.

The predominance of siliceous rocks in the Colorado Front Range has led to the formation of relatively mineral-poor soils that are heavily leached by the flush of spring snowmelt and the acid-producing conifer forest litter. Water derived from most watersheds in Rocky Mountain National Park is low in mineral nutrients because of the dominant effect of the pure snowmelt water on the chemistry of runoff and aquifers and the few mineral nutrients that can be leached from the hard rocks.

In northern Minnesota peatlands, Glaser (1987) documented the pH and Ca++ concentrations for water in different types of peatlands (Table 2). Overlap in these categories indicates the complexity of determining the type of peatland from pH and Ca++ alone.

The Ca++ concentrations in water at station 13 (Fig. 24) are 1.62 in mid-June, 2.28 in mid-July, 1.66 in early August, and 1.91 in early October, showing a fairly consistent nutrient content at the lowest part of the poor-fen range. The pH at this station was > 5.0 throughout the season. Most stations in the peatland where water was collected for analysis show fairly similar trends to station 13, being fairly constant over the summer; concentrations of Ca++ ranged from 1.62 to 2.41.

The Big Meadows peatland is a soligenous (fed by water running from slopes), minerotrophic (fed by mineral soil water) fen. Its status along the rich- to poor-fen gradient is somewhat uncertain. In Scandinavia, Europe, and the northern United States, many plant species have been identified that are exacting in their nutrient requirements and that only occur in rich fens. These species can be used to help determine the status of fens. Preliminary research on extremely rich fens in the Colorado Rocky Mountains indicates that species such as *Carex dioica*, *Carex microglochin*, and *Kobresia simpliciuscula*, occur only in rich fens (Cooper, unpublished data). These species are not present in Big Meadows.

Table 2. *Calcium (Ca++) and pH recorded in water in northern Minnesota peatlands.*

Area	pH	Ca++ (mg/L)
Ombrotrophic bog	3.9–4.1	0.6–1.6
Poor fen	3.7–5.2	0.6–5.5
Rich fen	5.0–6.2	3.6–30.4
Extremely rich fen	7.0+	20.0+

Some circumpolar rich-fen indicators such as the moss *Campylium stellatum* occur in small scattered tufts in the main part of the Big Meadows peatland, and known calcicoles such as *Thalictrum alpinum* occur on hummocks on the peatland edge. However, the two dominant species in the peatland, *Carex aquatilis* and *C. utriculata*, are known indicators of poor-fen conditions (Glaser 1983; Sjors 1983).

The ecological gradient from mire margins (mire is a general term used for all peatland ecosystems), where nutrients are received from the adjacent uplands, to mire expanses, usually the most nutrient-poor areas (Sjors 1948, 1983; Persson 1961; Malmer 1962, 1986), is fairly well expressed in the study area. Seeps on the western wetland edge have high nutrient concentrations, and this mineral-rich water is gradually diluted as it mixes with water in the mire expanse. A nutrient gradient exists from west (station 10) to east (station 13) along transect 3 (see Fig. 10); a similar gradient exists for extractable Ca in soils (Table 3).

Groundwater discharge into the peat from the alluvial

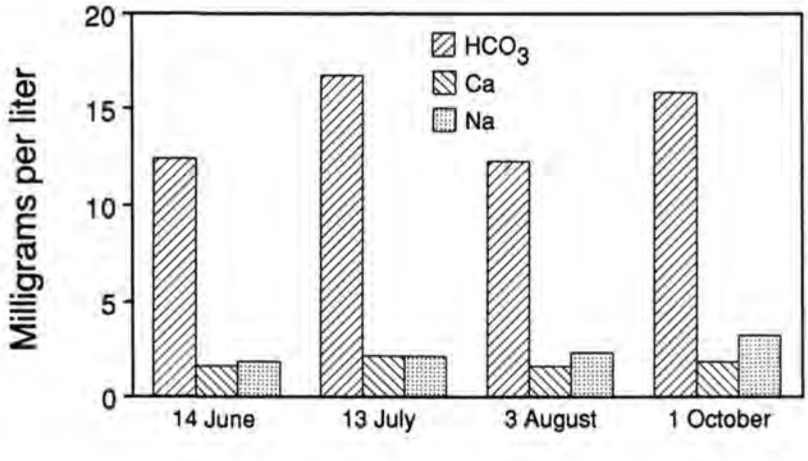


Fig. 24. Water chemistry (concentration of HCO_3^-, Ca++, and Na++ in ppm) at station 13 for four sample dates in 1988. Na++ showed a slight but steady increase during summer, while Ca++ and HCO_3^- were more variable and showed no pattern.

aquifer under the peat was collected at piezometer station 52. Here the concentration of nutrients decreased throughout the summer, but even at its lowest the concentration was still higher than in surface or groundwater elsewhere in the study area. This rich flow indicates that where peat is shallow and plants can root into the substrates supplied by this water, more nutrient-rich systems can occur. Peat accumulation over time, however, leads to the isolation of the root zone from this rich water source.

When the high mountain snowpack has melted and the aquifers supplying water to Big Meadows are depleted, water tables quickly drop. Precipitation is insufficient to maintain saturated conditions except during occasional rainy periods. The development of ombrogenous peat (tertiary peats) that is never in contact with mineral soil water cannot occur in the southern Rocky Mountains because summer precipitation and atmospheric humidity are too low, and peat oxidation occurs. In addition, so much snowmelt water flushes peatlands in the study area (and all other wetlands in the Rocky Mountains) that the water in all peatlands has been in contact with mineral soil. A similar situation occurs in the aapa mire regions of central Finland and northeastern Canada (Damman 1979, 1986).

Soils

Soil Classification

Three soil orders, classified according to *Soil Taxonomy* (Soil Survey Staff 1975), support wetlands in the study area: Histosols, Mollisols, and Inceptisols (Fig. 25). Soils belonging to the order Entisols occur on rocky and sandy point bar deposits along Tonahutu Creek, but these small patches were not considered in the present study.

Histosols are deep peat soils and are abundant in the northern and western portions of Big Meadows and at the Green Mountain Trail Pond. All Histosols in the study area are classified as Cryohemists, which are cold, little-decomposed peat deposits. The thickness of the peat deposits and the stratigraphy differ somewhat throughout the study area, as discussed later in this report.

Mollisols are base-rich, fine-textured soils characteristic of grasslands. They are rare in humid environments where abundant water and subsequent leaching remove bases from soils. Most mineral soils in the study area lack enough base saturation (> 50%) to meet that criterion for a mollic epipedon. Soils with high base saturation occur in three settings: where springs rich in bases enter the western side of Big Meadows, where peat has been drained by the ditch and peat decomposition has created a base-rich histic epipedon, and in the more mesic grass-dominated vegetation characterized by *Calamagrostis canadensis*. The soils at stations 28, 50, and 60 are classified as Typic Cryaquolls. They have mollic epipedons and dark colors.

Table 3. *Calcium (Ca^{++}) content (mg/L) of surface water or soil pore water and surface soils on a west to east profile along transect 1 on 3 August 1988.*

Station	Ca++ in water	Ca++ in soil
10	7.86	5,930
11	4.26	4,350
12	2.93	2,910
13	1.66	2,040

Inceptisols are soils of recent origin. They do not have high base saturation or argillic horizons. Three subgroups of Inceptisols, all belonging to the great group Cryaquepts, occur in Big Meadows: Typic Cryaquepts, Humic Cryaquepts, and Histic Cryaquepts. Histic Cryaquepts have a histic epipedon and occur on the edge of the main peat body at stations 16, 23, 34, 48, 49, and 56. Humic Cryaquepts have umbric epipedons, a dark surface horizon that cannot be distinguished by eye from a mollic epipedon but which has base saturation < 50%.

Figure 26 lists the soil type for each station (Histosols, Mollisols, or Inceptisols) on a June centimeter-day and July centimeter-day gradient. The Histosols, as expected, occupy the wetter portion of the gradient; they occur at most stations that have > 2,300 centimeter-days for both June and July. Inceptisols have < 2,800 centimeter-days for both months. Stations with between 2,300 and 2,800 centimeter-days for both June and July have developed into Inceptisols or Histosols, for unknown reasons. The hydrologic situation that leads to the formation of Mollisols is not clear in this figure.

Peat Characteristics

The Big Meadows peat is autochthonous, having originated with the growth of the sedges *Carex aquatilis* and *C. utriculata*. The peat is largely sedge-root peat composed of structural cell wall carbohydrates. Little wood or moss occurs in the peat. Most wood is found near the base of the peat body, indicating that willows probably grew across the bottom of the mire expanse when the peat was thin and shrubs could root into the nutrient-rich mineral soils.

A basal peat sample from near station 13 was C-14 dated as 11,230 ± 170 years B.P. (laboratory sample I-15,632). This is a minimum age for the stabilization of the glacial outwash in Big Meadows and the formation of the wetland. Winding River kettle, a pond at 2,640 m in elevation in the Colorado River valley about 8 km southwest of the study area, has a basal peat date of 10,320 ± 200 years B.P. (Madole 1976).

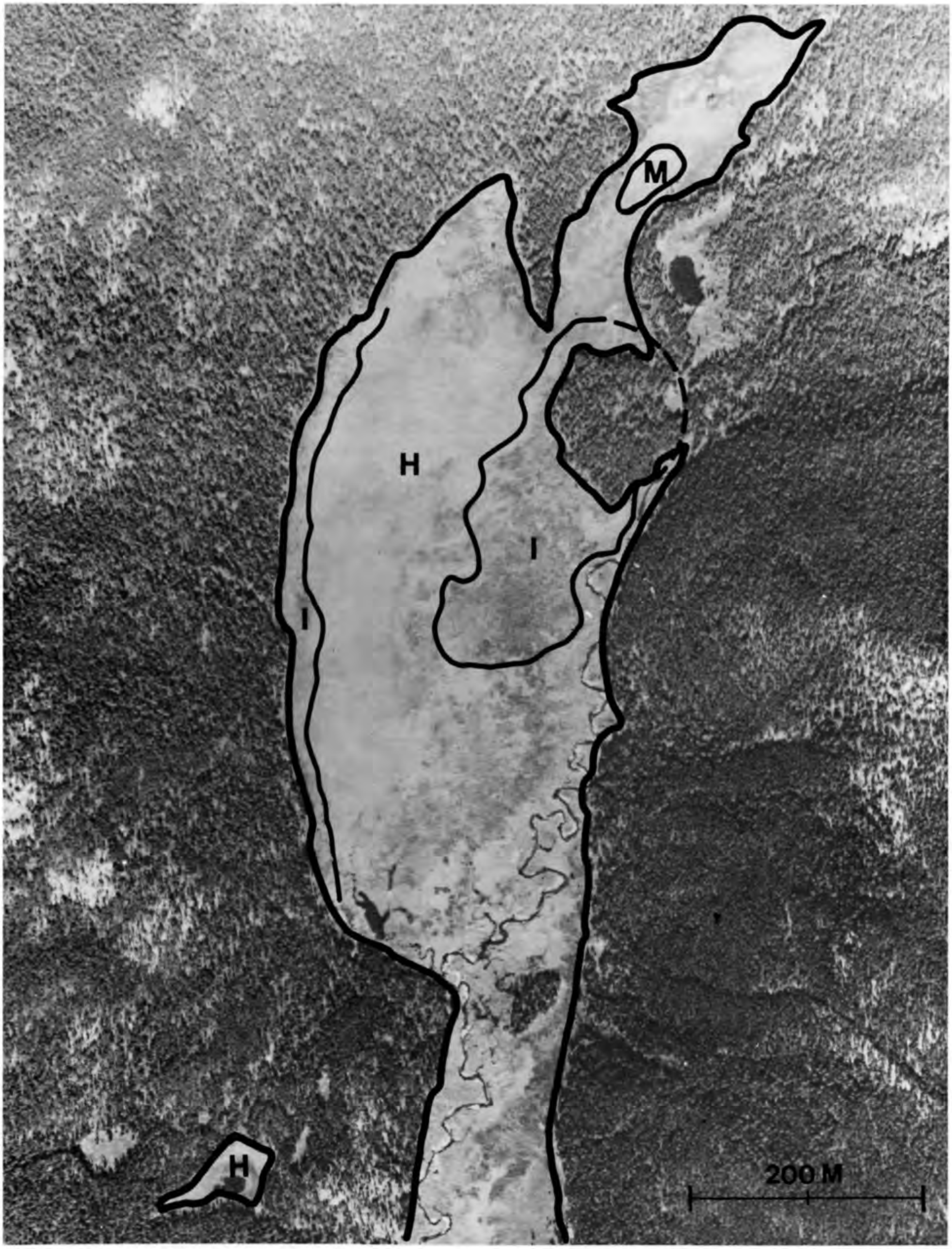


Fig. 25. Generalized soils map for the study area (Inceptisols = I, Histosols = H).

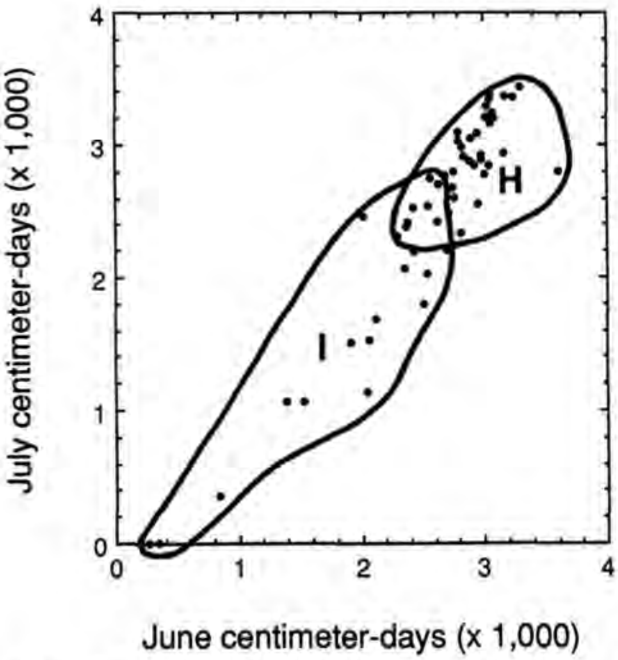


Fig. 26. Two-dimensional direct gradient analysis showing the water table regimes for Histosols (H) and Inceptisols (I) soils along the June and July centimeter-day gradients. Most Inceptisols are drier in June and July than Histosols.

Most of the peat accumulated in the Green Mountain Trail Pond study site is primary peat that has filled a pond basin. The basal peats are C-14 dated at 11,820 ± 170 years B.P. (laboratory sample I-15,631). This peat can also be termed limnic (Tallis 1983) because it formed below the water level. Peat in Big Meadows is largely secondary peat and can be classified as semiterrestric peat (Tallis 1983), with plants rooted above the water table, although seasonal flooding typically occurs. Secondary peat accumulation in Big Meadows has resulted in a raising of the water table. No tertiary peats (developed above the physical limits of groundwater, such as in ombrogenous mires) occur.

Peat deposits in the study area are as thick as 195 cm. The thickest deposits occur at the Green Mountain Trail Pond (just west of station 2) and in the southern portion of Big Meadows (e.g., station 13). In the northern portion of Big Meadows (station 51), the peat is 38 cm thick and has accumulated above coarse sand and gravel. The difference in peat thickness may indicate differences in site stability. Stations at the Green Mountain Trail Pond have been stable and peat accumulating for much of the Holocene, while other stations seem to have been repeatedly disturbed by either large floods and erosion or the deposition of alluvium.

The peat at most stations ranges from 51.9–66.3% organic matter, indicating that sediment is deposited on these peatlands during spring flooding. The sources of this sediment are probably the unnamed northern tributary that empties into Big Meadows and soil erosion from the forested slopes west of Big Meadows. Soil profiles for stations 10, 11, 18, 19, 29, 30, 56, and others show that a distinct and large burial event occurred in the past. For example, consider the following soil profile for station 18:

Horizon	Depth (cm)	Description
O11	0–2	fibric peat
O12	2–13	hemic peat, 10YR 2/1
A1	13–32	silty, and highly organic, 5Y 2.5/1
C1	32–58	clay, grayish 5Y 5/1, with many large streaks and mottles 10YR 4/6
O21	58–182	hemic peat, 10YR 2/2
C21	182+	cobbles and coarse sand

In this profile, 124 cm of peat is buried by 26 cm of clay and 19 cm of silty, organic sediments. Thirteen cm of peat occur above this soil. The C1 horizon described for station 18 also occurs at the other stations having this buried soil. The location and thickness of this buried horizon is illustrated for transect 1 in Fig. 27, and transect 2 in Fig. 28. Stations 38, 46, and others in the northern portion of Big Meadows have several buried soils, each separated by peat horizons.

Profiles of peat thickness across Big Meadows from west to east were constructed to examine the shape and bounds of the peat body. Along transect 2 (Fig. 28), the main peat body is confined between the valley wall on the west and the large alluvial deposit that forms a high terrace between the peatland and Tonahutu Creek. The peat body thins on both the western and eastern edges. This thinning occurs coincident with an increase in elevation along the wetland edge. The peat body surface is concave and nearly fills its basin. The concavity channels water into and through the peatland. If the peat in the center of the peat body were to thicken by more than 30–50 cm it would create a flat or even-domed surface that would channel surface water toward the sides of the peat body. Thus, the peat body may be near its maximum size.

The peat is confined by the valley sides but has not spread out of its basin into adjacent areas. There is evidence of paludification (the spread of mire peat into adjacent uplands). Paludification occurs in unconfined mires such as muskeg or blanket bogs, and is restricted to humid climates where mires and the accumulation of peat can be supported by precipitation alone. In low humidity and sunny climates, such as the southern Rocky Mountains, peat can only be supported where abundant water from snowmelt, springs, and high groundwater tables occur. Peatlands can only occur within the confines of a basin that concentrates, accumulates, and slows the runoff of water,

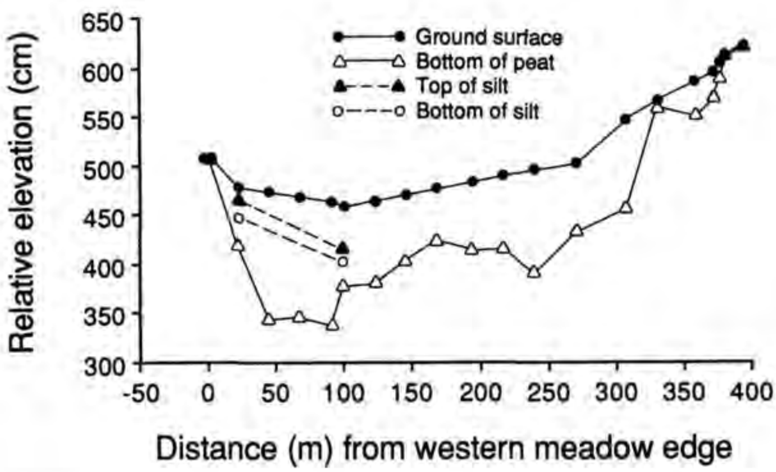


Fig. 27. Thickness of peat along transect 1. A buried mineral horizon occurs within the peat body on the western side of Big Meadows.

or at springs or other sources of water.

The buried clay horizon on the western side of the peatland is an obvious feature in the profile of transect 2 as well. The buried mineral matter is thickest and occurs at higher elevations on the west. A perplexing feature of this buried horizon is its slope, which does not indicate a simple burial of a flat surface.

The alluvial terrace east of the peat body may be quite old. It has a distinctive surface pattern that seems to be either fossil-sorted polygons (a periglacial feature), or fossil beaver channels typical of streamside environments (which would indicate that Tonahutu Creek once meandered across this area). Tonahutu Creek cuts into this alluvium on the east side of Big Meadows.

The thickness of peat in Big Meadows was studied in relation to the water table in two ways: centimeter-days for July, and average depth to water table for June, July, and August. Figure 29 shows peat thickness along a gradient of increasing July centimeter-days. A clear trend is that stations with < 2,200 centimeter-days in July do not support thick peat deposits, and probably are not able to support thick peat deposits. During June, most stations, with or without thick peat deposits, have water tables near the soil surface; therefore, these data are of little value in distinguishing patterns of soil moisture and peat preservation. During August, stations with thick peat deposits may have deep water tables. It thus seems that for peat preservation, soil saturation during July is critical.

Average water tables for June 1988 (Fig. 30) indicate that stations with standing water all accumulate peat, and all stations with peat accumulation have a water table within about 20 cm of the soil surface. During July 1988, the average water table for stations supporting peat is generally within 30 cm of the soil surface (Fig. 31). No stations with an average water table deeper than 30 cm in July are within the peat-accumulating ecosystem. In August (Fig. 32), much drier conditions occur in the peatlands, and the water table at some stations averages ≥ 60 cm below the soil surface. These data indicate that for the support of peatlands in the Rocky Mountain region a water table within 20–30 cm of the soil surface in early summer is necessary.

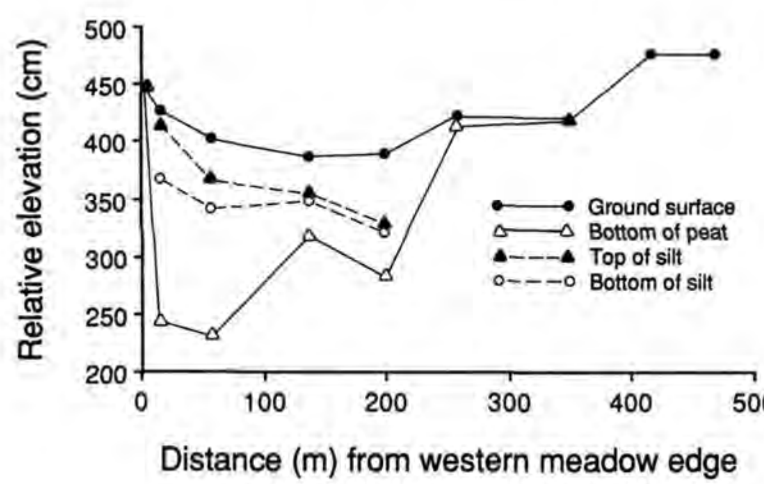


Fig. 28. Thickness of peat along transect 2. A buried mineral horizon occurs within the peat body.

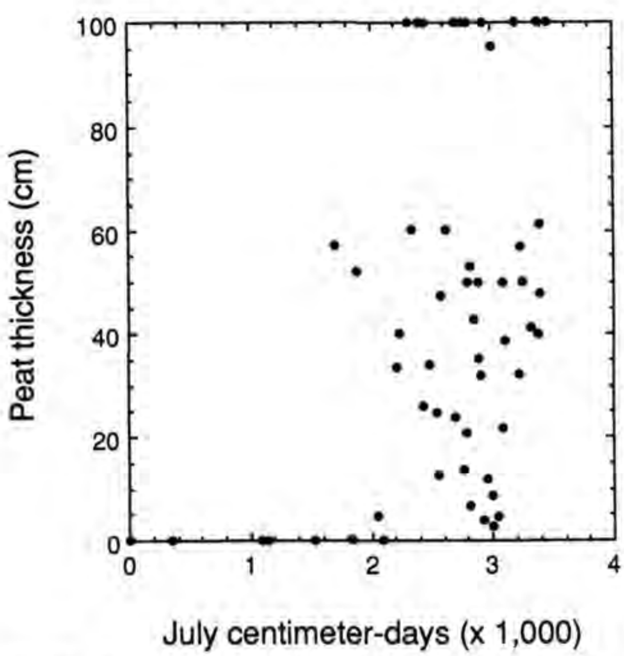


Fig. 29. Thickness of peat along the July 1988 centimeter-day index gradient. Peat only accumulates on sites with more than 2,000 centimeter-days.

Soil Temperature

Soil temperature was monitored from June 1987 to December 1988. Soil temperature for station 46 is shown in Fig. 33. Peak soil temperature occurs in August, and minimum soil temperature occurs in late winter. Surface soils are warmest in late summer and coldest in late winter. Soils are of equal temperature through the entire profile in May and October. The rising limb of soil temperature in May and June follows the descending limb of the groundwater table hydrograph in most stations.

Surface soils are above biological zero, or 5° C, for the entire time between early June and late October; however, soils at 45 cm do not rise above 5° C until July. Most living roots of all plant species investigated are within 45 cm of the soil surface. The growing season is traditionally defined as the time when the root zone is above 5° C; in the study area this is from early June to mid-September, about 100 days. However, by 1 June 1988, the plant shoots had already elongated as much as 1 cm in length, and they were fully elongated by late July, indicating that the concept of biological zero is not meaningful for plants adapted to cold temperatures.

Soil Oxidation–Reduction Potential

Oxidation–reduction potential (redox or Eh) was measured at stations 1, 9, 10, 28, 29, 32, 36, 44, 46, and 49. These measurements are used to determine spatial and temporal changes in redox potential in relation to depth to water table changes, and in relation to the distribution of different plant species and soil types.

The method used to measure redox is known to have inherent problems, but if used within recognized limitations is a useful and rapid method for evaluating the redox status of soils (Clymo 1983, Sikora and Keeney 1983). Reproducible results with this type of electrode are possible only for reducing soil conditions (Sikora and Keeney 1983). Reproducible results were obtained in this study with the redox electrodes.

According to Pearsall and Mortimer (1939), when oxygen saturation is reduced to < 8% the soil can become reduced. This change happens at Eh values between +320 and +350 mV according to Pearsall and Mortimer (1939), and at values greater than +350 mV according to Sikora and Keeney (1983). For this study, the boundary between the aerobic and anaerobic soil horizons was considered to be in the range 320–350 mV. All measurements > +350 mV were considered to be in aerobic soil, and no real difference was attributed to +350 versus +500 mV.

In 1988, the water table dropped steadily at station 44, with a slight rise after the rain in early July. The upper portion of the soil (7 and 15 cm in depth) became aerobic

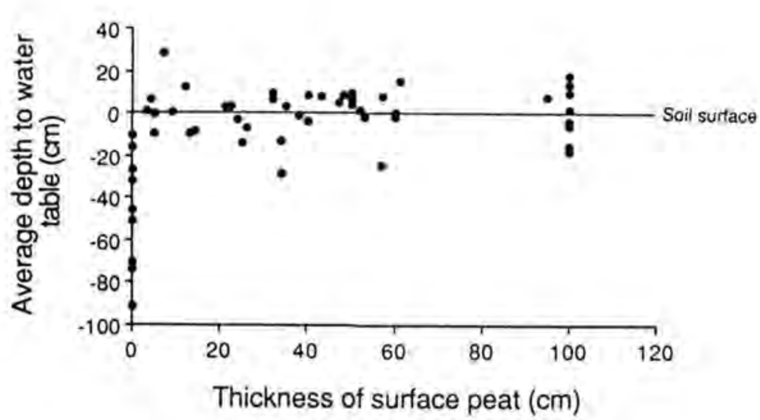


Fig. 30. Thickness of peat by station along average depth to water table for June 1988. Most stations that have accumulated peat have a water table close to the soil surface. Stations on the *right* side of the figure all have peat more than 1 m deep.

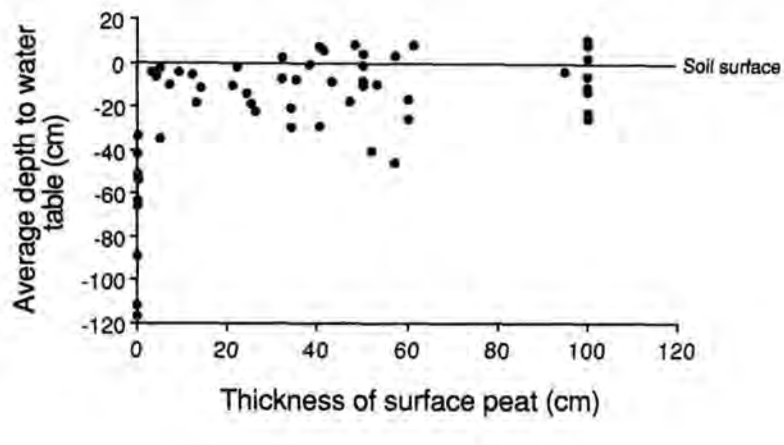


Fig. 31. Thickness of peat by station along average depth to water table for July 1988. Most stations that accumulate peat have a water table within 30 cm of the soil surface.

in mid-July, and the soil at 30 cm did so in late July (Fig. 34). The soil at 15 cm became aerobic within 1 week after the water table dropped below 15 cm, indicating that even organic soils (station 44 soil has 23% organic matter in the upper 18 cm) can drain and rapidly become aerobic.

Stations 10, 28, and 46 were reduced through the whole soil profile throughout the growing seasons of 1987 and 1988. Urquahart and Gore (1973) showed a significant linear relation between temperature and Eh; as temperature rose, Eh also rose. This relation does not seem to hold in my study because as the temperature rose at stations 10 and 28, the Eh did not rise.

Vegetation

Vegetation Description and Classification

Difficulties in the classification of wetland vegetation in the Rocky Mountains are to be expected because the wetland flora is depauperate, and like wetlands elsewhere, few species have high fidelity to any one particular habitat or community. Also, a few species impress themselves on the vegetation, dominating broad areas and obscuring important ecological regularities (Ruuhijärvi 1983). These problems are typical of wet, peaty, and cold soils, and of cold climates in general. Complexity is due to the many independently functioning ecological factors that contribute to mire vegetation. Thus, water table gradients and nutrient gradients do not necessarily correspond.

Vegetation classification is also difficult because spatial complexity is controlled by microtopography, and broad homogenous areas may be uncommon. Ecological conditions (e.g., water table and nutrients) on hummocks differ markedly from interhummock areas. Thus, hummocks and interhummock areas are distinctly different, and the vegetation responds to these differences.

Dominant and character species (sensu Mueller-Dombois and Ellenberg 1974) must be used in classification. The few dominant species in the study area have broad tolerances for duration of soil saturation, and probably for soil and water chemistry as well. The classifiation of vegetation in any peatland ecosystem in the Rocky Mountains of the United States must focus on *Calamagrostis canadensis*, *Carex aquatilis*, *C. utriculata*, *Deschampsia cespitosa*, *Salix planifolia*, and a few other locally or regionally important taxa. These common species, and other uncommon species, must be used to differentiate communities. At the drier and wetter ends of the

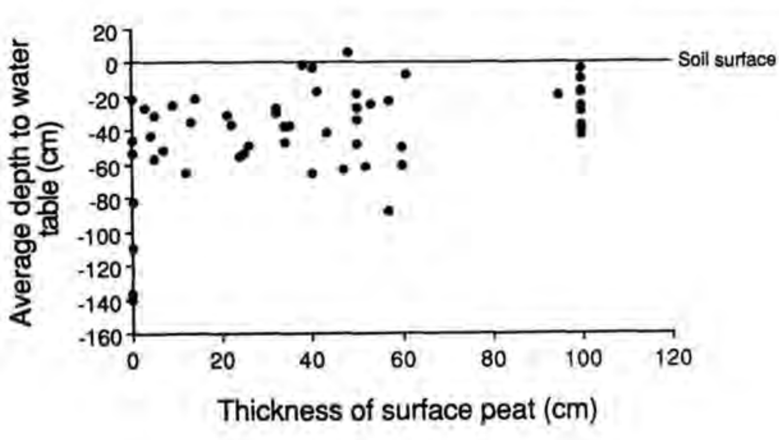
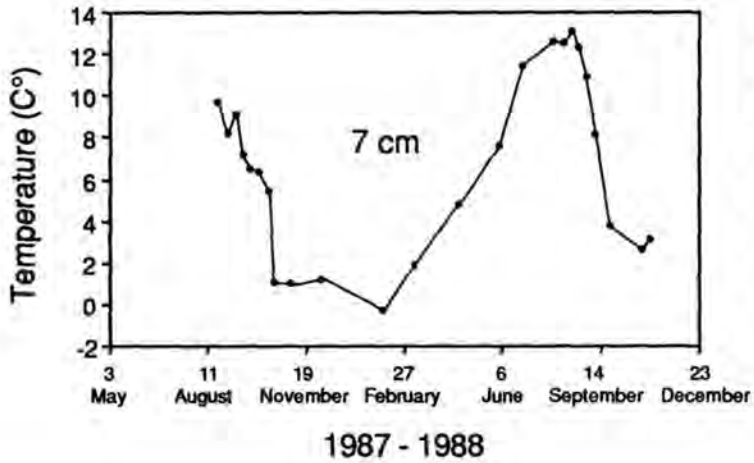
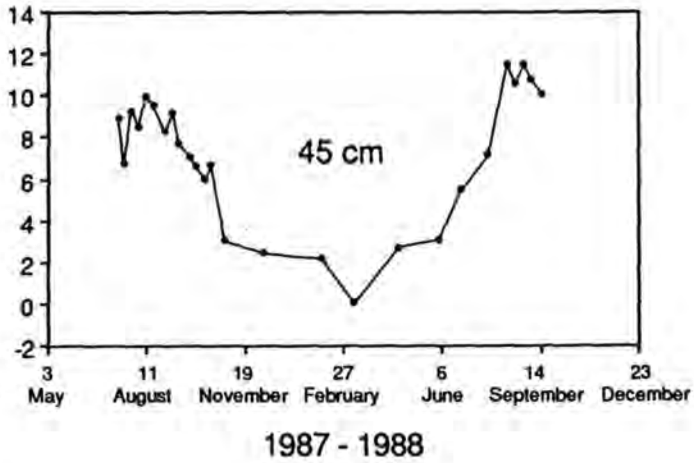
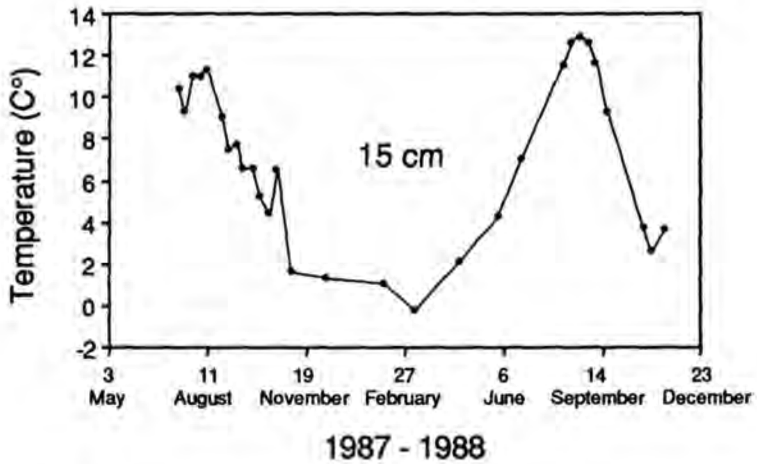


Fig. 32. Thickness of peat by station along average depth to water table for August 1988. Most stations that accumulate peat have a water table within 60 cm of the soil surface, indicating that many of these stations dry out by late summer.







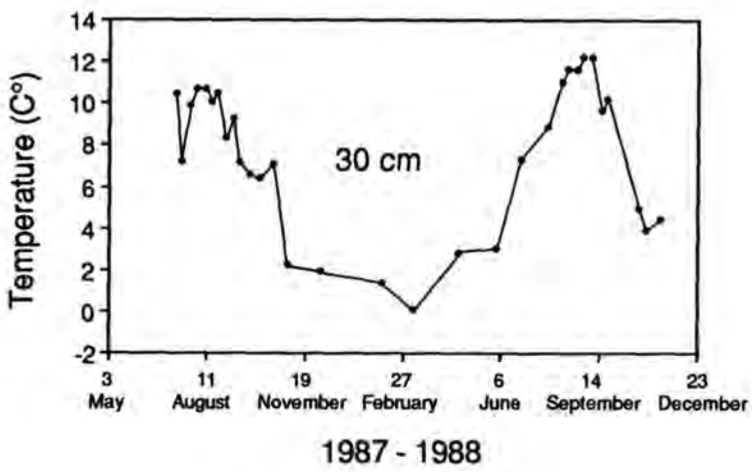


Fig. 33. Temperature of the soil at 7-, 15-, 30-, and 45- cm soil depth at station 44 in 1987 and 1988.

moisture gradient many species exist that can be used in classification. Mosses generally have low cover values or are absent in the study area, but many mosses are specific in their nutrient requirements and help greatly in developing an understanding of a wetland's ecology.

Vegetation stands were sampled at each of the 60 stations indicated in Fig. 10; thus, stand and station numbers are interchangeable. Stand tables were created to show the floristic relations between stands. The table method (Mueller-Dombois and Ellenberg 1974) and cluster anal-

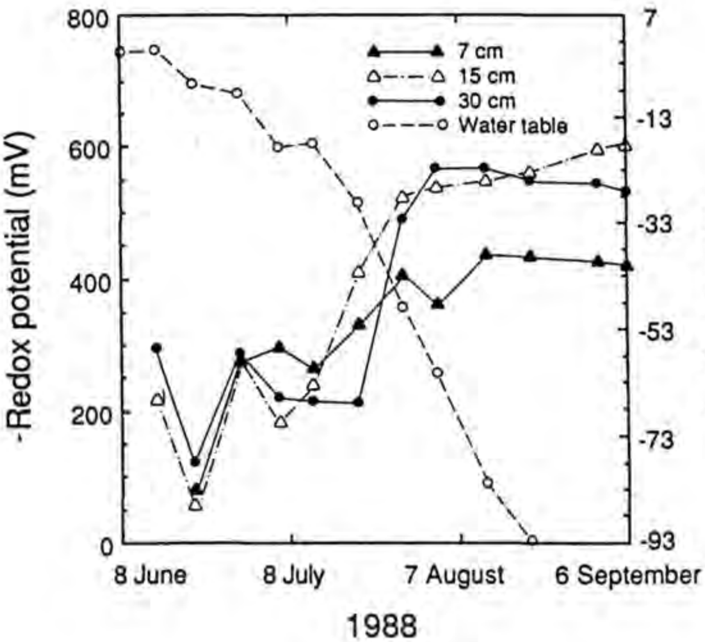


Fig. 34. Oxidation-reduction (redox) potential (mV) at 7-, 15-, and 30- cm soil depths, and water table at station 44 from June to September 1988. As the water table drops, redox potential rises. Soils with redox potential greater than about +350 mV are considered to be oxidized, while those below this are reduced.

ysis were used simultaneously to identify and describe 11 community types. Dendrograms were created using the vegetation data as an aid to classification. The results of this cluster analysis are shown in Fig. 35. A 12th community type was identified for the deepwater portion of the Green Mountain Trail Pond but was not sampled because of the water depth.

The cluster analysis helped to bring this data set into focus and linked a large number of stands, all dominated by *Carex aquatilis*, with *C. utriculata*, *Psychrophila leptosepala*, and other species at a high percentage of similarity. In general, stands with enough floristic similarity to be considered as part of the same community clustered together at ≥ 84% similarity. These communities are distinguished on the cluster analysis. Summary tables showing the average cover and constancy class values for all vascular plant species occurring in the community types are presented in Tables 4 and 5. Sample sizes were too small to compute cover and constancy values for some community types. A generalized vegetation map is presented in Fig. 36. Each of the 12 communities in the study area is described below.

1. *Nuphar luteum* spp. *polysepalum–Potamogeton gramineus*. No groundwater wells were placed in this community, which occupies the central deepwater portion of the Green Mountain Trail Pond (Fig. 6). Standing water is always present and ranges from < 0.1 m deep to > 1 m deep. The substrate is loosely consolidated organics. This community once dominated the entire pond complex, but terrestrialization is occurring because of peat accumulation. This has led to the filling of most of the pond, greatly reducing the extent of this community. Basal peat from a core extracted from the pond edge was C-14 dated and had an age of 11,840 ± 170 years B.P. (laboratory sample I-15,631), which indicates a very long period of stability and succession to create the ecological conditions observed today. Seeds of *Nuphar* that occur at the base of the peat core indicate that a population of this species has occupied this pond the entire time. A water sample collected on 13 July 1988 had a pH of 5.8, conductance of 5.8 µmhos/cm, Ca^{++} 1.68 of mg/L, Na^{++} of 0.95 mg/L, and Mg^{++} of 0.48 mg/L, indicating extremely poor fen conditions with regard to nutrient supply.
2. *Carex limosa*. This community (Table 4), which is largely a monoculture of *C. limosa*, occurs as floating mats on the edge of the Green Mountain Trail Pond. *Carex limosa* has long, almost stoloniferous rhizomes, and is well adapted for building the floating mats of a quagmire. A similar stand has been described for the West Elk Range (Weber 1961), and it also occurs in the Tarryall Mountains (Cooper, unpublished data) and other areas of Colorado. This species is important in primary succession, spreading onto the water column and shading out the submergent and floating-leaved aquatic species. Soils are classified as Cryohemists. *Carex utriculata* occurs as scattered inviduals in this community, as does *Menyanthes trifoliata*.
3. *Menyanthes trifoliata–Carex utriculata*. This community occurs on the margins of the Green Mountain Trail Pond (Fig. 6). *Menyanthes* is a broadleaf emergent that roots in unconsolidated peat at the pond margins. Its

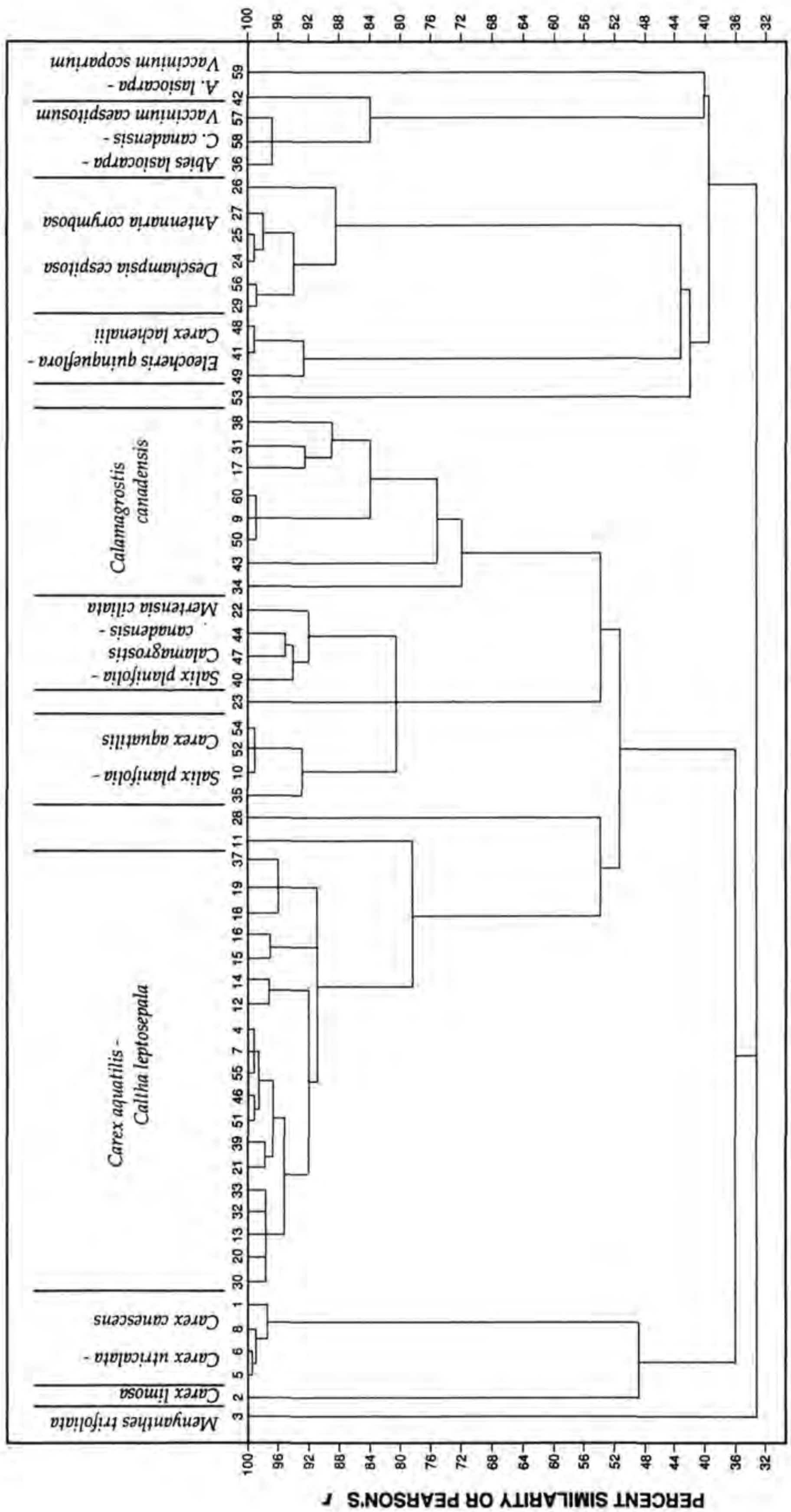


Fig. 35. Hierarchical dendrogram of the vegetation at all stations within the study area. The 60 vegetation stands are classified into 11 communities; each community is described in the text.

Table 4. *Percent of occurrence for the plants encountered in the Big Meadows–Green Mountain Trail Pond wetland complex in Rocky Mountain National Park.*

Community type

	Carex limosa	Menyanthes trifoliata - Carex utriculata	Carex utriculata - Carex canescens	Carex aquatilis - Psychrophila leptosepala	Salix planifolia - Carex aquatilis	Salix planifolia - Calamagrostis canadensis - Mertensia ciliata	Calamagrostis canadensis	Eleocharis quinqueflora - Carex lachenalii	Deschampsia cespitosa - Antennaria corymbosa	Abies lasiocarpa - Calamagrostis canadensis - Vaccinium cespitosum	Abies lasiocarpa - Vaccinium scoparium
Number of Stands	1	1	4	19	6	4	8	3	6	3	2
Species											
Carex limosa	15.0	.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Menyanthes trifoliata	0.0	80.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carex utriculata	10.0	2.0	77.5	1.8	5.0	0.0	.9	1.0	0.0	0.0	0.0
Eleocharis quinqueflora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	68.3	0.0	0.0	0.0
Carex lachenalii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Eriophorum angustifolium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Carex aquatilis	0.0	0.0	.3	61.4	27.5	6.0	18.4	11.7	1.3	.1	0.0
Psychrophila leptosepala	0.0	0.0	0.0	12.0	7.7	4.5	3.1	2.0	4.3	0.0	0.0
Clementsia rhodantha	0.0	0.0	0.0	.4	1.2	1.8	.0	.7	.1	.0	0.0
Epilobium lactiflorum	0.0	0.0	0.0	.0	.4	.0	.1	0.0	0.0	.0	0.0
Pedicularis groenlandica	0.0	0.0	0.0	.7	.6	0.0	0.0	.1	0.0	0.0	0.0
Crunocallis chamissoi	0.0	0.0	0.0	.1	0.0	0.0	.0	0.0	0.0	0.0	0.0
Carex canescens	0.0	0.0	2.5	2.4	0.0	0.0	0.0	1.0	0.0	0.0	1.0
Galium trifidum	0.0	0.0	0.0	.1	.1	.3	.1	.0	0.0	0.0	0.0
Senecio crocatus	0.0	0.0	0.0	.2	0.0	0.0	.9	0.0	0.0	0.0	0.0
Calamagrostis canadensis	0.0	0.0	0.0	3.0	2.8	47.5	58.8	0.0	.4	8.3	.5
Conioselinum scopulorum	0.0	0.0	0.0	.0	.0	.5	.3	0.0	0.0	0.0	0.0
Mertensia ciliata	0.0	0.0	0.0	.1	.0	7.5	0.0	0.0	0.0	0.0	0.0
Senecio triangularis	0.0	0.0	0.0	0.0	0.0	1.5	1.1	0.0	0.0	0.0	0.0
Salix planifolia	0.0	0.0	0.0	.1	56.7	62.5	6.3	0.0	2.2	.3	0.0
Deschampsia cespitosa	0.0	0.0	0.0	5.0	2.0	2.3	1.0	1.3	50.8	.7	0.0
Antennaria corymbosa	0.0	0.0	0.0	0.0	0.0	.3	.0	0.0	15.3	0.0	.1
Penstemon c. procerus	0.0	0.0	0.0	0.0	0.0	0.0	.3	0.0	1.5	.0	0.0
Carex festivella	0.0	0.0	0.0	.8	3.3	.8	.1	0.0	4.5	0.0	0.0
Fragaria ovalis	0.0	0.0	0.0	0.0	.0	1.0	.1	0.0	1.7	1.0	1.6
Achillea lanulosa	0.0	0.0	0.0	0.0	.0	.3	.4	0.0	1.0	.1	.1
Potentilla diversifolia	0.0	0.0	0.0	.0	0.0	.0	.4	0.0	.9	.1	.1
Taraxacum officinale	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	.0	0.0	.1
Pinus contorta	0.0	0.0	0.0	0.0	0.0	0.0	.0	0.0	0.0	50.0	35.0
Picea engelmannii	0.0	0.0	0.0	0.0	0.0	0.0	.0	0.0	0.0	8.3	30.0
Abies lasiocarpa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5
Juniperus communis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	1.5
Vaccinium cespitosum	0.0	0.0	0.0	0.0	0.0	.5	2.5	0.0	.2	33.3	5.0
Shepherdia canadensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Lonicera involucrata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	3.0
Pentaphylloides floribunda	0.0	0.0	0.0	0.0	0.0	1.5	1.9	0.0	4.8	1.3	0.0
Vaccinium scoparium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	12.5
Betula glandulosa	0.0	0.0	0.0	0.0	.4	5.8	3.8	0.0	1.2	3.7	0.C
Ribes lacustre	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Linnaea borealis	0.0	0.0	0.0	.1	0.0	0.0	0.0	0.0	0.0	.3	1.5
Arnica cordifolia	0.0	0.0	0.0	0.0	.2	0.0	0.0	0.0	0.0	0.0	7.5
Chamerion angustifolium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	.1	.6
Psilochenia runcinata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	.1

Table 5. *Constancy class values for the plants occurring in the Big Meadows–Green Mountain Trail Pond wetland complex in Rocky Mountain National Park.*

	Community type								
	Carex utriculata - Carex canescens	Carex aquatilis - Psychrophila leptosepala	Salix planifolia - Carex aquatilis	Salix planifolia - Calamagrostis canadensis - Mertensia ciliata	Calamagrostis canadensis	Eleocharis quinqueflora - Carex lachenalii	Deschampsia cespitosa - Antennaria corymbosa	Abies lasiocarpa - Calamagrostis canadensis - Vaccinium cespitosum	Abies lasiocarpa - Vaccinium scoparium
Number of Stands	4	19	6	4	8	3	6	3	2
Species									
Carex utriculata	X	III	III		I	III			
Eleocharis quinqueflora						X			
Carex lachenalii						VI			
Eriophorum angustifolium						VI			
Carex aquatilis	II	X	X	VII	VIII	X	V	VI	
Psychrophila leptosepala		X	X	X	V	X	VI		
Clementsia rhodantha		V	X	X		X	V		
Epilobium lactiflorum			III		VI				
Pedicularis groenlandica		IV	VIII			VI			
Crunocallis chamissoi		II							
Carex canescens	II	IV				III			V
Galium trifidum		VII	V	V	VI				
Senecio crocatus		III			I				
Calamagrostis canadensis		V	V	X	X		VIII	X	V
Conioselinum scopulorum				V	II				
Mertensia ciliata		I		VII					
Senecio triangularis				VII	III				
Salix planifolia		II	X	X	III		VIII	III	
Deschampsia cespitosa		VI	VI	VII	III	X	X	VI	
Antennaria corymbosa				V			X		V
Penstemon c. procerus					I		X		
Carex festivella		I	I	II	I		X		
Fragaria ovalis				V	I		VI	X	X
Achillea lanulosa				V	II		X	X	X
Potentilla diversifolia					II		VIII	X	X
Taraxacum officinale									V
Pinus contorta								X	X
Picea engelmannii								X	X
Abies lasiocarpa									V
Juniperus communis								X	X
Vaccinium cespitosum				II	II		III	X	X
Shepherdia canadensis									V
Lonicera involucrata								VI	X
Pentaphylloides floribunda				V	I		VI	X	
Vaccinium scoparium								VI	X
Betula glandulosa			III	V	I		V	X	
Ribes lacustre									V
Linnaea borealis		I						III	V
Arnica cordifolia			I						X
Chamerion angustifolium								X	X
Psilochenia runcinata									V

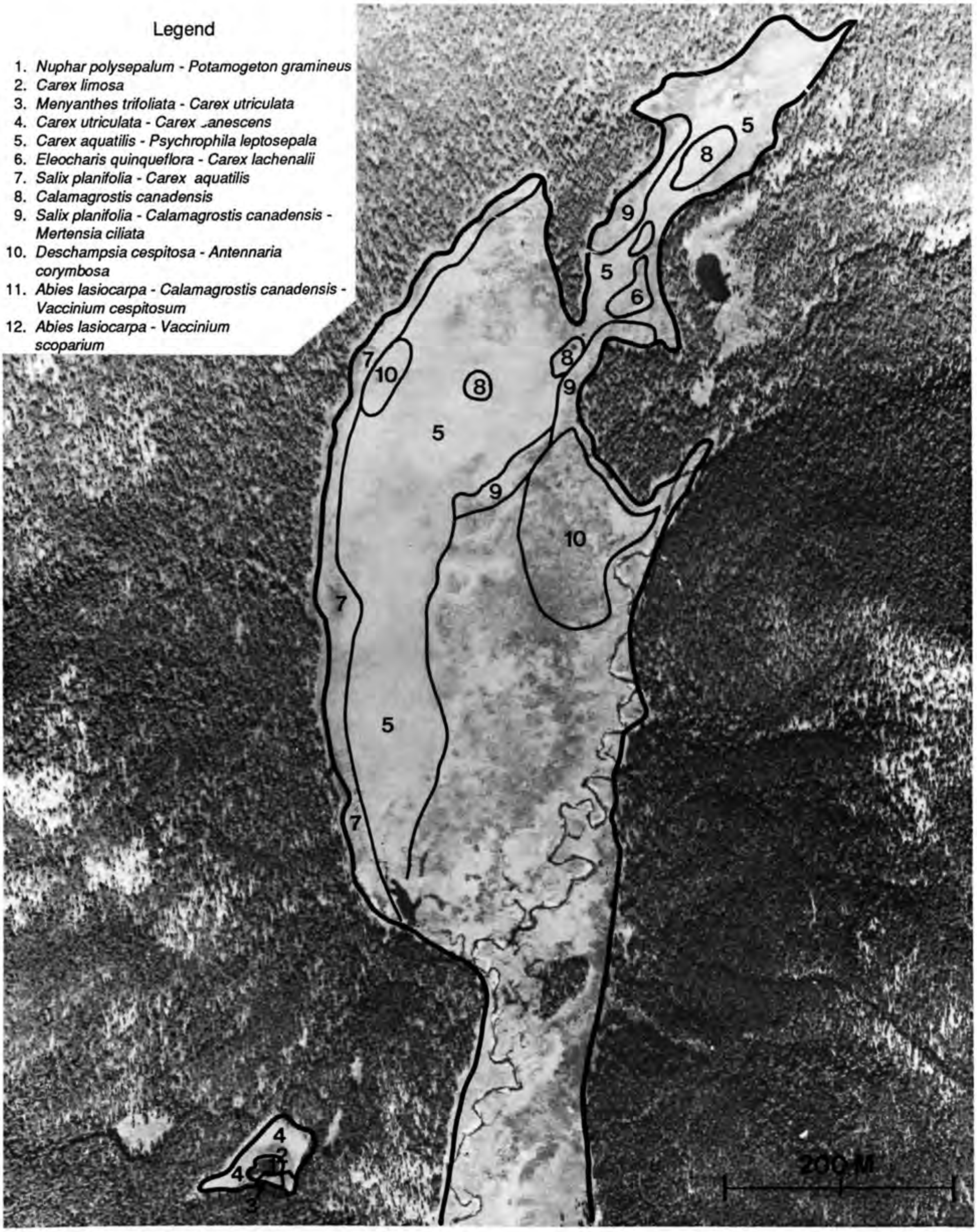


Fig. 36. Generalized vegetaion map of Big Meadows and Green Mountain Trail Pond. Numbers represent the communities described in detail in the text.

seeds occur throughout the peat core taken from this pond edge, indicating that a population of this species has been at the pond for about 12,000 years. Soils are Cryohemists.

4. *Carex utriculata–Carex canescens*. This community is largely characterized by monocultures of *C. utriculata*, a coarse sedge capable of growing in water that is ponded ≥ 20 cm deep for a considerable portion of the growing season. *Carex canescens* is the only other plant to occur in these stands. All stands sampled are at the Green Mountain Trail Pond. Where the water is deeper, *C. utriculata* occurs in a pure monoculture and grows up to 60 cm tall. This community type had the highest standing crop of any herbaceous or shrub wetland community in the study area. Stand 5 (Fig. 10) had a standing crop of 470 g/m^2, and the average for the four stands (Fig. 35) sampled was 399 g/m^2. Soils are deep peats and classified as Cryohemists.

5. *Carex aquatilis–Psychrophila leptosepala*. This community occupies the large central portion of the mire expanse in Big Meadows (Fig. 4). A basal peat sample from a site adjacent to station 13 was C-14 dated to be 11,230 $\pm$ 170 years B.P. (laboratory sample I-15,632), indicating the great antiquity of this mire expanse. Significant variation in the abundance of the herbs *Clementsia rhodantha*, *Pedicularis groenlandica*, *Psychrophila leptosepala*, and other species occurs. In addition, the abundance of *Carex utriculata* also varies. This community is adapted to the low nutrient levels present in the peat soils and the flush of weakly minerotrophic water from the northern tributary early in summer.

Several variants of this community occur. For example, nearly pure stands of *Carex aquatilis* occupy the water track in the northern portion of Big Meadows (Fig. 10, stands 46 and 51). This is the wettest and least disturbed part of the Big Meadows fen, and *C. utriculata* is almost entirely absent. The water chemistry for stands 46 and 51 indicates that they are poor-fen communities, even though fen communities in water tracks in other peatlands in North America tend to be rich fens (Heinselman 1970; Glaser 1983). Calcium content of water at station 46 varies from 1.76 to 2.98 mg/L on different dates. Soils are deep peats with many buried mineral soil horizons and are classified as Cryohemists.

Another variant of this community is characterized by *Carex aquatilis* and *Sphagnum russowii* (Fig. 10, stand 4) and occurs on the southern side of the Green Mountain Trail Pond. A similar *S. russowii*-dominated community occurs on the edge of fens in Wild Basin in the southeastern portion of Rocky Mountain National Park. Most likely, the abundant *Sphagnum* growth is supported by the reduced evapotranspiration created by shading of the peatland by tall trees on the adjacent hillside. This illustrates that even a small change in the moisture of a site can dramatically change its ecology and vegetation.

Some stands (e.g., stands 15, 16, and 53) support an abundance of *Carex canescens*, but the environmental factors this species is responding to are unclear. This community is Bierly's (1972) wet sedge fen.

6. *Eleocharis quinqueflora–Carex lachenalii*. This community, represented by stands 41, 48, and 49, occurs on quartzite sands and has a thin peat layer. It occurs in the northeastern portion of Big Meadows. Water collected from the well at station 48 on 3 August 1988 had 2.41 mg/L of Ca++, typical of poor fens. However, the soils here are the most nutrient poor in the study area (3 ppm of extractable Ca++, and less than 1 ppm of Na++ and Mg++), indicating that the low-growing *Eleocharis* (maximum height of 20 cm) and the rare species *Carex lachenalii* and *Eriophorum angustifolium* escape competition by growing on sites too poor in nutrients to support the more robust *Carex* species, which are so ubiquitous and dominant in Colorado wetlands at this elevation. Soils are peat over sand and gravel and are Cryohemists.

7. *Salix planifolia–Carex aquatilis*. This community occupies the western mire margin, where more mineral-rich water from seeps keeps the groundwater table near the soil surface for the first half of the summer (Fig. 37). It is restricted to the western and southeastern sides of Big Meadows. Stands 10 and 52 (Fig. 10) are characteristic of this community type. These stands have a dense and tall canopy of *S. planifolia* with an understory dominated by *C. aquatilis*; herbs such as *Clementsia rhodantha* also occur. Soils in this community type may be classified as Cryaquolls because of the organic and base-rich mollic epipedon. The soils are high in Ca++ and other metallic ions, and peats are thin, allowing the shrubs to root into mineral soils. This is probably the wet shrub fen of Bierly (1972). A similar community is described by Hansen et al. (1988) for southwestern Montana and also occurs throughout northern Colorado (Cooper, unpublished data).

8. *Calamagrostis canadensis*. This community is characterized by a near monoculture of *C. canadensis*, with small populations of *Carex aquatilis* and *Deschampsia cespitosa* and a few forbs (Table 4). It occupies better drained sites than those dominated by *C. aquatilis*, yet these sites are still wetter than those dominated by *D. cespitosa*. This is a peat-forming community, with Cryohemists or Cryaquolls soil, although the peats are not as deep as in wetter communities. Stands 9, 31, 50, and 60 are characteristic of this type. This community is probably similar to the mesic grass meadow described by Bierly (1972).

Fig. 37. This *Salix planifolia–Carex aquatilis* community occupies the mire margin in Big Meadows where mineral-rich groundwaters saturate the soil for much of the first half of the summer.

9. *Salix planifolia–Calamagrostis canadensis–Mertensia ciliata*. This distinctive community occupies mesic portions of the mire margin where seeps are not present. Stands 22, 40, 44, and 47 are characteristic of this type. The soils are Cryohemists where stable conditions have allowed peat to accumulate, or Cryaquepts where deep peats are not present. These stands usually have high concentrations of extractable Ca++ in the soil (e.g., 2,770 ppm at stand 40 and 3,260 ppm at stand 44), but the soil water is typical of other stands in the study area, with a concentration of only 1.72 mg/L of Ca++ found at stand 44 on 13 July 1988. This stand could be called a willow carr.

10. *Deschampsia cespitosa–Antennaria corymbosa*. This community (Fig. 38) occupies the most mesic portions of the Big Meadows wetlands. It may have a water table that is deeper than some of the stands for the two forested communities described next. *Achillea lanulosa*, *Carex festivella*, *Fragaria ovalis*, *Penstemon confertus* ssp. *procerus*, *Potentilla diversifolia*, *Salix wolfii*, and other species are common. These species do not occur, or have low cover (Table 4) and constancy (Table 5), in wetter stands. Soils in this community type are typically Cryaquepts, although one Histosol (stand 56) occurs. *Deschampsia cespitosa* seems to be an aggressive species, invading disturbed sites, such as the buried soils at stations 29 and 56, and the mire expanse where the ditch has affected the water table of some stands. *Deschampsia* may also be effective at keeping conifers from invading those meadows that are suitable for tree growth. Cooper (1986) reviewed data on other *D. cespitosa*-dominated communities that occur in the Rocky Mountains. This community type may be closely related to Bierly's (1972) dry grass meadow. I have also included Bierley's dry shrub meadow here.

11. *Abies lasiocarpa–Calamagrostis canadensis–Vaccinium cespitosum*. This community occurs in the wettest sites occupied by forests in the study area. It is closely allied with the *A. lasiocarpa–C. canadensis* habitat type described by several researchers developing forest habitat type classifications for the U.S. Forest Service (Alexander 1985, 1988; Hess and Alexander 1986; Komarkova et al. 1988). However, the three stands (36, 57, and 58) examined in the study area have a ground cover of *V. cespitosum*, which puts them more closely in line with the concept of the *A. lasiocarpa–C. can-*

Fig. 38. *Deschampsia cespitosa–Antennaria corymbosa* communities occur on the driest portion of the Big Meadows wetlands.

adensis habitat type, *Vaccinium cespitosum* phase, as described by Pfister et al. (1977) for Montana.

Hess and Alexander (1986) noted that this habitat type occupies the coldest, wettest environment in the *A. lasiocarpa* series because of high groundwater levels and cold air drainage. They described the soils as primarily Typic Cryaquolls. In Big Meadows the soils are Cryaquepts, with insufficient base saturation to support a mollic epipedon. The three stands have a water table near the soil surface for the first several weeks of the growing season (late May, early and mid-June). Soil temperature does not go above 5° C until mid-June.

12. *Abies lasiocarpa–Vaccinium scoparium.* This community is represented in the study area by stands 42 and 59. It has a deeper water table than stands of community 11. *Calamagrostis canadensis* and *Vaccinium cespitosum* are generally absent or have low cover values in this community.

Analysis of Vegetation Along Environmental Gradients

The dominant species in the vegetation were ordinated along several measured environmental gradients. Direct gradient analysis (Whittaker 1967; Mueller-Dombois and Ellenberg 1974; sensu Gauch 1982) attempts to answer the fundamental question, "How are species distributed in relation to one another along environmental gradients?" The environmental gradients used in these analyses are water table, oxidation-reduction potential and the seasonality of reducing conditions in the root zone, and percent of the growing season that the upper 30 cm of soil is aerobic.

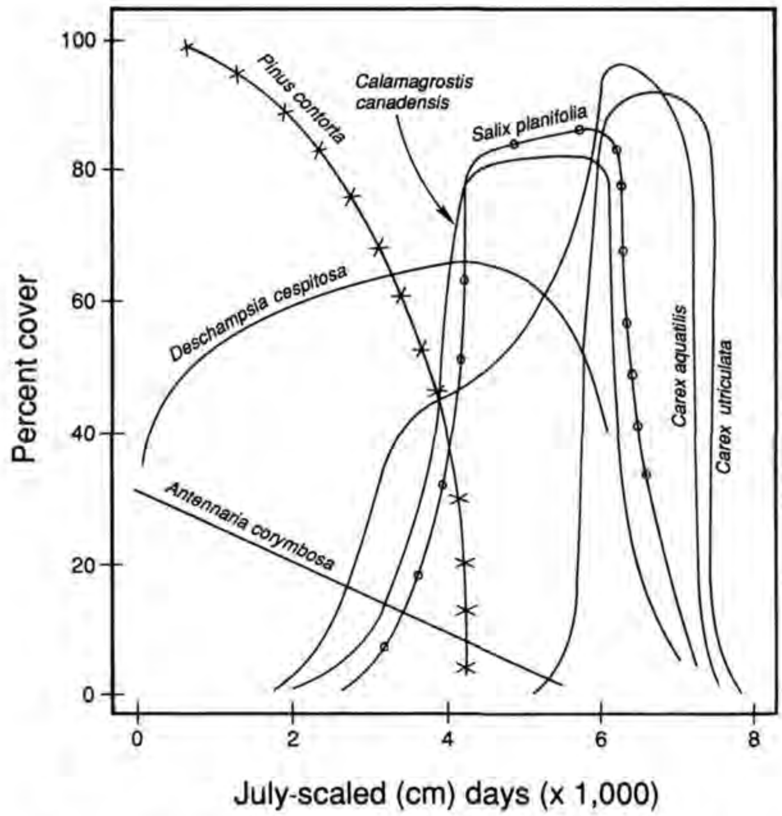


Fig. 39. Percent canopy cover (Y-axis) of dominant plant species along July-scaled centimeter-day gradient (X-axis). The line for each plant species was drawn outside of all points for that species and thus is the maximum portion of the ordination space occupied by that species.

Analysis of plant species along water table gradients. A two-dimensional direct gradient analysis of species canopy cover along a scaled July 1988 water table cumulative centimeter-days index gradient is presented in Fig. 39. This scaled index was developed similarly to the centimeter-day index; however, more emphasis was placed on water table characteristics that influence plants. The total centimeters of water table above the ground surface (inundation) was multiplied by 3. The total centimeters where the water table was from the surface to 30 cm below the soil surface was multiplied by 2. All centimeters below 30 cm were multiplied by 1. These totals were added to develop the scaled index. The line for each species in this figure represents the maximum realized niche for that species. The line was drawn around the space occupied by all data points for each species in every stand.

Figure 39 indicates that *Carex utriculata* occupies the wettest sites of any species considered in this analysis. Its niche has considerable overlap with *Carex aquatilis*, which explains why these two species occur together over much of the mire expanse in the study area and in mires elsewhere in the Rocky Mountains.

Salix planifolia and *Calamagrostis canadensis* have similar niche widths, which explains why they commonly occur together, particularly in the *S. planifolia–C. canadensis–Mertensia ciliata* community. *Salix planifolia* also overlaps with *Carex aquatilis*, which illustrates that the community *S. planifolia–C. aquatilis* occurs on wetter sites than the *S. planifolia–Calamagrostis canadensis–M. ciliata* community. *Pinus contorta*'s niche is on the dry end of the gradient as is that of *Antennaria corymbosa*. *Deschampsia cespitosa* occupies a wide portion of this gradient, indicating its flexibility in dominating stable mesic to seasonally dry sites, and its ability to invade wetter sites that are somewhat disturbed.

Analysis of plant species along oxidation-reduction potential gradient. In many respects it is the anaerobic versus aerobic character of the soil root zone, and not the position of the water table, to which plants are responding. This redox gradient should present a meaningful analysis to compare with the water table gradient analyses. Weekly data from 3 soil depths (7, 15, and 30 cm) were used to determine the position of the aerobic-anaerobic boundary in the soil during the growing season of 1988 at 9 redox stations (1, 9, 10, 28, 29, 36, 44, 46, and 49). These data were used to generate a plot showing the seasonal change in the position of this boundary for these stations (Fig. 40). The soil above the line was aerobic, while the soil below the line was anaerobic. As the boundary drops, more soil becomes aerobic.

As would be expected, since the water table is driving the redox potential, the results are somewhat similar to the water table gradient analysis. The forest stand at station 36 occupies a site where soils become aerobic during June. This illustrates again that healthy Rocky Mountain conifers grow on sites that have anaerobic conditions in the

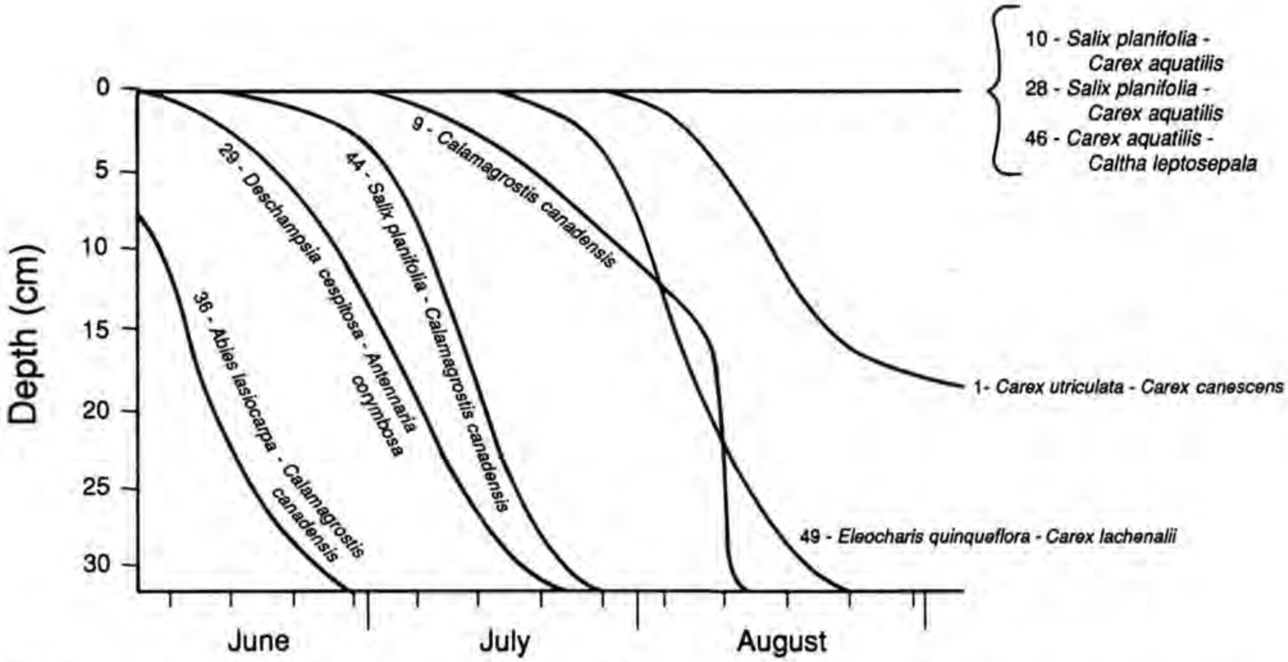


Fig. 40. Approximate position within the upper 30 cm of soil of the contact between the aerobic and anaerobic zones at nine stations during summer 1988. In the summer, contact drops deeper into the soil for all stations, except stations 10, 28, and 46 where soils remain reduced through the entire profile for the summer.

upper portion of the soil for up to several weeks during the growing season. Figure 40 also illustrates that the upper part of peat soils (for example, stations 9, 44, and 49) dry out during years with average precipitation (such as 1988) and become aerobic during the summer. In addition, these aerobic conditions occur simultaneously with the soil temperature maximum in August (see Fig. 33 for soil temperature data). Thus, some decomposition of leaf and root litter must occur. Peat accumulation in the Rocky Mountains may be a function of peat preservation during wet years.

The seasonal relations of the aerobic-anaerobic boundary surely change during wet and dry years, increasing or decreasing the duration of anaerobic conditions in the root zone of plants by up to several weeks. However, the relative positions of plant species and communities on this gradient would most likely remain the same because they are integrating long-term water table means and extremes.

For three stations (10, 17, and 46), all dominated by Carex aquatilis, no portion of the soil between 7 and 30 cm becomes aerobic at any point during the growing season. At the same time, a stand (station 1) dominated by *C. utriculata* was aerobic in the upper part in late summer. The gradient analysis constructed using water table data for July (Fig. 39) indicated that *C. utriculata* occupies a wetter position on the gradient than *C. aquatilis*. Thus, while *C. utriculata* can occupy sites subject to deeper and more prolonged flooding and ponding than *C. aquatilis*, the soils may dry out late in the growing season.

Data presented earlier (Fig. 34) show that it takes 1 to 3 weeks for a soil horizon to become aerobic once the water table has dropped significantly below that horizon. Thus, a general relation between water table and the aerobic-anaerobic conditions in the soil can be developed in the future. However, the use of water table data alone to determine whether a site has saturated and reduced soils, is not appropriate.

Number of Plant Species in Stands

The number of vascular plant species generally decreases as the cumulative wetness index of a site increases (Fig. 41). Stands with < 10 vascular plant species had > 2,100 centimeter-days (a water table at an average depth of 32 cm for the month of July), while stands with > 20 species generally had < 2,100 centimeter-days and many had < 1,800 centimeter-days. Regression analysis showed that the probability that the relation was due to chance is 0.00001 (R^2 = 42.5%); however, a straight line does not explain the variation in the data.

Standing Crop

Stands with the largest standing crop (in g/m^2) of herbaceous plants and greatest 1988 apical growth on shrub species occur on the wettest end of the moisture gradient (Fig. 42). I did not collect data on standing crop of tree species. All stands with 400 g/m^2 standing crop had >2,700 cumulative centimeter-days for July 1988. Stands

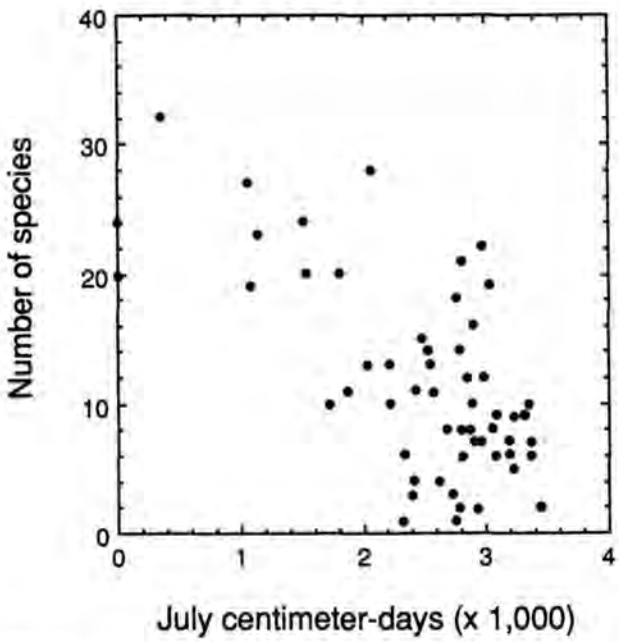


Fig. 41. Number of vascular plant species at stations along the July 1988 centimeter-day gradient. Stations with the largest number of species generally had fewer than 2,000 centimeter-days while those supporting fewer than 10 species all had more than 2,200 centimeter-days.

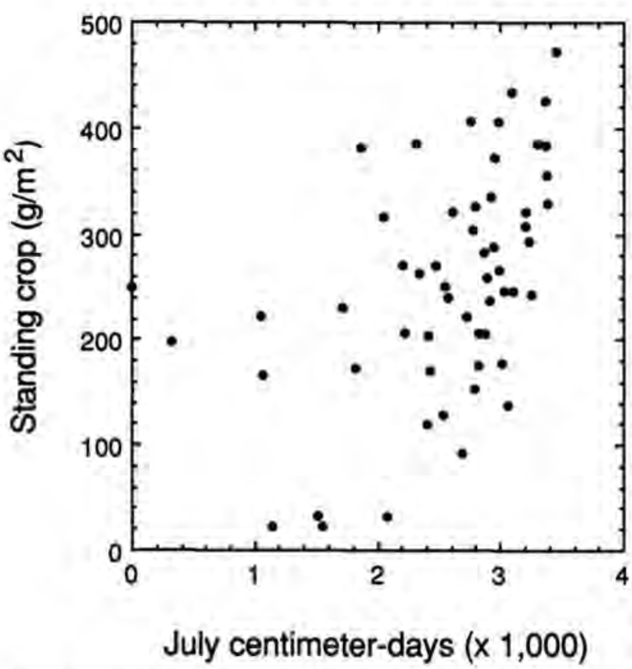


Fig. 42. Standing crop at stations along the July 1988 centimeter-day gradient. The stations with the greatest standing crop had the highest number of centimeter-days (i.e., they were the wettest stations).

with > 200 g/m^2 standing crop occurred in wet and dry sites. Regression analysis was used to determine if a linear relation existed in this data. The probability that this relation was due to chance is 0.00002 ($R^2 = 27.89\%$); however, a straight line explains little of the variation in the data.

The largest standing crop, 470 g/m^2, occurs in stand 5, a near monoculture of *Carex utriculata* that occupies a pool at the western end of the Green Mountain Trail Pond. Other stations with large standing crops (10, 21, 51, and 55) are dominated by *Carex aquatilis* and may also have significant cover by *Salix planifolia*. Large standing crops are also produced by some stands (9 and 50) dominated by *Calamagrostis canadensis*.

Large standing crops can be produced by very wet conditions that produce monocultures of tall individual plants and dense swards of sedge. Large standing crops can also be produced by more mesic conditions, such as in the *S. planifolia–C. canadensis–Mertensia ciliata* community, where luxuriant growth of shrubs, grasses, and forbs occurs.

Vegetation Successional Relations

The filling of the Green Mountain Trail Pond by processes of terrestrialization has been occurring for at least 11,840 ± 170 years B.P. Almost 2 m of peat has been deposited; the basal peats contain seeds of *Nuphar luteum* ssp. *polysepalum* and *Menyanthes trifoliata*, which still grow in the center and margin of the existing pond. Succession proceeds through the following generalized pattern:

Nuphar luteum ssp. *polysepalum–Potamogeton gramineus*

to

Menyanthes trifoliata–Carex utriculata

to

Carex limosa

to

Carex utriculata–Carex canescens.

The evolution of this primary mire seems to encompass the first three communities. The development of a secondary mire begins with the community dominated by *Carex utriculata*. Further terrestrialization toward communities dominated by *Calamagrostis canadensis* may occur; however, it would require the accumulation of peat well above the water table. Paludification (Cajander 1913; Heinselman 1963) does not occur in the study area and has not been reported from any Rocky Mountain peatlands. Peatlands in the Rocky Mountains are, with few exceptions, hydrologically confined to basins because the dry summer environment makes their spread into uplands impossible. Sjors (1983) stated that the larger part of the world's peatlands were formed by paludification; however, this generalization applies to climates that are much more humid than the southern Rocky Mountains of Colorado. Peats in the Rocky Mountains can only be supported by nearly constant early and midsummer irrigation from snowmelt water, groundwater discharge, or proximity to surface water. Peat cannot accumulate beyond the influence of this water. Radiocarbon dates of basal peats in Big Meadows and other locations in the Colorado Front Range (Pennak 1963; Madole 1976) indicate the great age of these peatlands and their inherent stability.

It seems that peatlands can be maintained in perpetuity. Most Rocky Mountain peatlands are climax ecosystems — succession from peatland to upland forest does not occur in the Rocky Mountains. Thus, the concept of a successional monoclimax for any elevation in the Rocky Mountains is invalid. Both forests and peatlands are climax ecosystems in this region, just as they are in Scandinavia and Canada (Sjors 1983).

Deschampsia cespitosa seems to be the most aggressive species in the study area. It has the ability to quickly colonize disturbed areas where mineral soil is deposited on peat or where the water table in a peatland is dropped and the surface peat oxidizes. This species probably exists as a number of genetically distinct populations with slightly different ecological requirements and tolerances. The pattern of succession once *Deschampsia* invades a site is difficult to interpret because it spreads rapidly to form stands of dense tussocks, such as at stations 56 and 29. These stands probably developed when a thick layer of mineral material buried the peat soil. There is no indication that further increase in peat thickness will drive succession further to reestablish *Carex* spp. as the community dominant.

Peat accumulation results in the isolation of plant roots from mineral soil, limiting nutrient uptake to that available in the peat and water. Species with high nutrient requirements cannot occur in the mire expanse. Wetland species that occur on the mire margin but are eliminated from the peatland expanse include *Carex aurea, Conioselinum scopulorum, Mertensia ciliata, Salix planifolia, Salix wolfii, and Senecio triangularis*. These species are tolerant of high water tables, but not high water tables and low nutrient availability. Thus, the analysis of wetland vegetation along a water table–drainage regime gradient provides only part of the ecological picture of species distribution.

The evolution of the Big Meadows wetland probably began on the broad glacial outwash floodplain of a braided Tonahutu Creek sometime between 15,000 and 12,000 years ago. Willows such as *Salix planifolia* and *S. wolfii* are pioneers on bare mineral substrate, as is *Deschampsia*, and probably were dominant species in the early stages of succession. Willow stems are abundant in basal peats of cores from Big Meadows. *Carex aquatilis* and *C. utriculata* probably invaded soon after, creating a lawn of coarse sedges beneath the willows. As peat accumulated, a flat or concave valley profile developed that resulted in the sheet flow of water from the northern tributary and springs across the peatland.

As peat thickness increased, the willows died out in all habitats except the mire margin and mineral soil areas. Stratigraphic work has not been completed to determine how deep the peat was before the willows and other species with high nutrient requirements were eliminated from what is now the peatland. However, it is not only the depth to mineral soil that is important, but also the height to which mineral-rich groundwater rising through the peat column could influence the nutrient regime of near-surface soils.

The fen vegetation that exists in Big Meadows today has been established for thousands of years; this stability may be produced by a dynamic system. During dry periods, a certain amount of peat oxidation may occur that would lead to the creation of a more distinctly concave peatland surface; this would hold more water. During wetter periods, the accumulation of peat would tend to flatten (from concave) the shape of the peat body and lead to the dispersion of surface water toward other portions of Big Meadows. This would dry the peat surface and lead to the redevelopment of a concave shape. This system might operate on a scale of hundreds to thousands of years.

Ditching can have a significant effect on a peatland by lowering the water table, thereby increasing oxidation of surface peats and subsequent decomposition (Verry and Boelter 1978). Peat oxidation is occurring in Big Meadows where water tables have been lowered by the ditch. Up to 1 dm of difference in the height of the peatland surface on either side of the ditch occurs between stations 15 and 16. Oxidation seems to occur rapidly, leading to the reduction of peat thickness. This thinning of the peat could lead to a change in species composition by changing the relation of depth to mineral soil and depth to the mineral-rich groundwater. Other types of successional relations for Rocky Mountain wetlands are reviewed elsewhere (Cooper 1986).

Interactions Among Vegetation, Soils, and Hydrology

Correlation of Vegetation and Hydrology

Direct gradient analysis reveals the close correlation between the characteristics of the water table and the realized niches of plant species. Recent research by Bertness and Ellison (1987) showed that the occurrence of the salt marsh species *Juncus gerardii, Spartina alterniflora,* and *S. patens* did not correspond to their potential performance (potential niche) across the same New England marsh in the absence of surrounding vegetation. While the high-marsh perennials, *S. patens* and *J. gerardii*, seem to be restricted to the high marsh, the low-marsh dominant, *S. alterniflora*, is capable of vigorous growth across the entire marsh. *Spartina alterniflora* seemed to be excluded from the high-marsh habitat by the high-marsh perennials. The organization of these salt marsh communities was structured by interspecific competition and also by disturbance (e.g., burial by wave-deposited debris), which species tolerate differently.

The interrelations of species along the water table gradient in Big Meadows probably are also structured by interspecific competition. As previously stated, low nutrient levels in the mire expanse limit many species to the mire margin or to mineral soil areas. Competition from species of the mire margin and mesic mineral soils may limit many species to the mire expanse. The main range of *Carex aquatilis*, *C. limosa*, *C. utriculata*, *Eleocharis quinqueflora*, *Galium trifidum*, *Menyanthes trifoliata*, *Pedicularis groenlandica*, and others may be limited to the mire expanse and to the colonization of pond edges because they have limited ability to compete with *Calamagrostis canadensis*, *Deschampsia cespitosa*, *Salix planifolia*, and other large, aggressive dominants of more mesic sites.

The wetland vegetation in the study area may not be structured solely by the stress placed on plants by saturated, anaerobic, and reducing soil environments. Two other factors are important: (1) the paucity of available nutrients limits the distribution of many species that can otherwise tolerate saturated soil conditions; and (2) interspecific competition for light and nutrients limits the ecological niche of species, restricting some species to the wetter, more nutrient-poor portion of their potential niche. *Carex aquatilis* and *C. utriculata* do not seem to be stressed by the wetland environment and in fact have greater annual standing crop in wetter areas than in more mesic ones. It may be that these two *Carex* species, which are so dominant in Rocky Mountain peatlands, have many ecotypes, some adapted to the wettest sites and nutrient-poor mire expanses.

Correlation of Vegetation and Soils

The correlation of vegetation and soils is simpler than the correlation of vegetation and water table characteristics because only a few soil types occur in the study area. The cold and generally wet conditions of the soils result in only three soil types (at the great group level of soil classification): Cryohemists, Cryaquepts, and Cryaquolls. In general, based on a comparison of Fig. 26 (soil types along water table gradients) and Fig. 39 (plant species along the July centimeter-days gradient), stands dominated by *Calamagrostis canadensis*, *Carex aquatilis*, *C. utriculata*, and *Salix planifolia* occur on Cryohemists. Stands dominated by *Deschampsia cespitosa*, *Picea engelmannii*, and *Pinus contorta* occur on Cryaquepts. Cryaquolls occur only where base saturation is high; they are limited to portions of the mire margin, where nutrient input occurs from groundwater or oxidation of peats.

Few wetland soil series are named in Colorado, and the Grand County Colorado Soil Survey (Alstatt and Miles 1983) does not describe all wetland soils (e.g., Histosols). In addition, some of the most common wetland soils (e.g., Cryaquepts) are classified to the great group or subgroup level, but not to the soil series level. In the study area, a variety of vegetation is encompassed in the great group Cryaquepts; this vegetation ranges from seasonally wet conifer forests to constantly wet mire margin shrublands to mesic grasslands.

Conclusions

Big Meadows is a complex mountain wetland system that fills the bottom of the Tonahutu Creek valley. The hydrologic template for wetland formation (sensu Moore and Bellamy 1974) was created by glaciers eroding bedrock and depositing till, thus shaping the topography to effectively retard the runoff of water, allowing the saturation of soils. The relatively flat valley floor, was created by the filling in of a lake that occupied the valley floor, and by the deposition of alluvial sediments about 45 m thick in the valley center. More recent surficial alluvial deposits occur on the eastern side of the valley, raising it above the western valley side. Tonahutu Creek is embedded in this alluvial debris.

The five water sources create a complex mosaic of hydrological and chemical variability: (1) Tonahutu Creek, which recharges the alluvial body on the eastern side of the valley; (2) the northern tributary, which sheetflows across Big Meadows; (3) seeps from the mountain side, west of Big Meadows; (4) groundwater, which discharges vertically up into the peat from the underlying alluvium; and (5) precipitation.

At least three distinct peat bodies occur in Big Meadows, one in the northeast, one in the southeast, and the large one that stretches along the entire western side. These peatlands are soligenous (sloping) fens. They are weakly minerotrophic in early summer when a flush of dilute snowmelt water flows through the system. Calcium concentrations in early summer surface water are less than 2.0 mg/L, typical for poor fens (Foster and King 1984). Later in the summer, groundwater in many portions of the peatland is more variable and in some sites more calcium-rich. The late season nutrient enrichment seems to create conditions characteristic of a richer fen and allows small coverage of rich-fen indicators, such as the moss *Campylium stellatum*, to occur. A strong Ca^{++} gradient from the mineral-rich mire margin on the western side of the fen into the mire expanse exists, particularly in late summer. The details of the nutrient regime of Colorado wetlands in relation to their vegetation must be further clarified.

Green Mountain Trail Pond seems to be a topogenous (influenced by flat topography and stagnant water) mire in a kettle that is slowly undergoing terrestrialization. Its hydrology is simpler than Big Meadows because it is not connected to any source of running water and is unaffected by alluvial processes. Green Mountain Trail Pond represents an environment that has been extremely stable during the Holocene. This environment supports populations of several rare boreal plant species (e.g., *Carex limosa* and *Menyanthes trifoliata*) that occur in small, disjunct populations in the southern Rocky Mountains well south of the main ranges of these species (Hultén 1968). These rare species occupy the ever-decreasing pond fringes, where there is little competition from the dominant *Carex* species.

The peatland expanses of Big Meadows are unpatterned, flat or concave, and relatively homogenous fens with low species diversity. Heterogeneity is created by the patterns of several ecological gradients: mire margins versus mire expanse, hummocks versus interhummock hollows, water track, alluvial versus peat soils, and disturbance due to the deposition of mineral matter over the peat and the grazing of small mammals. The principal gradients in the peatlands are similar to those described for other regions of the world where cold climates occur (Sjors 1948; Malmer 1986; Glaser 1987).

Several additional gradients may be important in Rocky Mountain peatlands. The effect of groundwater discharge patterns through peat of differing thickness may significantly influence the nutrients available to roots in mid- to late summer. Sites with thin peat over alluvial material (such as station 32) may be much more influenced by mineral-rich groundwater discharge than a site with deep peats (such as station 13), where most of the nutrients are adsorbed by the lower peat horizons. In addition, seasonal patterns of groundwater recharge and discharge may influence surface soil saturation. In Big Meadows there seems to be a groundwater recharge zone on the wetland edges and a discharge zone in the wetland center. The relation between these processes and the vegetation needs further study.

Stability and Instability of Rocky Mountain Wetlands

Peat thickness and peatland surface shape are influenced by the dry summer weather of the Rocky Mountains and probably are in a long-term balance with climate changes on a temporal scale of hundreds to thousands of years. Peat accumulation is slow in Big Meadows, averaging about 1 m every 5,000 to 6,000 years. Future tectonic events that will change the shape of the basin by even a few centimeters will change the hydrology and cause shifts in the distribution of species and processes. Human activities that modify the hydrology will also cause changes in the wetlands.

Regional gradients in peat types occur on both an elevational (vertical) and geographical (horizontal) scale. Southern Colorado and Arizona peatlands are more influenced by midsummer late summer monsoons than Big Meadows and other areas in central and northern Colorado where the monsoon pattern is weak. This rain may be a factor in maintaining high water tables and creating different peatland types in different regions of the Rocky Mountains. In addition, differences in wetlands on various bedrock types (e.g., volcanic, limestone, sandstone, and granite) on a regional scale should be explored.

With increasing elevation, patterned mires probably occur in response to a greater abundance of water and more steeply sloping mires. Poorly developed aapa mires, which are those mires containing strings (ridges) and flarks (elongate pools), occur in the Tonahutu Creek valley, as do large pools that seem to have grown up from the peatland surface controlled by local hydrology. Pool formation in some instances seems to be similar to processes occurring in Canada and Scandinavia (Foster and Fritz 1987; Foster et al. 1988). However, some pools in the Rocky Mountains seem to have developed from differential growth rates of peat in certain sheet-flow areas, and not through the development of hummocky topography, the joining of depressions across the slope, or the active degradation of peat in pools, as described by Foster and King (1984).

The data on peat thickness versus water table characteristics of the summer months (Figs. 30, 31, and 32) indicate that peatlands only exist where the water table is within 20–30 cm of the soil surface in midsummer. Sites that have a water table near the lower limit of that range can still maintain and perhaps accumulate peat, but they are susceptible to even slight hydrological effects that will change the balance of aerobic versus anaerobic conditions in the soil. Because the accumulation of peat brings the water table up, it should be expected that the degradation of peat would result in the lowering of the water table. However, a drop in water table of 20 cm does not necessarily mean a drop in the peat surface of only 20 cm because a water table drop caused by reduced water flow may not allow the development of a peat ecosystem of any kind. Reduction in the water source in a stream adjacent to a wetland would probably change the hydraulic head of aquifers beneath the wetland, resulting in changes in groundwater recharge–discharge processes.

Great annual differences in winter snowpack occur in the Rocky Mountains. Differences in winter snowpack and summer temperatures control the character of the runoff and the duration of high water tables in these mountain wetlands. Short-term ecological and hydrological studies that do not integrate information from wet and dry years cannot correctly interpret the relations between plant species, soils, and water tables. For example, the same study conducted during the very wet year 1983 and the dry year 1987 would end up with very different results in centimeter-days for each station, and in average depth to water table during any month for any station or community type. Annual precipitation differences between 1987 and 1988 were not great, but they resulted in up to a 20-cm difference in depth to water table for July dates in these 2 years and a 2-week shift in the time when water tables started to drop. Thus, long-term studies of hydrology, soils, and vegetation are essential.

Many Rocky Mountain wetlands similar to those described in this study are being affected by highway construction, water diversion, or other developmental activities that result in an interruption of major hydrologic regimes, soil moisture gradients, and nutrient gradients that dictate the distribution of soils and vegetation within these wetlands. The maintenance of Rocky Mountain wetlands is dependent on the continued functioning of these ecological processes. These wetlands provide critical elements of diversity in Rocky Mountain environments and they furnish habitat for many animal species in all or part of their life cycle. Studies such as this provide essential information for understanding, managing, and preserving these fragile wetland ecosystems.

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References

Alexander, R. R. 1985. Major habitat types, community types, and plant communities in the Rocky Mountains. U.S. For. Serv., Gen. Tech. Rep. RM-123. 105 pp.

Alexander, R. R. 1988. Forest vegetation on national forests in the Rocky Mountain and intermountain regions: habitat types and community types. U.S. For. Serv., Gen. Tech. Rep. RM-123. 47 pp.

Alstatt, D., and R. L. Miles. 1983. Soil survey of Grand County area, Colorado. U.S. Soil Conserv. Serv. 174 pp. + maps.

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. Ecol. Monogr. 57:129–147.

Bierly, K. F. 1972. Meadow and fen vegetation in Big Meadows, Rocky Mountain National Park. M.S. thesis, Colorado State University, Fort Collins. 102 pp.

Buol, S. W., F. D. Hole, and R. J. McCracken. 1980. Soil genesis and classification. 2nd ed. Iowa State University Press, Ames. 406 pp.

Cajander, A. K. 1913. Studien über die Moore Finnlands. Acta For. Fenn. 2:1–208.

Clymo, R. S. 1983. Peat. Pages 159–224 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. 4A. Elsevier Science Publishers, B. V., Amsterdam.

Cooper, D. J. 1986. Community structure and classification of Rocky Mountain wetland ecosystems. Pages 66–147 *in* J. T. Windell et al. An ecological characterization of Rocky Mountain montane and subalpine wetlands. U.S. Fish Wild. Serv., Biol. Rep. 86(11).

Cooper, D. J., and L. C. Lee. 1987. Rocky Mountain wetlands: ecosystems in transition. National Wetlands Newsletter 9(3): 2–6.

Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. Bioscience 39:24–30.

Damman, A. W. H. 1979. Geographical patterns in peatland development in eastern North America. Pages 42–57 *in* E. Kivinen, L. Heikurainen, and P. Pakarinen, eds. Classification of peat and peatlands. Proceedings of the International Peat Society symposium. Hyytiälä, Finland.

Damman, A. W. H. 1986. Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. Can. J. Bot. 64:384–394.

DuRietz, G. E. 1954. Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord und mitteleuropäischen Moore. Vegetatio 6:571–585.

Foster, D. R., and S. C. Fritz. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. J. Ecol. 75:409–437.

Foster, D., and G. King. 1984. Landscape features, vegetation and developmental history of a patterned fen in south-eastern Labrador, Canada. J. Ecol. 72:115–143.

Foster, D. R., H. E. Wright, Jr., M. Thelaus, and G. A. King. 1988. Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. J. Ecol. 76:1164–1185.

Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England. 298 pp.

Glaser, P. H. 1983. Vegetation patterns in the North Black River peatland, northern Minnesota. Can. J. Bot. 61:2085–2104.

Glaser, P. H. 1987. The ecology of patterned boreal peatlands of northern Minnesota: a community profile. U.S. Fish Wild. Serv., Biol. Rep. 85(7.14). 98 pp.

Hansen, P., S. Chadde, R. Pfister, J. Joy, D. Svoboda, J. Pierce, and L. Myers. 1988. Riparian site types, habitat types and community types of southwestern Montana. Montana Riparian Association, University of Montana, School of Forestry. Missoula. 140 pp. [unpublished report]

Heinselman, M. L. 1963. Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. Ecol. Monogr. 33:327–374.

Heinselman, M. L. 1970. Landscape evolution and peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol. Monogr. 40:235–261.

Hess, K., and R. R. Alexander. 1986. Forest vegetation of the Arapahoe and Roosevelt national forests in central Colorado: a habitat type classification. U.S. For. Serv., Res. Pap. RM-266. 48 pp.

Hultén, E. 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford, Calif. 1008 pp.

Knopf, F. L. 1989. Riparian wildlife habitats: more, worth less and under invasion. Pages 20–22 *in* K. Mutz, D. Cooper, M. Scott, and L. Miller, tech. coords. Restoration, creation and management of wetland and riparian ecosystems in the American West. Proceedings of a 14–16 November 1988 conference sponsored by Rocky Mountain Chapter of Society of Wetland Scientists, Denver, Colo.

Komarkova, V., R. R. Alexander, and B. C. Johnston. 1988. Forest vegetation of the Gunnison and parts of the Uncompahgre national forests: a preliminary habitat type classification. U.S. For. Serv., Gen. Tech. Rep. RM-163. 65 pp.

Kovach, W. L. 1986. Multivariate Statistics Package. Dept. of Biology, Indiana University, Bloomington. [computer disk]

Madole, R. F. 1976. Bog stratigraphy, radiocarbon dates, and Pinedale to Holocene glacial history in the Front Range, Colorado. J. Res. U.S. Geol. Sur. 4:163–169.

Malmer, N. 1962. Studies on mire vegetation in the Archaean area of southwestern Götaland (South Sweden). Opera Bot. 7:2.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. 64:375–383.

Marr, J. W. 1967. Ecosystems of the East Slope of the Front Range in Colorado. University of Colorado studies, Series in Biology 8. University of Colorado Press, Boulder. 134 pp.

Meierding, T. C. 1977. Age differentiation of till and gravel deposits in the Upper Colorado River basin. Ph.D. thesis, University of Colorado, Boulder. 353 pp.

Moore, P. D., and D. J. Bellamy. 1974. Peatlands. Springer-Verlag, Inc., New York. 221 pp.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

Pearsall, W. H., and C. H. Mortimer. 1939. Oxidation–reduction potentials in waterlogged soils, natural waters and muds. J. Ecol. 27:483–489.

Pennak, R. W. 1963. Ecological and radiocarbon correlations in some Colorado lake and bog deposits. Ecology 44:1–15.

Persson, A. 1961. Mire and spring vegetation in an area north of Lake Torneträsk, Torne Lappmark, Sweden. I. Description of the vegetation. Opera Bot. 6(3):1–100.

Pfister, R. D., R. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. U.S. For. Serv., Gen. Tech. Rep. INT-34. 174 pp.

Reed, P. B. 1988. National list of plant species that occur in wetlands: intermountain (Region 8). U.S. Fish Wild. Serv., Biol. Rep. 88(26.8). 76 pp.

Rutter, A. J. 1955. The composition of wet-heath vegetation in relation to the water table. J. Ecol. 43:507–543.

Ruuhijärvi, R. 1983. The Finnish mire types and their regional distribution. Pages 47–67 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. 4B. Elsevier Science Publishers B.V., Amsterdam.

Shuter, K. A. 1988. Surface and subsurface hydrologic processes in Big Meadows, Rocky Mountain National Park, Colorado. M.S. thesis, Department of Environmental Sciences and Engineering Ecology, Colorado School of Mines, Golden. 136 pp.

Siegel, D. I. 1983. Ground water and the evolution of patterned mires, glacial Lake Agassiz peatlands, northern Minnesota. J. Ecol. 71:913–921.

Siegel, D. I., and P. H. Glaser. 1987. Groundwater flow in a bog–fen complex, Lost River peatland, northern Minnesota. J. Ecol. 75:743–754.

Sikora, L. J., and D. R. Keeney. 1983. Further aspects of soil chemistry under anaerobic conditions. Pages 246–256 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. 4A. Elsevier Science Publishers B.V., Amsterdam.

Sjörs, H. 1948. Myrvegetationen i Bergslagen. Acta Phytogeogr. Suec. 21:1–299.

Sjörs, H. 1983. Mires of Sweden. Pages 68–94 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. 4B. Elsevier Science Publishers B.V., Amsterdam.

Soil Survey Staff. 1975. Soil taxonomy. U.S. Soil Conserv. Serv. Agriculture handbook 436. 754 pp.

Tallis, J. H. 1983. Changes in wetland communities. Pages 311–348 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. 4A. Elsevier Science Publisher B.V., Amsterdam.

Urquahart, C., and A. J. P. Gore. 1973. The redox characteristics of four peat profiles. Soil Biol. Biochem. 5:659–672.

Veery, E. S., and D. H. Boelter. 1978. Peatland hydrology. Page 674 *in* P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Proceedings of the national symposium on wetlands. American Water Resources Association, Minneapolis.

Weber, W. A. 1961. Additions to the flora of Colorado. University of Colorado Studies, Series in Biology 7: 1–26. University of Colorado Press, Boulder.

Weber, W. A. 1973. Guide to the mosses of Colorado. Occasional Paper 6, Institute of Arctic and Alpine Research, University of Colorado, Boulder. 48 pp.

Weber, W. A. 1987. Colorado flora: Western Slope. Colorado Associated University Press, Boulder. 530 pp.

Westoff, V., and E. van der Maarel. 1978. The Braun-Blanquet approach. Pages 617–726 *in* Handbook of vegetation science. Part V. Ordination and classification of communities. Dr. Junk, the Hague.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42:207–264.

Wright, H. E., Jr., D. H. Mann, and P. H. Glaser. 1984. Piston corers for peat and lake sediments. Ecology 65:657–659.

Appendix A. Plants of the Big Meadows Study Area[1]

Scientific name	English name
Abies lasiocarpa	subalpine fir
Achillea lanulosa	yarrow
Aconitum columbianum	monkshood
Agoseris glauca	false dandelion
Agrostis scabra	bentgrass
Alopecurus alpinus	alpine foxtail
Angelica pinnata	angelica
Antennaria corymbosa	pussy-toes
Arabis divaricarpa	rock cress
Arabis drummondii	rock cress
Arnica cordifolia	arnica
Aster foliaceus	aster
Betula glandulosa	bog birch
Bistorta bistortoides	bistort
Bistorta vivipara	bistort
Bromopsis canadensis	fringed brome
Calamagrostis canadensis	Canada reedgrass
Callitriche cf. *heterophylla*	water starwort
Cardamine pensylvanica	bittercress
Carex angustior	sedge
Carex aquatilis	water sedge
Carex aurea	golden sedge
Carex bella	sedge
Carex canescens	sedge
Carex dioica	sedge
Carex festivella	sedge
Carex foenea	sedge
Carex interior	sedge
Carex lachenalii	sedge
Carex limosa	sedge
Carex magellanica ssp. *irrigua*	sedge
Carex microglochii	sedge
Carex microptera	sedge
Carex rossii	sedge
Carex utriculata	beaked sedge
Castilleja sulphurea	paintbrush
Chamerion angustifolium (*Epilobium angustifolium*)	fireweed
Clementsia rhodantha (*Sedum rhodanthum*)	rose crown
Conioselinum scopulorum	hemlock-parsley
Crunocallis chamissoi	water spring-beauty
Danthonia parryi	Parry oatgrass
Deschampsia cespitosa	tufted hairgrass
Eleocharis quinqueflora	spike-rush
Elymus trachycaulus (*Agropyron trachycaulon*)	slender wheat grass
Epilobium lactiflorum	willow-herb
Erigeron peregrinus	fleabane
Erigeron speciosus	fleabane
Eriophorum angustifolium	cotton-sedge
Festuca idahoensis	Idaho fescue
Festuca saximontana	sheep fescue
Fragaria ovalis	strawberry
Galium trifidum	bedstraw
Gentianella acuta	little gentian
Gentianopsis thermalis	fringed gentian
Geum macrophyllum	large-leaved avens
Glyceria striata	mannagrass
Hierochloë hirta	sweetgrass
Juncus drummondii	rush
Juncus mertensianus	rush
Juncus parryi	rush
Juniperus communis	juniper
Kobresia sibirica	sedge
Kobresia simpliciuscula	sedge
Koeleria macrantha	junegrass
Linnaea borealis	twinflower
Lonicera involucrata	twinberry
Luzula campestris	woodrush
Luzula parviflora	woodrush
Lysiella obtusata	orchid
Menyanthes trifoliata	buckbean
Mertensia ciliata	chiming bells
Nuphar luteum ssp. *polysepalum*	yellow pond-lily or spatterdock
Orthilia secunda	one-sided wintergreen
Osmorhiza depauperata	sweet cicely
Oxypolis fendleri	cowbane
Pedicularis bracteosa	lousewort
Pedicularis groenlandica	elephantella
Penstemon confertus ssp. *procerus*	beard-tongue
Pentaphylloides floribunda	shrubby cinquefoil
Phleum alpinum ssp. *commutatum*	alpine timothy
Picea engelmannii	Engelmann spruce
Pinus contorta	lodgepole pine
Pneumonanthe parryi	bottle gentian
Poa leptocoma	bog bluegrass
Poa palustris	swamp bluegrass

Appendix A. *Continued.*

Scientific name	English name	Scientific name	English name
Poa pratensis	Kentucky bluegrass	*Stellaria laeta*	chickweed
Polemonium caeruleum	Jacob's ladder	*Stellaria longifolia*	stitchwart
Potamogeton gramineus	pondweed	*Streptopus fassettii*	twisted-stalk
Potentilla diversifolia	cinquefoil	*Swertia perennis*	star gentian
Pseudostellaria jamesiana	false chickweed	*Taraxacum officinale*	dandelion
Psilochenia runcinata (Crepis runcinata)	American hawksbeard	*Thalictrum alpinum*	alpine meadow-rue
		Thlaspi montanum	candytuft
Psychrophila leptosepala (Caltha leptosepala)	marsh-marigold	*Tragopogon porrifolius*	salsify
		Trisetum spicatum	spike trisetum
Pyrola chlorantha	shinleaf	*Trollius albiflorus*	globe-flower
Ranunculus reptans	spearwort	*Vaccinium cespitosum*	dwarf bilberry
Ribes lacustre	gooseberry	*Vaccinium scoparium*	broom huckleberry
Salix geyeriana	willow	*Valeriana edulis*	valerian
Salix monticola	willow	*Veronica nutans*	speedwell
Salix planifolia	willow	*Viola adunca*	mountain violet
Salix wolfii	willow	*Viola epipsiloides*	marsh violet
Senecio crocatus	groundsel		
Senecio triangularis	groundsel		
Shepherdia canadensis	buffalo berry		
Solidago multiradiata	goldenrod		
Stellaria calycantha	chickweed		

[1]For common species that have had recent nomenclature changes (Weber 1987) the old name is in parentheses.

Cooper, David J. 1990. **Ecology of Wetlands in Big Meadows, Rocky Mountain National Park, Colorado.** U.S. Fish Wildl. Serv., *Biol. Rep.* 90 (15). 45 pp.

This report describes in detail the results of 1987–1988 studies of hydrology, water chemistry, soils, and vegetation in the Big Meadows–Green Mountain Trail Pond wetland complex in the Rocky Mountain National Park in north-central Colorado. Five water sources affect the complex; each water source somewhat differently structures the hydrological character, vegetation, and water chemistry of various portions of the wetland complex. Twelve plant communities that make up the wetland complex are described and characterized.

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