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Mires, or peat-producing ecosystems, dominated by sedges, shrubs, and brown mosses, are common features in Cascade subalpine regions, occurring where moisture accumulates in small basins or on poorly-drained slopes. Although descriptions and classifications have been developed for mire vegetation in much of the world, there is little information of even a descriptive nature for these montane mires in Oregon and Washington. This thesis reports on phytosociological structure, environmental relations, and successional trends in one such mire in the Oregon Cascade mountains.

To characterize the general phytosociological structure of the mire vegetation at Sphagnum Bog, Crater Lake National Park, quantitative species cover data were used in conjunction with a Braun-Blanquet tabular analysis and two-dimensional stand ordinations, reciprocal averaging and a Bray-Curtis polar ordination. Defined community types correspond to physiognomic types as follows: *Carex rostrata* (reedswamp); *Eleocharis pauciflora*-*Carex limosa*, *Eleocharis pauciflora*/bryophytes (low sedge fens); *Carex sitchensis* (tall sedge fen); *Vaccinium*/

Aulacomnium palustre, *Vaccinium occidentale*/*Carex sitchensis* (shrub thickets; *Alnus incana*/*Brachythecium* sp. and *Salix barclayi* (marginal carrs).Phases were defined when appropriate. A vegetation map was made to illustrate the locations and extent of the various communities. Comparisons with other montane mires in the area determined that the physiognomic units defined are repeatable when appropriate habitat conditions are present, and that they usually include many of the same characteristic species, the dominant mosses being particularly constant.

Relationships of the vegetative patterns to the following environmental factors were investigated: topographic position, pH, water table depth, and nutrient concentrations. Concentration gradients of the nutrients calcium, magnesium, potassium, and phsophorus proved to be the most important in determining vegetation, with R^2 values ranging from .6 to .7. The role of topographic position was illustrated in several cross-sectional profiles. Water table measurements and, to a lesser degree, pH exhibit low correlation with the floristic gradients. It is suggested that the gradient determining vegetation patterns in this mire is a complex gradinet, dominated by nutrient regime, but also involving water table depths, water mobility, and topographic position. Some interaction of these factors is suggested.

Complete succession to terrestrial forest seems unlikely in these spring-fed, water-logged soils. Peat cores sampled show that little succession, even of the mire types has taken place within the peatland, where peat, sometimes greater than 2 m deep is underlain by pumice.

Limited invasion by *Pinus contorta* and *Picea engelmannii* is evident, however, in two drier community types--*Vaccinium*/*Carex sitchensis*, and *Carex sitchensis* (*Aster occidentalis* phase), as well as in a transitional meadow area. Establishment of these trees probably corresponds to favorable climatic periods 34 to 50 years ago, but some more recent establishment is also evident.

Comparison with pre-existing mire classification systems developed elsewhere in the world, indicates that Sphagnum Bog corresponds with moderately rich fen vegetation or *Philonotis fontana*-*Pohlia albicans* spring vegetation, on the bases of floristics, pH, and nutrient concentrations.

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INTRODUCTION

Potential for peat formation exists in surface features in which water collects. Relatively cool and moist climatic conditions further favor peat development. Thus, large expanses of peat-covered land occur through much of the higher latitudes, but at lower latitudes, especially in coastal regions or at high elevations, smaller peatlands are found under appropriate conditions. Much of the knowledge concerning the ecology of peat bogs and fens comes from groups of investigators in Fennoscandia, Russia, Britain, or more recently, in North America, particularly Canada and the upper Midwest and eastern United States. Remarkable similarities exist in the floristic composition of mires of similar types, particularly in the cryptogamic strata (Sjörs, 1963). Certain environmental factors consistently determine variation within and between peatland systems.

Objectives

Bogs and fens are common features along the Pacific Northwest coast and in subalpine areas; yet, very little ecological information is available on these ecosystems. This study serves as a preliminary to a more comprehensive survey of the mires of the mountainous regions of the Pacific Northwest. Sphagnum Bog at Crater Lake National Park, a montane mire, has been intensively studied with the following objectives:

(1) To characterize the composition, structure, and pattern of the vegetation, including both vascular and bryophytic species;

(2) To relate the distribution of communities to important environmental gradients; e.g., differences in topographic position, water table regime, pH, and nutrient status;

(3) To characterize the area as a whole, in terms of development, and type of mire system it represents; and,

(4) To compare the variability in floristic make-up and communities between Sphagnum Bog and other similar mires.

Future monitoring of the vegetation, and comparison with the baseline data obtained in this study, will provide useful insights into natural successional processes of montane mires, and into the degree of impact caused by human visitors and ungulates, both wild and domestic. Such information is necessary in formulating management policies that will maintain natural conditions, a primary concern of the National Park Service.

LITERATURE REVIEW

Terminology and Classification Systems

A plethora of confusing terms has developed in the various fields of wetland science. Unless clarifications as to specific usages are made, communication and understanding are difficult, if not impossible. Independent wetland schools have developed in different parts of the world, at different times in recent history. The reluctance to apply principles derived in one area to systems in another has contributed to the general confusion. In Europe, peatland studies have constituted a well-developed science since the turn of the century, yet their contributions have largely been overlooked by North Americans in recent studies (Sjörs, 1959). Furthermore, any classification is somewhat arbitrary, since there are numerous "directions of variation" in peatlands. Several of the systems, therefore, may be valid (Sjörs, 1959). As greater understanding of the systems is acquired, some convergence of ideas is becoming apparent (Heinselman, 1963).

In general, a wetland can be defined as any ecosystem having the water table above, at, or just below the substrate's surface, such that the surface is saturated for most of the year (Burrows and Dobson, 1972). Due to anaerobic conditions caused by the high water table, rates of production in many wetlands exceed rates of respiration and decomposition. Therefore, plant remains accumulate in varying stages of chemical, physical and microbial alteration. This mixture of complex organic compounds--celluloses, lignins, cutins, waxes, resins, alkaloids, pectins, fats, proteins, sugars, starches and decomposition products--is collectively termed peat, and ecosystems in which it accumulates, peatlands (Heinselman, 1963; Moore and Bellamy, 1974). The English term mire, or Swedish term myr, is equated by some researchers with peatland (Osvald, 1933; Godwin and Conway, 1939), but others use it in a broader sense to include macrophytic wetland vegetation that may or may nor actually form or grow on peat (Sjörs, 1959; Burrows and Dobson, 1972). Other general terms, as discussed by Sjörs (1959), are even more ambiguous; muskeg, although widely used in Canada, may specifically connote black spruce muskegs, and organic terrain may additionally imply terrestrial sites with thick humus, as found in some rich forests or tundra.

A summary of processes affecting variations within wetlands by Moore and Bellamy (1974) suggests these processes be divided into the abiotic template and biotic-abiotic interactions. The first level of the abiotic template consists of geomorphic, hydrologic, and macroclimatic conditions affecting gross morphology in the system; the second level consists of hydroedaphic conditions affecting biotic expression. Biotic-abiotic interactions include those modifying hydroedaphic conditions, such as changes in succession, and those modifying climate near the ground.

Classification systems have been founded on several of these criteria. Based on geomorphological, hydrological, and macroclimatic conditions, Moore and Bellamy (1974) suggest dividing peatlands into primary, secondary, and tertiary mire systems. The latter two are distinguished from primary mires as having large enough accumulations of peat to act as a water reservoir, and to develop a perched water table, respectively. Two early European systems, by Weber and Potonie (as reviewed by Moore and Bellamy, 1974), devided mires into Niedermoore or Flachmoore, Ubergangsmoore or Zwischenmoore, and Hochmoore, based strictly on ontogeny. Another early Fennoscandian syatem, based strictly on floristics,with no explanations of the differences, divided mires into comparable types called riekarr, karr, and moss (Moore and Bellamy, 1974). The use of hydroedaphic concepts in delimiting types was suggested as early as 1823 (Sjörs, 1959). Division of the mires into oligotrophic, mesotrophic, and eutrophic, with concepts borrowed from limnology, has now fallen into disuse in favor of looking at the source of the water and minerals, or the means of nutrition in the system (Heinselman, 1963).

More recently, classifications have been based on Thunmark's and DuRietz's theories that the ground waters of the three types are distinct. If classification is done according to the water source, soligenous mires fed by mineral-bearing waters percolating through them are distinguishable from onbrogenous mires, having convex surfaces that make them dependent on rainwater for nutrients. Contrast of minerotrophic with ombrotrophic mires emphasizes the nutrition of the vegetation; rheophilous versus ombrophilous mires emphasizes the mobility of the ground waters. Another recent classification by Tolpa is based strictly on floristic units (Moore and Bellamy, 1974).

In summary, Moore and Bellamy (1974) maintain that since mobility of mire waters is the most important factor, the terms rheotrophic, transition, and ombrotrophic should be adopted to distinguish the three groups. Rheotrophic mires are those deriving their nutrients from moving ground waters; transition mires represent types with insufficient ground water supplies, or mires in the process of change; and ombrotrophic mires represent systems deriving nutrients solely from direct precipitation. For ease in discussion, these terms are equated with the more commonly used terms fen, poor fen, and bog, respectively. Sjörs and Bellamy (Moore and Bellamy, 1974) both propose subclasses for each of these to account for the continuous nature of the variation between them.

This division into fen, poor fen, and bog is generally accepted by the Uppsala school of Swedish ecologists, including DuRietz, Sjörs, Malmer, Osvald, and others, but the English and Americans tend to deviate somewhat in usage, especially with the category of poor fen. In Britain, the transitional stage has often been called lacustrine bog, and various fens from regions unfavorable for bog development were called valley bogs (Gorham, 1957). Various Americans use the terms even more loosely, often including poor fen under the rubric of bog, considering only raised bogs as ombrotrophic (Heinselman, 1963; Stanek and Jeglum, 1977). Earlier American systems, as summarized by Dansereau and Segedas-Vianna (1952) as well as their own, were even more ambiguous and fraught with inconsistencies.

To further complicate the problem, other terms are occasionally used interchangeably with bog and fen. Heinselman (1963) defines a marsh as a wet, grassy place with little peat, yet Stanek and Jeglum (1977) combine marsh with fen in their classification system. Carr is a European term for a water-logged woodland, or wooded fen, generally with shallow peat, and better drained than other fens, consisting typically of alder, birch, or willow thickets (Sjörs, 1963; Gorham, 1957; Moore and Bellamy, 1974; Proctor, 1974). The term sallow is sometimes applied to willow carrs (Haslam, 1965; Godwin, et al., 1974) Stanek and Jeglum class Canadian alder carrs as thicket swamps. Reedswamp is another, special class of fens composed of reeds, or tall graminoids that have advanced into shallow water, often along shorelines, without a moss layer (Gorham, 1957; Moss, 1953). Strings and flarks are the elongate ridges and wetter depressions that form parallel bands in the patterned fens of the far North (Sjörs, 1959).

In conclusion, for purposes of consistency, the recent outline by Moore and Bellamy (1974), dividing mires into fens, poor fens, and bogs, based on mobility of ground water, will be used in this paper to characterize entire areas. When appropriate, terms such as carr will be employed for a more specific type of vegetation occurring within these.

Bogs, in general, are characterized as having a type of relief, such as updoming of the peat, that prevents the access of mineral soil water, so that the only supply of water is through direct precipitation. As a result, the peat acids have a low saturation by metal ions, pH values are quite low, and there is a general mineral deficiency for the plants. The vegetation is highly specialized, being poor in vascular species, and usually having a prominent bryophyte layer, particularly Sphagnum spp. (Sjörs, 1963; Heinselman, 1963). Fens, on the contrary, having convergent or parallel drainages, are influenced by water that has percolated through mineral soil. If this supply is small, intermittent, or from silicious soils, as in poor fens, they may be more or less acidic, but generally are not. Species indicative of minerotrophic areas will be present even if the degree of minerotrophy is slight (Sjörs, 1963). Often the vegetation is dominated by grasses, sedges, or reeds, with some shrub cover (Heinselman, 1963) and mosses other than *Sphagnum* spp. dominate.

Present Knowledge

Bogs and fens have been studied extensively in Europe for many years, particularly in the northern regions where peatlands are extensive. Gorham (1957) summarized early investigations of peatlands. Many European papers are unavailable to the English-speaking student, since the Scandinavian papers are usually in Finnish, Swedish, or German, and the Russian papers in Russian. For summaries of the Scandinavian school, one may refer to Sjörs (1950, 1959). The classic European studies were also reviewed by Vitt and Slack (1975). In addition, a number of important studies in North America have added to the general understanding of peatlands, generally in the north or east (Conway, 1949; Moss, 1953; Dansereau and Segadas-Vianna, 1952; Heinselman, 1963). Sjörs (1959) noted a strong similarity between vegetation of Northern Europe and Canada, particularly among the bryophytes. More recent studies have also delved into environmental gradients, employed ordination methods for interpreting the vegetation data, and have carefully examined the moss flora (Heinselman, 1970; Vitt and Slack, 1975; Vitt, et al., 1975; Stanek and Jeglum, 1977).

Climatic conditions at relatively high elevations in the mountains can provide favorable conditions for development of mires in regions where they are otherwise less common. In Sweden, mires are common in the subalpine zone and may cover large areas. Persson (1965) characterized the various subalpine types and reviewed previous work from Scandinavia. The high altitude mires in Scotland have also been described by Ratcliffe (1964). In the mountains of the eastern escarpment of Southern Africa, two types of bogs are found in the alpine belt; one in seepage areas and another in cirque-like riverheads. The vegetation of the latter type was classified using Braun-Blanquet association tables (van Zindern Bakker and Werger, 1974).

In the Pacific Northwest, mires are common features of the subalpine zone, or less frequently, of the lower elevation *Abies amabilis* or *Abies magnifica* var. *shastensis* zones (Franklin and Dyrness, 1973). The typical subalpine bog is listed as a Research Natural Area cell for the Western Slopes and Crest Province of the Oregon Cascades (Dyrness, et al., 1975), and presently is represented by Gold Lake Bog RNA (Franklin, et al., 1972). Yet, very few descriptions for these montane mires in Oregon or Washington exist(Franklin and Dyrness, 1973), and investigations into the accompanying environmental variables are even less frequent. Complete community descriptions are not available for Gold Lake Bog RNA or the proposed RNA Goat Marsh, in Washington; the vascular floras of several other recently designated bog RNAs are presently being described (Frenkel, pers. comm., 1979).

In the earlier part of the century, several investigators concentrated on mire types in the Pacific Northwest, but their descriptions are largely incomplete. Osvald (1933), a Swedish botanist, made general descriptions of coastal bogs. Although Rigg (1922, 1940) visited large numbers of bogs, only a few were in the Oregon Cascades. Observations of a very general nature were the extent of his descriptions of these areas; no species identifications were made for bryophytes or sedges, and a description of the peat stratigraphy was his only method of investigating the environmental relations of the bogs. Hansen (1947) also visited numerous bogs, but, as his primary interest was palynology, descriptions of the areas consisted mainly of a determination of the origin of the basin and composition of the adjacent vegetation, with brief notes on vegetation of the mire and peat stratigraphy and depth. Frye (1935) gave only very general descriptions, naming a few obvious species.

In recent years, mires have been included in several larger studies in the Pacific Northwest. Roach (1952) presented quantitative descriptions of the mire associations of a sedge-peat bog at 4200 ft (1280 m) in the Oregon Cascades, in addition to descriptions of forest associations of the area. Again bryophytes were not included in the study, nor were environmental variables. Campbell (1973), in a study of a subalpine meadow complex, characterized four hydric communities, in which she included moss flora, as well as assessments of soil chemistry and snow relationships. A peaty melt seep, the _Caltha biflora_/_Carex sitchensis_/_Dodecatheon jeffreyi_ bog association was described by Hickman (1968, 1976) as part of a study of non-forest communities of the western Oregon Cascades. Brooke et al. (1970), in the coastal mountains of British Columbia, briefly discussed an _Eriophorum-sphagnetum_ moor as part of a vegetation study in the subalpine mountain hemlock zone. Other studies of subalpine meadows in the Pacific Northwest dealt with drier meadows having smaller amounts of peat than a typical mire (Van Vechten, 1960; Kuramoto and Bliss, 1970).

Major and Taylor (1977) reviewed recent work on bogs and fens in alpine regions of California. Mire communities at Grass Lake on Luther Pass were described and mapped by Beguin and Major (1975), ranging from eutrophic *Caricetum nebraskensis* meadows to *Mimulo-Caricetum limosae* fens, with various accessory communities, including several hydric types and a willow community. Other relevant studies include a description of the coastal Inglenook Fen by Baker (1972 (in Major and Taylor, 1977)), species checklists and descriptions of the vegetation and ecology of a sloping, neutral, montane, non-Sphagnum bog dominated by Cratoneuron and Drepanocladus (Rae, 1970; Savage, 1973). Several "wet meadow" subtypes dominated by *Sphagnum* species and fine-leaved sedges, in the Sierras, were also described by Bennett (1965) and Strand (1972) (in Rundel, et al., 1977).

Major and Taylor (1977) maintain that much work is still required on Californian wetlands, which are rapidly being destroyed by development. Based on a classification system of comparable types by Guinochet and Vilmorin in the French Alps, they list potential wetland vegetation units for California, including the floating Potametea, seasonally submerged Littorelletea, flowing water Montio-Caricetea fuscae, Oxycocco-Sphagnetea acid bogs, Scheuaerio-Caricetea fuscae fens, and Salicetea purpurae thickets.

DESCRIPTION OF THE AREA

Physical Features

Sphagnum Bog, the study area, lies on the lower slopes of Mt. Mazama, in the southern Cascades of Oregon, at 43° 00'N latitude, 120° 15'W longitude. It lies 0.5 to 1.0 miles within the western border of Crater Lake National Park (Fig. 1) in Klamath County, Oregon. Township and range designations have not been assigned for the park, which falls between approximately T28S and T31S, R4E and R7.5E. Sphagnum Bog occurs within the Oregon Cascades Physioggraphic Province (Dyrness, et al., 1975).

Sphagnum Bog formed in a large, gradually sloping basin at the head of Crater Creek where two large springs at the higher, northwest end form a broad, but shallow stream, Crater Creek, that courses southwest through the forest between expanses of mire. The stream gradient in the area of the mire is low to moderate, with a drop in elevation from 1630.7 m to 1600.2 m. Although not indicated on the topographic map, elevation also decreases from the outer edges to the center of the system. The open areas of the mire are not directly adjacent to the main stream in most cases, but numerous smaller spring-fed rivulets occur throughout the system. Sphagnum Bog comprises approximately 1/4 mi^2 (.65 km^2).

Climate

Only general trends and estimates of the weather and climate in the vicinity of Sphagnum Bog can be discerned. The nearest U.S. weather

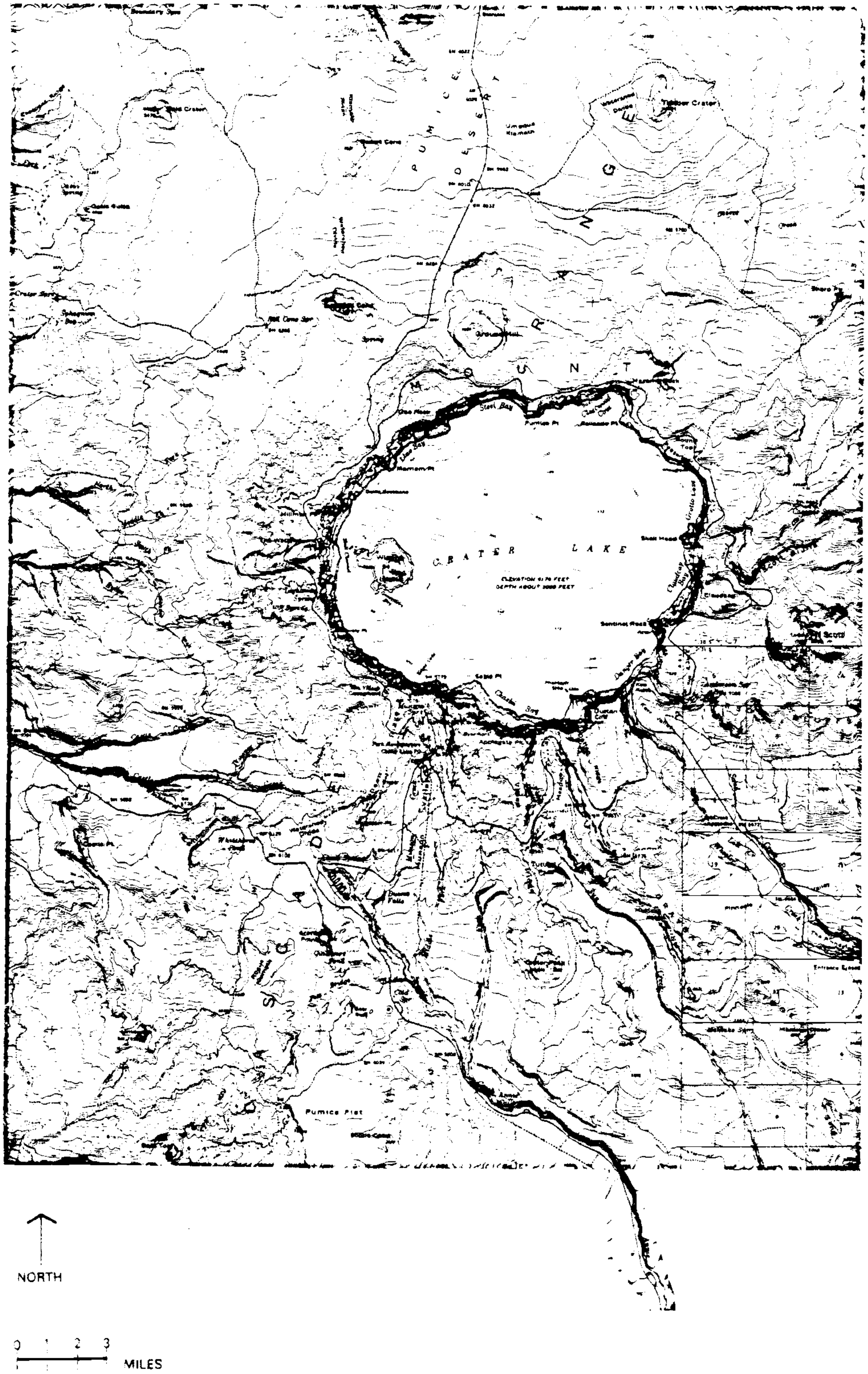

Figure 1. Location and environs of Sphagnum Bog study area in Crater Lake National Park, Oregon.

service station is at Crater Lake park headquarters, at 1990 m, 390 m higher than the bog. Precipitation patterns can be quite variable within the park, due to wide diffences in elevation, topographic position, and wind patterns. The following account of climatic conditions is summarized from Sternes (1963) and personal observations. Crater Lake has a winter rainfall climate, with 70 percent of the annual precipitation, mostly in the form of snow, falling between November and March, when moisture-laden air masses moving in from the Pacific are warmer than land. Only six percent falls in the summer months of June through August, when air masses from off the coast are cooler than land, and humidity, typically, is quite low. Though in lower amounts, rain can and does occur at all time of the year. A period of nearly two weeks of showers was experienced at Sphagnum Bog during September, 1978; September, 1977 was also quite rainy. The average annual precipitation is 170.8 cm, although the amount received at the bog would be somewhat lower. Winter temperatures average about -2.8°C. Heavy snow that accumulates in this portion of the park would moderate the effect of this extremely low temperature on vegetation near the ground. There is no evidence of frost heaving. Average summer temperatures are 11.8°C, with mean maxima and minima of 19.3°C and 4.3°C. At the lower elevations of the bog, the temperatures would be somewhat higher. On the average, snowpack at park headquarters ends by June 22 and the average date of the first permanent snow is October 31. Visits to the bog in 1978 demonstrated that the snow was gone from all but the edges by mid-June, and that no permanent snow had accumulated until after the first week of November, in 1978.

Winter the previous year was exceptionally dry.

Geology

The geologic history of Mt. Mazama has been outlined by Williams in 1942, with recent additional information summarized in the Andesite Conference Guidebook (Dole, ed., 1968) and by Harris (1976). Most of the following account is taken from Williams (1942). The main cone forming Mazama had its inception toward the end of the Pliocene. It was a composite cone of hypersthene-andesite, with glacial deposits between the flows, that was split by radial fissures. In the latter part of the life of the volcano, the magma changed to the more silicious dacite. Two major glacial advances and retreats left the mountain essentially bare of vegetation above 4500 ft (1372 m). Culminating eruptions, just prior to the mountain's subsidence, initially consisted of dacite pumice carried high above the mountain and eventually deposited over an area of 500 square miles (1295 km^2), mostly to the northeast. Following this ash rain, dacite pumice poured out at tremendous speeds as glowing avalanches, flowing down the major glacial valleys, where deposition began after descending steeper slopes. Immediately following the pumice avalanches, basic scoria flows of more limited extent carved channels in the earlier flows. Subsequent to ejection of all this magma, and some concurrent subterranean withdrawal, the magma chamber was left empty, and the summit areas of the mountain collapsed into the void, resulting in the caldera that formed Crater Lake (Harris, 1976). Radiocarbon dating of charred remains from the pumice flow, sets the time of the culminating explosions at 6600 ± 200 years ago (Rubin and Alexander, 1960 (in Blank,1968)).

Three principle rock types are found within the park boundaries: andesitic lava flows, basaltic lava flows and scoria, and pumiceous volcanic flow breccias and tuffs of dacite and andesite. The area surrounding Sphagnum Bog is a composite of geologic types, resulting from different periods of activity. Reference to the earlier geologic map by Diller (1902) suggests that the area is underlain by an old basalt flow, probably concurrent with the older volcanic series of the High Cascades (Williams, 1941). The basalt is fine-grained and rich in olivine (Williams, 1941). In relatively flat areas, there is a thin covering of pumice from Mazama's culminating eruptions (Diller, 1902; Williams, 1941), but occasionally domes of basalt rise through the pumice. This dacite pumice is siliceous, with numerous small crystals of feldspar, horneblende, augite and hypersthene comprising 10 to 15 percent of the total volume (Williams, 1961). A more current geologic map, however, simply designates this area as Mazama dacite pyroclastics (Blank, 1968). Explorations of Sphagnum Bog verify that on the lower flat areas now covered by peat, pumice forms a more or less continyous layer, but scattered, basaltic rocks were found on the higher forested islands within the mire.

The surface is well glaciated, having numerous striated ledges, as can be observed on the trail just to the north of the bog. Especially near the western park border, the topography of the basalt becomes irregular and rugged, with lava dams in narrow parts of some valleys. The presence of these lava dams, or of buried hummocky mounds of coarse drift left by the glaciers may have acted to block drainage of subterranean water in the area of Sphagnum Bog, thereby accounting for the hydric conditions necessary for the formation of the mire.

The mire can be no older than 6600 years, since the underlying mineral substrate consists of pumice ejected immediately before the mountain collapsed (Fig. 10). These pumice flows occurred during the Hypsithermal period (Hansen, 1947), when the surrounding landscape presumably was unforested, as a result of the glaciation that had scoured the mountainside down to 4500 ft (1372 m) (Williams, 1942). A cooler, wetter trend began 4000 years ago. Since very small amounts of woody remains were found in the peat, it can be assumed that the mire began with an invasion of sedges and herbs into shallow ponds formed overly the poorly drained blanket of pumice.

Soils

The soils in the Sphagnum Bog complex are highly organic and are here discussed as distinct types of peat, after a system summarized by Moore and Bellamy (1974). Three types are found; limnic, formed below the water level; telmatic, formed in a periodically emersed and immersed zone; and terrestric, formed above the general water level. All peat depositions are underlain by granular pumice. Limnic peats are of limited extent, occurring only in the very wettest parts of the area with standing water and also associated with reedswamp vegetation, evident in only a few instances as very narrow bands at the bottoms of deposits. The majority of peat deposits are telmatic fibrous peats, probably derived from *Carex sitchensis*, a sedge that currently dominates much of the mire. *Eleocharis pauciflora* co-occurs with the coarser sedges in some places. Roots, twigs, and leaves of *Vaccinium occidentale* are mixed with sedge peat in areas where the shrub dominates. In some areas, there is moss peat, mostly derived from *Drepanocladus* . Moss peat is quite spongy and often reddish in color. Wood remains are mixed with sedge remains in peat at the bottoms of some deposits. Finally, in carrs, terrestric peat is found. Terrestric peat has a higher mineral content, since mineral sediments are readily washed in from the adjacent mineral soil. Numerous alder or willow leaves and twigs are found in this peat, as well as fine roots of herbaceous species.

Peat depths range from less than one m to an average of one to two m over much of the area, the deepest deposits somewhat over two m. Hansen (1947) lists 2.3m as an average peat depth for deposits on Mazama pumice. This shallower depth reflects both the younger age of these bogs compared with those on glacial drifts, and possibly, also, the shorter growing season, drier summers, and colder waters and substrata (Hansen, 1947). According to various estimates of rates of peat accumulation (Hansen, 1947 (in Kuramoto, 1970); Rigg, 1958), the oldest parts of Sphagnum Bog may be 3000 to 3800 years old. This coincides with the beginning of the cooler, wetter climatic period 4000 years ago.

Soils in the surrounding forest were not described in this study. The nearest previously described soils are those of the *Pinus contorta* forest in Crater Lake National Park (Zeigler, 1978), incuding a sample soil pit approximately ½ mi northeast of Sphagnum Bog, with a similar mixed forest community designated as Abies lasiocarpa/ Haplopappus/Aster-Elymus (Zeigler, 1978). Since both the nearby soil sample site and the uplands immediately adjacent to Sphagnum Bog are in areas of dacite pumice flow parent material, and have similar vegetation, the general correspondence of the soils should be close. According to Zeigler (1978), these soils belong to the Steiger series, previously described by the U.S. Bureau of Indian Affairs, formed from water-transported flow material, rather than original deposits, as in the park. The other, more prevalent soil series of central Oregon, the Lapine series, developed, instead, on ash fall deposits. The Steiger series soils are well to excessively well-drained mixtures of pumice and scoria sand, gravel, and cobble, with a fine sandy to sandy loam texture. Profile development is weak, with a typical horizon sequence of A1, AC, C. Fertility, particularly of nitrogen, is quite low (Youngberg and Dyrness, 1964).

Vegetation

The forests surrounding Sphagnum Bog, though somewhat mixed, generally fall within the subalpine Abies magnifica var. shastensis zone, depauperate Chimaphila type (Franklin and Dyrness, 1973). This zone is part of Merriam's Canadian Life Zone, a classification system used by some of the earlier botanists in the park. A somewhat transitional nature with the higher subalpine Tsuga mertensiana zone is evident. No recent vegetation studies in Crater Lake Park have included this zone; Zeigler (1978) surveyed Pinus contorta forests, McNeil (1976) studied Pinus ponderosa-Abies concolor forests in lower portions of the park, and two specialized areas were investigated by Horn (1968) and Jackson and Faller (1973). Two comprehensive surveys of the park are available, but are old and highly generalized (Applegate, 1939; Wynd, 1941). They characterize the forests of this zone as having a depauperate understory, and seral stages with dense invasion of *Abies* sp. and *Tsuga mertensiana*. A recent study 19 km west of the park boundary, at Abbott Creek Natural Area, includes examples of *Abies magnifica shastensis* types forests with an abundance of evergreen sclerophyll taxa, as *Ceanothus* or *Arctostaphylos* in seral or drier habitats (Mitchell and Moir, 1976).

Due to its position near the southern end of the Cascades, the flora of Mt. Mazama reflects a mixture of North Cascades and Sierra Nevada elements. Mitchell and Moir (1976) maintain that the presence of evergreen sclerophyll taxa in drier areas of the nearby Abbott Creek *Abies magnifica shastensis* forests is suggestive of the Mediterranean climate of the southern Oregon Cascades, and that while there are important floristic elements of the Cascades, that these forest are very similar to California Sierran types. Within the mire, there are certain hygric, mire species that are circumboreal, and otherwise uncommon in the Sierra Nevada and probably also in the southern Cascades (Beguin and Major (in Major and Taylor, 1977).

METHODS

Field Methods

Vegetation

Initial reconnaissance of the bog complex was made in early summer 1977, to gain familiarity with the variation in vegetation and to determine sampling strategy. Sampling was by subjective choice of stands representing recurrent or unique units of homogeneous vegetation within the system. Twenty-five stands were sampled, with 40 or 50 standard 20 x 50 cm microplots placed at regular intervals along a stretched tape. Cover estimates were recorded for all vascular species and bryophytes occurring in the plots, using the standard cover classes described by Daubenmire (1959), with the slight modification of an additional class, +, for species with cover less than one percent. The canopy-coverage method outlined by Daubenmire (1959) was further modified to better distinguish cover of sedges occurring at different densities. For graminoids, the percentage of area covered by the foliage was used in determining cover class, rather than the total area delineated by the canopy's outline.
From this data, a preliminary classification of the communities was accomplished, by incorporating presence-absence data for all species into a stand similarity ordination (SIMORD) (Dick-Peddie and Moir,1970).

In the summer, 1978, an alternate, more objective approach of sampling across communities and gradients was employed. Five permanent transects were established along recorded compass bearings, each extending from forest edge to forest edge across the bog. The preliminary classification scheme waw used in selecting locations for these such that a diversity of community types would be represented. Percent cover was recorded for all vascular species and bryophytes in 20 x 50 cm microplots, using the cover-class method employed in 1977. The microplots were placed at two meter intervals over broad areas of homogeneous vegetation, or at one meter intervals where communities were narrower, and in transition areas. A total of 477 microplots was sampled. Figure 2 displays orientation and location of the transects.

A list of all vascular and bryophyte species was compiled for the mire areas. Phenological records were maintained for vascular species in 1978, by walking zigzag patterns throughout the mire complex, approximately every two weeks, so as to check examples of all community types. Additional species were searched for, and phenological activities of the species were recorded.

Authority names for the majority of the vascular plants follow Hitchcock, et al.(1976). Species not included in this flora because they are south of its range were named according to Munz and Keck (1959), and the monograph on Pinus contorta was utilized for that species (Critchfield, 1957). Verifications were made at Oregon State University's herbarium. A set of voucher specimens is located at the Natural History Museum, Crater Lake National Park, and some duplicate specimens are filed in the herbaria of Oreon State University and Southern Oregon State College. Mosses were identified using Lawton's Moss Flora of the Pacific Northwest (1971). The Sphagna, not covered by Lawton (1971), were identified using Nyholm's moss flora (1969).

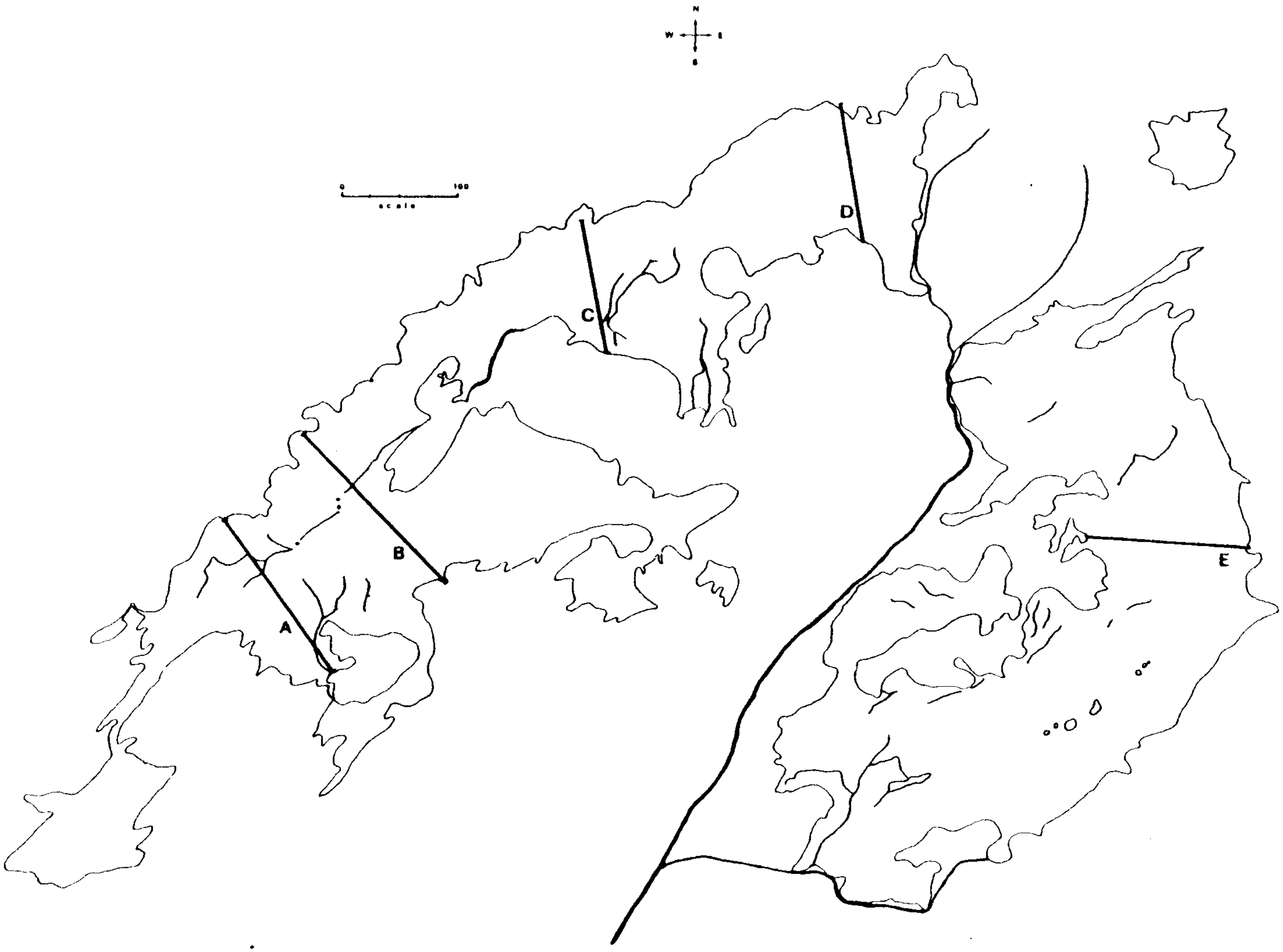

Figure 2. Location and orientation of permanent vegetation sampling transects, Sphagnum Bog, Crater Lake National Park.

Most bryophytes were verified by W.B. Schofield, University of British Columbia. Moss nomenclature follows a revised list by Crum, et al. (1973). Liverworts are named according to Schuster (1974). Bryophyte voucher specimens are at Crater Lake's Natural History Museum, and duplicate specimens are in the herbaria of University of British Columbia, Oregon State University, and the author's personal collection.

For mapping the bog communities, a series of parallel baselines, from forest edge to forest edge across the bog, with stakes set every 60 ft (18.3 m) was established perpendicular to, and intersecting a long line in each section of the bog complex. Locations for the ends of the lines were recorded on an air photo, and bearings recorded with a staff compass. The recorded locations of baselines and the grid they established were drawn onto a sketch map derived from a black-and-white photo flown during the summer of 1978 by the Oregon National Guard. The photo was of poor quality, distinguishing clearly only the marginal woodland communities and areas where water had accumulated. These areas were sketched onto the map from the photo while in the lab with the aid of a zoom transfer scope, but most of the mapping had to be done in the field, using the numbered stakes as a guide to the stands' locations.

Environmental Factors

Superficial bog topography was determined with an automatic optical level mounted on a tripod, stadia rod, and paced-off distances along permanent transects.

Along two of the transects, samples of the underlying peat were taken with a Hillyer peat borer, for construction of a profile relating surface topography with underlying mineral substrata and peat type. Vegetation data was correlated with these profiles using microplot data.

From the preliminary classification system developed in 1977, sixteen sites were selected to represent the different communities. Replications were included for the more widespread types. Two community types not studied in the first summer's work were also sampled.

Water table depths were measured at these sites according to the basic method outlined by Damman (n.d.). Three inch (7.62cm) diameter polyvinylchloride pipes three or four ft long (91.5 or 122.0 cm) were installed into cylindrical holes of the same diameter dug with a soil auger. The ground surface was used as a reference point for water level measurements. Positive values were used to record water depths below the surface; negative values for depths of water standing above the surface. Water levels were measured at irregular intervals from mid-summer to late fall, 1978, thereby including seasonal periods of high and low general water levels.

Measurements of pH were made at each of these sites, using the following methods: a soil pH kit; "panpeha" colorimetric paper; and two, single-unit, portable instruments (the Kelway soil tester and Accutronics soil tester). A portable pH meter was unavailable. At eight of the sites, a peat sample was dug from the first ten centimeters of the soil and brought to the laboratory for analysis within three days. Samples were oven-dried at 60° overnight, then finely ground and passed through a 40-mesh screen. One gram samples from each site were analyzed for total contents of N,P,K,Ca,Mg, and Na. Results were expressed in percent oven-dry weight. Total N was determined by the micro-Kjeldahl method. Perchloric acid digestion was used for the other analyses. Cations were determined by atomic absorption spectrophotometry on the solution, and total P colorimetrically with molybdenum blue.

Vegetation Analyses

Data collected from the five permanent transects formed a matrix of 477 samples and 97 species. Most available ordination and classification programs would not accept such a large matrix; therefore, before analyses were begun, two procedures to reduce numbers of samples and species were employed. The data screening program CEP-8A (Cornell Ecology Program) successively eliminated species according to four criteria for which I set limits as follows: the number of positive entries for a species was less than three out of 477, the species maximum percent cover value was less than 2.0, species with small variances were eliminated if the percentage of total variance remaining was above 90 percent, and until no more than 50 species remained. The number of samples was reduced by grouping the microplots by stands, where a stand was defined as a homogeneous unit of vegetation crossed by the transects. This was accomplished by looking for natural breaks in species composition and structure as expressed in plot data and incorporating information of obvious changes observed while sampling along the transects from field notes and memory. Occasional plots that fell in obvious ecotones between two stands were not used in subsequent analyses. The two data reduction procedures resulted in a new matrix of 67 stand samples and 50 species.

Two different approaches were employed in deriving a community classification from the reduced data set. First, the clustering program CLUS-B was employed, which did not require subjective judgements in the grouping of similar stands. CLUS-B is a non-agglomerative cluster analysis that minimizes the sums of squares around the means of cluster variances of observations in the data. Second, a more flexible, inductive approach was used; namely, the Braun-Blanquet tabular analysis as outlined by Mueller-Dombois and Ellenberg (1974). Average species cover values in stand samples were used in analysis rather than presence-absence data. The relatively continuous nature of vegetation variation made use of quantitative data imperative. The limits normally suggested for constancy e.g., between 10 and 75 percent for the differential species, often had to be abandoned. Species groupings showing similar abundance in several stands, or mutually exclusive species groups, were chosen as differentiating species for different stand groupings. In some cases, differentiating species for a unit of vegetation had very low overall constancy if the vegetation unit was poorly represented in the total data set. The derived groups were considered to be representative of the various communities and community phases in the system.

Several ordinations of the vegetation data were conducted so as to display the patterns of composition with reference to one or two major axes following the indirect gradient approach described by Whittaker (1967). Floristic gradients displayed in this manner often relate to simple or complex environmental gradients. Reciprocal averaging, as presented by Hill (1973), was selected as the first means of ordination because it offers several advantages. Reciprocal averaging does not require a priori knowledge of the underlying environmental gradients and the computer program selects endstands. The problem of linearity inherent in principal components analysis (another means of ordination) is circumvented because it inflates the species weightings at the extremes of the underlying gradient (Nichols, 1977); and, reciprocal averaging is not as subject to distortion and involution (Gauch, et al., 1977). Computationally, it is an eigenanalysis problem. It is quite appropriate for displaying strong floristic gradients in that it combines the concept behind Whittaker's gradient analysis with a method of successive approximations that simultaneously ordinates both species and stands (Hill, 1973).

Although reciptocal averaging gives a good, first axis, it may be ineffective for additional axes. In some cases, a polar ordination may prove more effective for this purpose (Gauch, 1977). A Bray-Curtis polar ordination was performed on the data set, from which two outlier stands had been removed during the reciprocal averaging. The endstands used for the first axis were those selected by the reciprocal averaging for the first axis. The similarity index employed was percent similarity, PS, with the equation:

$$PD_{jk} = IA - PS_{jk}, \text{ where } PS_{jk} = \frac{200 \cdot \sum_{i=1}^{l} \min(D_{ij}, D_{ik})}{\sum_{i=1}^{l} (D_{ij} + D_{ik})}$$

where summations are over all species (l), D_{ij} and D_{ik} are abundances of species i in samples j and k, IA is the internal association equal to 100 in most cases, and PD equals percent dissimilarity (Gauch, 1977). The second axis was chosen automatically, using a procedure similar to that of Bray and Curtis (1957). From stands close to the midpoint of the first axis, the pair with the greatest separation is selected. If either fewer than two stands are available, or if the second axis is less than 1/5 the length of the first, it will be bypassed (Gauch, 1977).

Various transformations were used initially on the data. For reciprocal averaging, the data was relativized by stands; for subsequent polar ordination, both a log transformation and a double standardization, i.e., relativization according to both sample and species, were performed.

Relation of Vegetation to Environment

For interpretation of the floristic gradients displayed by the ordination techniques, simple linear correlations were run. Environmental data was correlated with the ordination scores; i.e., the relative position along the ordination axis, for corresponding stands, using the environmental data as the independent variable. Since the sites for environmental data collection were not always in the same locations as the permanent transects, sampled stands from the transects were chosen to represent the collection sites, using the criteria of same community and community phase. R^2 values were generated (Austin, 1971).

RESULTS AND DISCUSSION

Vegetation

Classification of Communities and Phases

On the basis of the Braun-Blanquet classification table, eight community types were defined. These are presented in Figure 3 in the order in which they were displayed by the reciprocal averaging. Several of the communities were subdivided into phases, and a marginal ecotone was also defined, resulting in a total of eleven units. Distribution of species across the communities illustrates that the units are not discrete (Fig. 3). Certain species, particularly *Carex sitchensis*, are nearly ubiquitous, differing only in relative cover between the various communities. Most other range across at least several closely related communities. Only communities at the extremes of the gradient, i.e., the *Carex rostrata* reedswamp and the deciduous fen carr communities, exhibit definite breaks in species occurrences from the rest of the mire communities. However, although divisions into types may occasionally be somewhat arbitrary, a presentation of community types and phases is quite useful for ease in describing and discussing the vegetation. Classification of the communities confirms the continuity of the vegetation. Rather than initially breaking the samples into a small number of distinct groups, to be subsequently further subdivided, the CLUSB analysis provided a succession of very small clusters, leaving a large, heterogeneous

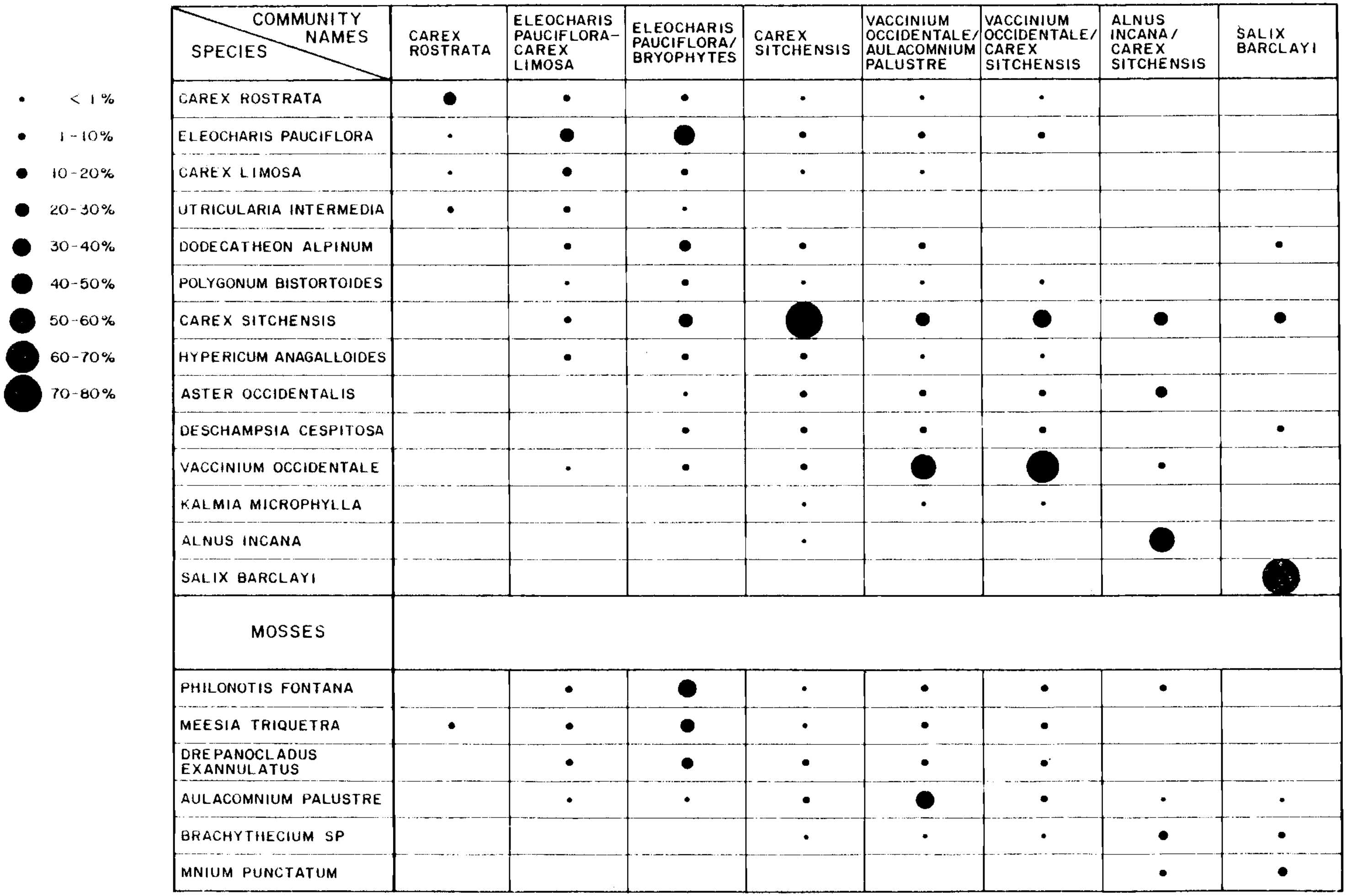

Figure 3. Representations of average cover values for characteristic species in the various communities.

cluster undivided.* Since this method apparently is unsuitable for such data, the classification is based solely on the Braun-Blanquet association table.

Vitt and Slack (1975) also found that bog communities in northern Michigan tended to overlap, and that well-separated species groupings are not consistently present. The species associations present, they attributed to similar physiological tolerances of species pairs. Under rigorous habitat conditions, associations might be very tight, but in the more typical case where several factors interact to determine a species' distribution, complete association between species in a group was unlikely. They also found that several species with sufficiently broad tolerances occurred across all of the community types.

Four physiognomic types are present at Sphagnum Bog: reedswamp, sedge fen, deciduous shrub thicket, and deciduous fen carr. The community types and phases fall into these types under appropriate subdivisions (Fig. 4).

I. Reedswamp

    Carex _rostrata_ community

II. Sedge fen

    A. Low sedge fen with no moss carpet (dominant sedges less than 50 cm in height)

        Eleocharis _pauciflora_-_Carex_ _limosa_ community

    B. Low sedge fen with moss carpet

        Eleocharis _pauciflora_/bryophyte community

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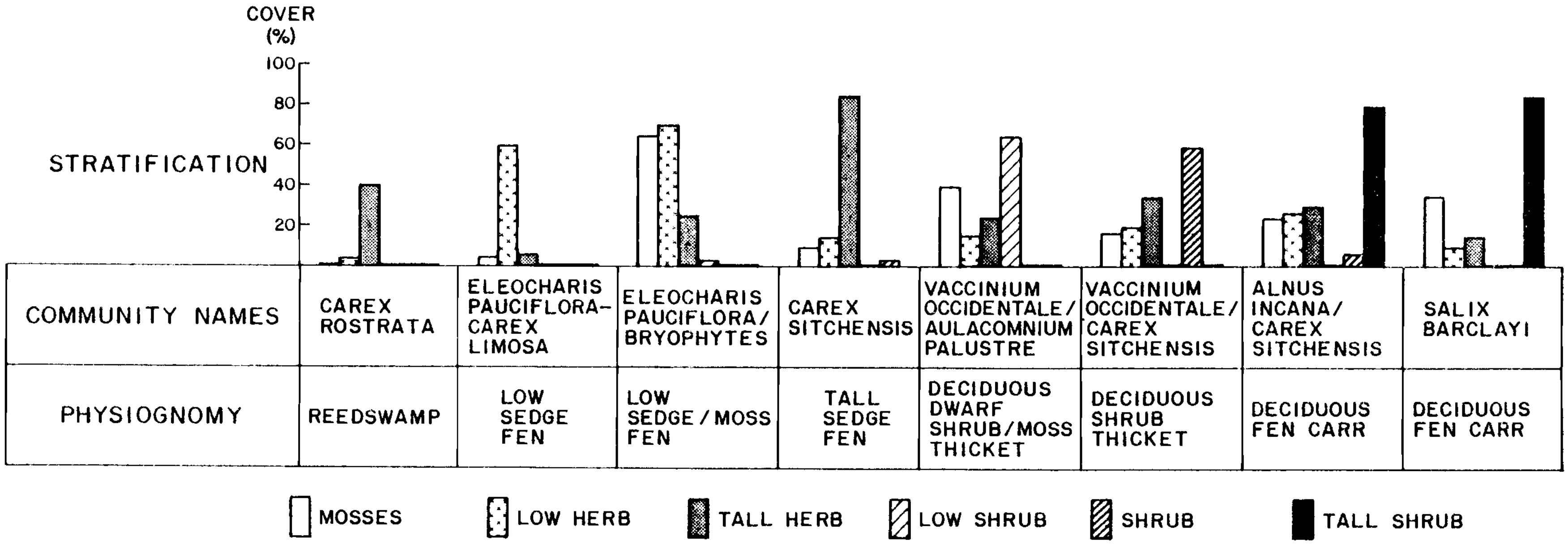
* For a discussion of the CLUSB method, see Chapter II B.



COMMUNITY NAMES	CAREX ROSTRATA	ELEOCHARIS PAUCIFLORA-CAREX LIMOSA	ELEOCHARIS PAUCIFLORA/ BRYOPHYTES	CAREX SITCHENSIS	VACCINIUM OCCIDENTALE/ AULACOMNIUM PALUSTRE	VACCINIUM OCCIDENTALE/ CAREX SITCHENSIS	ALNUS INCANA/ CAREX SITCHENSIS	SALIX BARCLAYI
PHYSIOGNOMY	REEDSWAMP	LOW SEDGE FEN	LOW SEDGE / MOSS FEN	TALL SEDGE FEN	DECIDUOUS DWARF SHRUB/MOSS THICKET	DECIDUOUS SHRUB THICKET	DECIDUOUS FEN CARR	DECIDUOUS FEN CARR

Figure 4. Comparisons of physiognomy and stratification between the communities at Sphagnum Bog.

- Meesia triquetra phase
- Philonotis fontana phase

C. Tall sedge fen (dominant sedges greater than 50 cm in height)

- Carex sitchensis community
  - Hypericum anagalloides phase
  - Aster occidentalis phase

III. Deciduous shrub thicket

A. Dwarf deciduous shrub thicket with moss carpet

- Vaccinium occidentale/Aulacomnium palustre community

B. Deciduous shrub thicket

- Vaccinium occidentale/Carex sitchensis community

1. Transition to low sedge/moss type

   - Vaccinium occidentale/Carex sitchensis-Eleocharis pauciflora phase

IV. Deciduous fen carr

- Alnus incana/Brachythecium sp. community
- Salix barclayii community

V. Marginal ecotonal zone

- Vaccinium scoparium/Clintonia uniflora community

Community Descriptions

Carex rostrata community. Reedswamps, as defined in the literature review, are characterized by tall, coarse graminoids that have invaded areas of shallow standing water, and have little or no moss layer. The Carex rostrata community, restricted to a small area in the southern portion of the western arm of Sphagnum Bog, originally occupied by a shallow pond, corresponds to this physiognomic type. Approximately two to three dm of standing water remain above the surface of an unstable sedge rhizome mat throughout the summer. Although the sedge mat is spread across the entire wetland, shoots are rather thinly distributed, with evident open water between. Tall graminoids, defined as 50 cm in height or greater, predominate, but their average cover amounts to only about 40 percent. *Carex rostrata*, a robust sedge averaging 1.0 to 1.5 m in height, accounts for nearly 100 percent of this tall graminoid element; *Carex sitchensis* and *Puccinellia pauciflora* also occur very sporadically in the area. Low herbs and sedges contribute a much lower percentage of the total cover. *Hippurus vulgaris* and *Menyanthes trifoliata*, species with a patchy distribution, are also characteristic. *Bidens cernua* and *Sparganium minimum* are restricted to this community, and are particularly prominent in the muddy edges. *Utricularia intermedia* is also fairly common. *Meesia triquetra* was the only bryophyte noted; it is limited to the extreme edges.

Eleven species were recorded in the twelve microplots sampled of this community type, but several other other species grew sporadically outside the sample plots. Average species richness per microplot is 4.25 (Table 1).

Patchiness within this community may perhaps be explained by differences in species' optimal water depth ranges. *Hippurus vulgaris*, *Sparganium minimum*, *Potamogeton*, and *Utricularia intermedia* are reported by Jeglum (1971) as exhibiting optimal growth in standing water of medium depth, 60 cm or less; *Glyceria borealis*, of shallow water, 40-59 cm in depth; *Carex rostrata* of surface water, where depth ranges from 1.0 to 19 cm; and *Bidens cernua* and *Menyanthes trifoliata* of areas where depth to the water table averages from 0 to 19 cm. He also indicated, however, that each species could also exist across a broader range of conditions. Water depths were not measured at the various plot sites, but it was observed that conditions are not uniform across the area. It is not known, therefore, if patchiness results from variation in levels of standing water, at Sphagnum Bog, or from variation in other factors, as pH or water movement; e.g., slow-moving streams bounded two sides of the old pond.

Eleocharis pauciflora-Carex limosa community. Sedge fens are divided into low sedge and tall sedge fens, according to height of the dominant sedges, 50 cm being the critical measurement. Low sedge fen is further divided into types with or withour a moss carpet. The *Eleocharis pauciflora-Carex limosa* community represents low sedge fen without a continuous moss carpet. The community is typical of areas with shallow standing water, or where the soil surface is saturated, and a considerable portion of the surface is unvegetated. Approximately 60 percent cover is provided by low sedges and herbs; other elements are insignificant. The dominant, *Eleocharis pauciflora*, and codominant, *Carex limosa*, average approximately 20 cm in height.

Other characteristic species are *Utricularia intermedia*, *Drosera rotundifolia*, *D. anglica*, *Carex rostrata*, generally much shorter in this community than in the reedswamp, and the ubiquitous *Carex sitchensis*.

Seven stands, including thirty-five microplots, were sampled of this community type. Twenty-nine species were recorded from these sample plots, but average species richness is only 6.97 per microplot.

This community type occurs throughout the Sphagnum Bog area, but is always of restricted extent, and corresponds to low spots.

Eleocharis pauciflora/bryophyte communities. The low sedge fen with moss carpet is typified by the *Eleocharis*/bryophyte communities. It is similar to the former community, having the same dominant *Eleocharis*, and comparable total low herb and graminoid cover of approximately 65 percent. The bryophyte layer, however, is strikingly more prominent, having an average cover of 60 percent as opposed to 5 percent in the *Eleocharis-Carex limosa* sedge fen. Tall herbs and graminoids are also slightly more important in this bryophyte community. In general, it occurs on slightly higher or drier spots than the *Eleocharis-Carex limosa* type.

Two phases have been defined, based on the dominant moss. The *Meesia triquetra* phase is characterized by high constancy and moderate cover of three mosses: *Meesia triquetra*, *Drepanocladus exannulatus*, and *Sphagnum subsecundum.* Species richness is quite high, averaging 9.78 per microplot. The number of low herbs is conspicuous, including such characteristic species as *Epilobium alpinum* var. *gracillimum*, *Dodecatheon alpinum*, *Polygonum bistortoides*, and *Mimulus primuloides*. *Carex sitchensis* is slightly more important here, with an average cover of 22 percent and 100 percent constancy.

The *Philonotis fontana* phase represents the drier end of the community, and *Eleocharis* dominates the areas more completely.

Philonotis fontana replaces the three major mosses of the *Meesia* phase. The tall, airy, bunchgrass *Deschampsia cespitosa* is scattered, but nearly always present. *Epilobium alpinum* var. *gracillimum* is much less prominent, but *Dodecatheon alpinum* and *Polygonum bistortoites* are more abundant. *Carex sitchensis* again occurs with moderate cover values.

The average species richness is only slightly lower, than in the *Meesia* phase, being 9.24 per microplot. Among the 58 microplots of the seven stands, 36 species were encountered. Eight stands of the *Meesia* phase were sampled, including 55 microplots, and a total of 32 species was recorded in the sampling.

These two phases of the *Eleocharis*/bryophyte community are common throughout the Sphagnum Bog area. They may occur as narrow bands,often around the edges of the *Eleocharis-Carex limosa* stands, or may cover relatively broad and flat, or slightly sloping areas, that are wet early in the summer and after periods of heavy precipitation.

Carex sitchensis communities. The vigorous sedge, *Carex sitchensis*, dominates the tall sedge fens, where it achieves a somewhat greater height of 0.8 to 1.0 m, than in the low sedge fens. *Carex sitchensis* is quite dense in these communities, with average cover values ranging from 48 to 99 percent. Only in a few small, selected sites that are very wet, is a more or less continuous moss carpet present. In general, only small fragments of mosses, usually different species than in the low sedge fens, were found on the ubiquitous, deep leaf litter (Figs. 3 & 4). Two phases of this community were defined— the *Hypericum anagalloides* phase and the *Aster occidentalis* phase.

The Hypericum phase represents the wetter end of this community, and is often associated with drainage channels, or other places occasionally flushed with moving water. As a result, the extent of these stands is fairly limited, and they appear as linear bands. Carex sitchensis has a higher average cover in this phase, and species richness is also higher, at 6.57 per microplot. Prominent herbs are Hypericum anagalloides, forming rather dense ground mats in places, and Oxypolis occidentalis, a tall, leafy umbel. Drepanocladus exannulatus, Amblystegium serpens, and Philonotis fontana are the characteristic bryophytes found in this community, but they are generally quite sparse.

Sampling of this phase included six stands, with a total of 184 microplots, and 51 species were recorded in the plots.

The Aster occidentalis phase covers fairly broad expanses in better drained portions of the bog. Cover values of the dominant, Carex sitchensis, vary widely from 48 to 97 percent. Codominant in most stands of this phase are the tall bunchgrass Deschampsia cespitosa and Aster occidentalis, with average cover values 15 and 16.3, respectively. The small herbs Stellaria longifolia, Galium trifidum, and Viola adunca,having average cover of 5.0 percent, are characteristic and exclusive menbers of this community and phase.

Species richness in this phase is notably lower than in the Hypericum phase, averaging only 4.5 per microplot, attributable possibly to the much drier conditions. A total of 54 microplots in seven stands were sampled of this phase, and included 37 species.

Vaccinium occidentale communities. Dense shrubs, primarily *Vaccinium occidentale*, cover approximately 60 percent in deciduous shrub communities, and *Carex sitchensis* cover is only 30 percent. Low herbs have low cover; bryophyte cover varies between types and phases. A dwarf deciduous shrub thicket/moss type, with the dominant *Vaccinium occidentale* averaging less than 50 cm in height, is differentiated from the taller, deciduous shrub thicket.

This dwarf shrub thicket/moss type is represented by the *Vaccinium occidentale/Aulacomnium* palustre community. *Vaccinium* is dwarfed, averaging only 30 to 40 cm in height, and is not so dense as in the other shrub communities, its average cover in this community only 53 percent. *Aulacomnium palustre*, a typical bog moss, has an average cover of 36 percent and 88 percent constancy, and frequently forms a more or less continuous carpet. The smaller bog shrub, *Kalmia microphylla*, averaging about 20 cm in height, is particularly prominent at the outer edges of this community and is almost exclusive to this type. However, *Kalmia* cover averages only about 15 percent. The herb *Tofieldia glutinosa* is abundant, though of low cover. A number of small mosses and liverworts occur sporadically, with *Aulacomnium*, in patches at the bases of *Vaccinium* branches, or on leaf litter. Species richness is high, at 8.41 per microplot. Fifty-one microplots, in eight stands were sampled, and included 50 species.

One fairly large stand of this community occurs in the lower end of the west arm of the bog, but more frequently this community occurs as small raised islands or hummocks between wetter *Eleocharis*/bryophyte communities, or as a band at the edge of the taller *Vaccinium* *occidentale* community.

In the typical taller deciduous shrub *Vaccinium occidentale* community, *Vaccinium* averaged between 60 and 70 cm in height, and forms dense thickets with only occasional openings, such that average cover equals about 72 percent. *Carex sitchensis* grows between the shrubs, and the taller portion of the population protrudes above the flat thicket tops. A slightly smaller, less dense-growing shrub, *Lonicera caerulea*, infrequently grows intermingled with the *Vaccinium* in some stands. The understory is quite sparse, contrary to the dwarf shrub stands, consisting of a few herbs and graminoids, and an assortment of bryophytes that form small patches on the lower *Vaccinium* branches, or on the leaf litter. *Sphenosciadium capitellatum*, a tall forb, is prominent is some stands, but absent or of limited occurrence in others. Characteristic bryophytes are the mosses, *Amblystegium serpens*, and *Brachythecium* sp., and two liverworts, *Lophocolia heterophylla* and *Chiloscyphus polyanthus*.

Low species richness is evident in this community, averaging only 4.8 per microplot. The extremely dense cover by the taller *Vaccinium* may account for this. A total of 91 microplots in 10 stands were sampled, including 48 species.

Finally, there is a group of *Vaccinium occidentale*/*Carex sitchensis* stands that appear to be transitional to the *Eleocharis*/bryophyte community. These are presented as the *Eleocharis*/bryophyte phase of the *Vaccinium* community. Several of the stands occur as narrow, poorly developed examples of the *Vaccinium* ocmmunity and one stand was an obvious ecotone between the typical tall *Vaccinium* community and a low sedge fen. Floristic elements of the *Eleocharis*/bryophyte community characterize this phase, particularly *Eleocharis pauciflora* and *Dodecatheon alpinum* among the vascular species, and *Meesia triquetra*, *Drepanocladus exannulatus*, *Sphagnum subsecundum*, and to a lesser extent *Philonotis fontana*,among the bryophytes. Richness is quite high, averaging 10.8 per microplot, due probably to the mixture of types. Thirty-two species were noted in the sampled plots.

Alnus incana/Brachythecium community and *Salix barclayi* community.

Carrs, as defined in the literature review, represent waterlogged woodlands, or wooded fens, with shallow, somewhat better drained peat, dominated generally by alder, birch, or willow thickets. Two carr communities are found at Sphagnum Bog--the *Alnus incana*/*Brachythecium* community and the *Salix barclayi* community. In both, the dominant tall shrubs, willow or alder, provide dense, extensive cover, and bryophyte cover averages between 20 and 30 percent. However, whereas low and tall herbs are of moderate total cover in the alder community, the understory of the willow carr is quite depauperate.

Alnus incana/*Brachythecium* carr occurs mainly along the edges of Sphagnum Bog between forest margins and open fens. The trees average between two and four meters in height, with numerous decumbent branches, all pointing away from the forest edge, or the center of the clump, and form dense thickets which are difficult to penetrate. Average *Alnus* cover is 52 percent. Occasionally shorter shrubs, such as *Spiraea douglasii* and *Vaccinium occidentale*, occur. Low and tall herbs and mosses generally dominate the understory, however. *Carex sitchensis* has moderate cover of 25 percent, and is 100 percent constant in the stands. Herbs such as Aster occidentalis, Senecio triangularis, Galium triflorum and Aconitum columbianum are characteristic of well-developed stands, and the shorter sedge, Carex disperma is a prominent member of the community. The characteristic mosses Brachythecium sp., Mnium rugicum, and Mnium punctatum, and several others occur in small, frequently intermingled patches, particularly at the bases of the branches.

Species richness is fairly high, at an average of 7.9 per microplot, probably reflecting the somewhat ecotonal position of this community between forest and open fen. A total of 18 microplots in four stands were sampled, and included 32 species.

Well-developed examples of willow carr, the Salix barclayi community, are somewhat limited in extent. The best example is a large dense stand along the eastern edge of the fen. Salix shrubs average about two meters in height. At the base, the branches are decumbent, but soon become stiffly erect and tangled. The understory is quite depauperate, consisting mostly of Carex sitchensis, Equisetum arvense, and a number of mosses, concentrated at the bases of the branches. Another species characteristic of this community, but not encountered in the sampled microplots is Pyrola asarifolia. Small patches of Carex disperma occur, especially along small drainage channels. Characteristic mosses are Bryum weigelii, Mnium punctatum, Drepanocladus aduncus, Brachythecium sp. and Amblystegium serpens, and the liverwort Chiloscyphus polyanthus is also common. The depauperate nature of the understory is reflected in the low average species richness of

5.9 per microplot. Fifteen microplots, in one stand, were sampled, and included a total of 17 species.

Forest edge communities. Finally, there is a set of communities of quite restricted extent, occurring in very narrow zones or specialized habitats. The first is a rather amorphous collection of stands representing the forest edge transition zone, that is shaded by the adjacent large forest trees, as well as being influenced by the wetness of the adjacent bog. Sixteen microplots of this type in four stands were sampled. *Vaccinium scoparium* and *Clintonia uniflora* are are characteristic species for which the type is named. *Carex sitchensis* and *Vaccinium occidentale* also exhibit relatively high cover, at least in some areas. Mosses present are those typical of wet forests, such as *Dicranum pallidisetum*, *Polytrichum juniperinum* and the drier bog moss *Aulacomnium palustre*. In contrast to the surrounding forest, the low understory vegetation is quite dense.

Stream community. Communities restricted to small, highly specialized areas were not adequately covered by the system of permanent transects, but were either sampled or described independently during the general overview made in 1977. A distinctive community comprised of floating moss mats of *Fontinalis antipyretica* is found in the larger streams. Lesser amounts of *Drepanocladus exannulatus*, *D. fluitans*, and *Hygrohypnum bestii*, or the vascular species, *Mimulus guttatus*, grow on these mats or form separate smaller mats. *Veronica americana*, and the grass *Glyceria borealis*, are rooted in the bottom of the streams and are emergent. Vegetative cover is sparse, with much clear, open water between patches. A moderate to high number of species is present, however. The water is cold, clear, and flowing, but not too swiftly. In some places the channels are discontinuous, with deep holes in between, up to two meters or more in depth. The best-developed streams average about 70 to 100 cm in width and 30 to 70 cm in depth. The bottom consists mostly of peat, but some stream depositional particles are present.

Deep pool communities. In the lower portion of the eastern arm of the bog, there are no major channels, but a discontinuous series of deep pools arranged linearly. These range in size from 1.5 to 2 m or more in depth. Vegetation varies between the different pools. In some, only the moss *Fontinalis* grows; in others, a fairly dense growth of emergent, aquatic *Sparganium minimum* with *Potamogeton berchtoldii*; and in still others, an almost complete dominance by floating *Potentilla palustre*. Algal growth is abundant in all.

Nuphar polysepalum community. In a bowl-shaped depression in the forest between the east and west parts of Sphagnum Bog is a small shallow pond, 28 cm in depth, at the center, and $800m^2$. The submerged area is dominated solely by *Nuphar polysepalum*, covering 30 percent of of the surface. Proceeding outwards from the pond, one encounters several bands of vegetation, representing progressively drier conditions. The emergent aquatics *Sparganium minimum* and *Carex rostrata* occupy a two meter band along the edge of the pond, where water may reach a depth of 8 cm. The next band is occupied by a dense growth of *Carex sitchensis*. Terrestrial vegetation follows, dominated either by

Deschampsia atropurpurea and associated forbs, or *Vaccinium occidentale* with *Spiraea douglasii*, *Salix* sp. small amounts of *Carex sitchensis*, and occasional forest edge forbs.

Average Species Richness

From a comparison of average species richness per microplot among different community types and phases, hypotheses as to distributions of resources and relative microenvironment harshness can be drawn (Table I). It appears that communities having lowest average species richness are those in which either conditions are quite restrictive to the growth of most species, as in the *Carex rostrata* reedswamp, in which only species adapted to moderately deep standing water can exist; or, those in which there is very high dominance by a large species. The latter is the case in some stands of the *Aster* phase of the *Carex sitchensis* community, in which the *C. sitchensis* grows so densely that little light gets through to the understory. Similar conditions occur in the dense *Vaccinium* thickets and the dense *Salix barclayi* carrs. The greater richness in the alders may be due to a slightly less dense canopy, allowing more light to filter through to the understory, or to the narrowness of the zone, giving it somewhat ecotonal characteristics, and allowing species from either adjacent zone to overlap somewhat into this community, augmenting its species richness. The *Eleocharis pauciflora-Carex limosa* community probably represents an area of intermediate harshness, with standing water present during at least the early part of the summer, but not as deep as in the reedswamp, or permanent. Highest richness is

Table I. Comparison of average species richness in the various communities at Sphagnum Bog.

COMMUNITY	AVERAGE SPECIES RICHNESS PER MICROPLOT
Carex rostrata reedswamp	4.3
Carex sitchensis (*Aster occidentalis* phase)	4.5
Vaccinium occidentale/ *Carex sitchensis*	4.8
Salix barclayi carr	5.9
Carex sitchensis fen (*Hypericum anagalloides* phase)	6.6
Eleocharis pauciflora-*Carex limosa* fen	7.0
Alnus incana/*Brachythecium* carr	7.9
Vaccinium occidentale/*Aulacomnium palustre*	8.4
Eleocharis pauciflora/bryophyte (*Philonotis* phase)	9.2
Eleocharis pauciflora/bryophyte (*Meesia* phase)	9.8
Vaccinium occidentale/*Eleocharis*/bryophyte	10.8

attained in the ecotonal Eleocharis phase of the Vaccinium occidentale community and the Eleocharis/bryophyte communities. In the latter, conditions are not extreme; these areas are wet, but not inundated with standing water. Further, they are not strongly dominated by any large species, and as a result, an abundance of light reaches ground level.

Vegetation Map

A map of communities and phases is useful in formulating hypotheses as to the causes underlying the distribution of these types (Fig. 5). Due to the extremely limited extent of some of the different phases, and difficulty in reconnaissance mapping, some phases were not distinguished on the map, particularly phases of the Eleocharis/ bryophyte community and different Vaccinium occidentale communities.

In general, the two carr communities are limited to where forest and associated mineral soils border the mire. Salix barclayi communities form a more or less continuous narrow band along the slightly higher edge of the east arm of the bog, and at a narrow isthmus of the bog, approximately midway along the length of the border, the carr expands to a large stand (30 x 50 m) that extends nearly halfway to the opposite forest border. Aside from the band and broader stand, there are only occasional small patches of willow carr, usually at, or near, the western or southeastern border of the eastern arm. These patches often occur where a bog drainage channel enters the forest, or in a depression with some accumulation of standing water from a drainage channel. Few willow patches occur in

Figure 5. Color-coded sketch map showing approximate distribution of major mire vegetation types at Sphagnum Bog Complex, Crater Lake National Park.

the west arm. Those that do are quite small, shorter, and usually in low, wet spots. It is not even certain that all the willows are the same species, since at the time of mapping, young fruits required for identification were unavailable. A different *Salix* species of lower stature had been found when specimens were collected, in the upper end of the west arm of the bog, in a mixed *Vaccinium* community.

The *Alnus incana/Brachythecium* community also forms a narrow band along the upper end of the slope where the western edge of the bog borders the forest. This band is limited to the west arm of the bog. Like the willow carr, the alder carr achieves its greatest development at a point where the bog becomes only a narrow isthmus surrounded by forest. Covering approximately 20 by 15 m, this alder stand is considerably smaller than the large stand of willows. Patches also occur along the lower, eastern edge of the west arm of the bog, especially in low, wet areas near creeks. One small shrub even grows in the open part of the bog, although it is still close to a stream, and not too far from the forest edge.

Several community types are quite limited in extent, occurring only in specialized habitats. The *Carex rostrata* reedswamp is restricted to a former pond with shallow standing water, in the lower end of the west arm, covering approximately 10 by 15 m^2.

The deep pool communities are limited to several pools in a linear pattern in the lower half of the east arm, symbolized by dark blue, for standing water.

The *Nuphar polysepalum* community is restricted to the shallow pond surrounded by forest, near Crater Creek, between the two major arms of the bog.

Of the major community types, the Vaccinium occidentale/Carex sitchensis type is the most extensive. Invasion by stunted conifers is prominent in some portions of this community, particularly in those areas close to a forest border. Such invaded areas are marked on the map with intersecting diagonal lines. The wetter phase of the Carex sitchensis community also covers large areas, especially at the lower end of the west arm, where the slope decreases and bog run-off accumulates, and in the wet, discontinuous portions of bog surrounded by forest, toward the middle of the bog system. This type also often appears as short lines on the map, since it is frequently associated with the edges of small drainages. At the edges of the bog, the Carex community tends to grade into a meadow, characterized by the presence of Deschampsia atropurpurea and more typical meadow forbs as Senecio triangularis. Drier phases are more limited, being most prominent in the lower portion of the west arm, in areas drained by small streams.

The Eleocharis communities are widespread, but examples of some types, particularly the Eleocharis-Carex limosa community, were often too small to illustrate at the scale of the map. An enlargement of certain portions would illustrate a typical zonation, with the Eleocharis-Carex limosa at the center of a depression, an Eleocharis bryophyte community at the edge, and a Vaccinium community on the higher portions, occurring as isolated hummocks, or as narrow ridges, where several hummocks wholly or partially coalesce. Such an intricate mosaic of vegetation types, common in the central portions of the mire, appear to be, at least in part, a reflection of the complex hydrology of the system, with its numerous seeps, channels for water movement, and low areas of water accumulation and stagnation. For other large mires, it has been suggested that such patterns reflect a number of changing environmental conditions (Burrows and Dobson, 1972), particularly the water flow patterns (Sparling, 1966).

Phenology and Reproductive Dynamics

Within a community or tight mosaic of communities, interspecific competition is an important component of the system. It is difficult to evaluate the role of competition,however, without conducting experimental studies. Competition for pollinators, or for the resources required for reproduction,--water, light, nutrients--, cna be considered in terms of the timing by various species in a system of reproductive activities. Several recent phenological studies suggest that in response to competition for pollinators, or for energy resources, bog plants have staggered blooming periods, spread more or less evenly across the season (Pojar, 1974; Reader, 1975; Heinrich, 1976).

In the Pacific Northwest, phenological studies including two Sphagnum bogs, a salt marsh and subalpine meadow (Pojar, 1974), and on a _Carex sitchensis-Vaccinium occidentale_ association of a montane bog in Oregon (Roach, 1952) are relevant. The phenological record from Sphagnum Bog for 1978 demonstrates a general staggering of the blooming periods across the season. The overall growing season is also obviously shortened relative to more low-elevation communities.

Comparison of the phenological pattern with those obtained by Pojar (1974) in three herbaceous community types, shows that Sphagnum Bog most closely approximates the subalpine meadow (Table II). Subalpine mires have particularly short growing periods because of the length of time the permanent snow pack remains. The meadows generally retain snow longer than the surrounding forest (Campbell, 1973), and drier, shaded parts of the meadow are the last to become snow-free. In poorly-drained areas, excessive water from snow-melt may delay the beginning of the growing season for some species (Roach, 1952), and in well-drained communities, end-of season drought may limit growth for others (Campbell, 1973). As a result of the short growing season at Sphagnum Bog and Nash Crater Bog (Roach, 1952) individual species' growing seasons might be reduced. Pojar (1974) suggests an inverse relationship between the number of species and the average blooming period. Additionally, species known to be at least partially autogamous,--*Drosera rotundifolia* and *D. anglica*, and probably *Kalmia microphylla* and *Vaccinium occidentale* (Pojar, 1974), generally have staggered blooming times also.

In light of the shortened growing season, one might conclude that the staggered blooming periods are a means of avoiding competition for insect pollinators. Subalpine meadow species are predominantly insect-pollinated; species of Sphagnum bogs are about equally divided between anemophily and entomophily (Pojar, 1975). The ericaceous bog species particularly, are dependent on insect visitation (Reader, 1975). However, a major portion of the vegetation at Sphagnum Bog consists of sedges and graminoids, and the number of ericaceous species is rather

Table II. Flowering phenologies of the species at Sphagnum Bog, 1978.

OBSERVATION DATES	JUNE......		JULY.....		AUG.......		SEPT.......	OCT....
SPECIES	11	25	8	24	5	25	15	18
Salix pseudocordata	x							
Salix barclayi	x o							
Alnus incana	x		x					
Kalmia microphylla	x		x					
Lonicera cerulea	x							
Caltha biflora	x	x	x o					
Ranunculus gormanii	x	x	x o					
Viola adunca	x		x					
Viola macloskeyi	x	x	x					
Viola glabella	x							
Polygonum bistortoides	+ x	+ x	+ x	x	x o	x o	x o	x o
Dodecatheon alpinum	+ x	x	x	x o	x o			
Pedicularis groenlandica	x	x	x o	x o				
Carex limosa	x		x					
Scirpus congdonii	+ x		x					
Vaccinium occidentale	+	+ x	x	x				
Mimulus guttatus		x	x	x	x	x	x	
Tofieldia glutinosa		x	x	x	x			
Carex sitchensis		x	x	x o				
Rubus lasiococcus			x					
Montia chamissoi			x	x				
Stellaria simcoei			x					
Mitella pentandra			x					
Vicia americana			x	x				
Hypericum anagalloides			x o	x	x	x o		
Epilobium alpinum			x	x	x	x o		
Epilobium glandulosum			x	x	x			
Mimulus primuloides			x	x	x	x o		
Veronica americana			x	x	x			
Veronica serpyllifolia			x	x				
Utricularia intermedia			x			x		
Senecio triangularis			+ x	x	x o	x o		
Camassia leichtlinii		+	x	x o	x o			
Clintonia uniflora			x					
Habenaria dilatata			x	x	x	x		
Habenaria saccata			x	x	x		x	

+: in bud; x: in flower; o: in fruit

Table II. Flowering phenologies of the species at Sphagnum Bog, 1978.

OBSERVATION DATES	JUNE		JULY		AUG		SEPT	OCT
SPECIES	11	25	8	24	5	25	15	18
Luzula campestris			o	x				
Carex cusickii			x					
Carex disperma				o				
Carex jonesii			x					
Carex muricata			o					
Carex rostrata			x	x				
Eriophorum gracile			x	x o				
Agrostis idahoensis			x	x	x			
Agrostis thurberiana			x	x				
Spiraea densiflora				x				
Spiraea douglasii				+ x	x	x	x	
Stellaria longifolia				x	x	x		
Nuphar polysepalum				x	x			
Cardamine pennsylvanica				x				
Drosera anglica				+ x	x			
Drosera rotundifolia				+ x	x	x		
Potentilla drummondiana				x				
Ligusticum grayii				x	x			
Oxypolis occidentalis			+	x	x	x	x	
Pyrola minor				x				
Galium trifida				x	x	x	x	
Galium triflorum				x	x			
Aster occidentale				+ x	x	x	x	
Juncus orthophyllus				x	x o			
Deschampsia cespitosa				x	x			
Glyceria borealis				+ x	x			
Muhlenbergia filiformis				+ x		x		
Puccinellia pauciflora				x	x			
Sparganium minimum				+ x	x	o		
Linnaea borealis					x			
Sphenosciadium capitellatum					x	x	x o	
Pyrola asarifolia					x			
Castilleja miniata					x			
Stachys rigida						x		
Bidens cernua						x	x	x
Madia bolanderi						x		

+: in bud; x: in flower; o: in fruit

small, compared to typical bogs elsewhere. Of these, *Kalmia* and *Vaccinium* may be partly autogamous. Therefore the timing of the phenological events at Sphagnum Bog more likely reflects a response to some other factor, as competition for energy (Heinrich, 1976), or climate.

Most of the shrubs,--*Salix* sp., *Alnus incana, Kalmia microphylla, Vaccinium occidentale, Lonicera cerulea*,-- bloomed early, as in bogs of the Northeast (Heinrich, 1976). The length of time necessary for seed set in these shrubs may dictate the early flowering. A group of herbaceous early bloomers, particularly *Ranunculus gormanii* and *Viola* spp., may be competing for light. They exhibit a very low growth habit in the dense *Carex sitchensis* communities. The dominant *Carex sitchensis* was just beginning to emerge above the leaf layer when they bloomed, and consequently, adequate light was still available to these ground layer species. The situation is analagous to that of the herbaceous species of deciduous woodlands completing their reproductive activities before the trees have leated-uot (Heinrich, 1976).

Carex sitchensis and many of the other taller herbaceous species as *Oxypolis occidentalis*, exhibit peak bloom in the middle-to-latter part of the season. This strategy probably represents a compromise between the length of time subsequent to snow melt required to acheive maturity, and the length of time after pollination required for maturation of seeds. Other species that are shorter at maturity, as *Mimulus primuloides* and *Utricularia intermedia*, are delayed in their growth and blooming only until the wet *Eleocharis* communities in which they grow have drained sufficiently of snowmelt. Similar phenological behavior is seen at Nash Crater Bog (Roach, 1952). The blooming of the sedges, Carex sitchensis and Carex rostrata, and the grass Agrostis thurberiana, corresponds well with blooming times of these species at Sphagnum Bog, falling in July, approximately the middle of the season. Carex sitchensis and Agrostis thurberiana are two weeks later in blooming at Crater Lake, but considering year-to-year differences in snow pack and general weather conditions, the correspondence is quite close. The flowering of the codominant of both areas, Vaccinium occidentale, also corresponds closely, beginning in late June. Lower stature plants, as Mimulus primuloides and Hypericum anagalloides, exhibit very different behavior at Nash Crater Bog. Roach (1952) suggests that these species are pushed into vernal flowering by the slow drainage, since only in autumn does outflow lower the water table into the peat. Nash Crater mire is obviously more poorly drained than Sphagnum Bog.

Of the later bloomers, Aster occidentalis corresponds to the late blooming stage in subalpine meadows dominated by showy-flowered composites (Pojar, 1975) Bidens cernua, one of the last to bloom, grows in the wettest community, the Carex rostrata reedswamp. The cold water may slow its growth considerably. Species characteristic of carr understories, Aconitum columbianum, Pyrola spp. and Galium triflorum, are also fairly late to develop. The reduced light under the tall shrubs may delay their development.

It is of interest that several of the aquatic species, such as Menyanthes trifoliata, were never observed to flower. They appear to rely heavily on a vegetative reproduction strategy, rather than on seed production. Possibly, the aquatic habitat is more amenable to the vegetative habit. In the absence of the extremes presented by a terrestrial environment, these species can reproduce vegetatively across the whole season.

Neither modes of dispersal, nor pollinating agents were examined at Sphagnum Bog, but these considerations raise interesting questions relevant to reproductive dynamics and geographical considerations of mire habitats. Pojar (1975) lists reproductive features for the species in his bog, marsh, and subalpine meadow study areas. Vegetative reproduction, according to this list, is also characteristic of the hydric genera, Eriophorum and Kalmia. Bumblebees and flies are typical pollinators, but butterflies and skippers are also important for some meadow species. Many of the species in the mires are at least partially dependent for dispersal on epizoochory in mud, or hydrochory, as well as anemophily or more typical means of animal dispersal. Hydrochory is effective only over short distances, whereas wind-dispersal and animal-dispersal can act over larger distances (Pojar, 1975). More intensive examination of the reproductive dynamics of these mire systems would be of interest, not only from the standpoint of interspecific competition in a tight mosaic of communities, but also for the answers it might suggest to questions of geographical distributions of species in these systems, and of community dynamics in terms of invasion of different species.

Stand Ordinations

Indirect gradient analysis, based strictly on the floristic similarities of the samples, was performed in order to investigate hypotheses concerning distribution of the communities within the mire.

From the first ordination performed by reciprocal averaging, an abscissa was obtained that scattered the stands along its length (Fig. 6). Very little information, however, was added by the ordinate. Carex rostrata reedswamp and low sedge fen types appear at one end of the x axis, alder carr, forest edge, and willow carr are at the opposite end, and the Vaccinium thickets and sedge fens are in the center. The Carex sitchensis communities are not well-separated from portions of the Vaccinium communities on this axis, nor are the carr elements well-separated from the forest edge types.

The ordinate separated the Carex sitchensis communities from the various Vaccinium communities, and the alder carr from the forest edge and willow carr. However, it emphasized the diversity within the forest edge samples and between alder carr and forest edge, and has less discriminating power in the central portion of the abscissa. Although this may reflect real conditions, it would be desirable to have greater separation in the middle portion to help elucidate obscure differences there, since these are the communities of interest in the study.

Therefore, a second type of indirect ordination, a modified Bray-Curtis polar ordination, was performed (Fig. 7). Since the first axis of the reciprocal ordination displayed the communities well, the end-stands from that ordination were preselected fpr the polar ordination. Unfortunately, this method of ordination tended to clump stands closer toward the center, than did the reciprocal ordination, reflecting the extreme nature of the endstands. The second axis spread the stands in

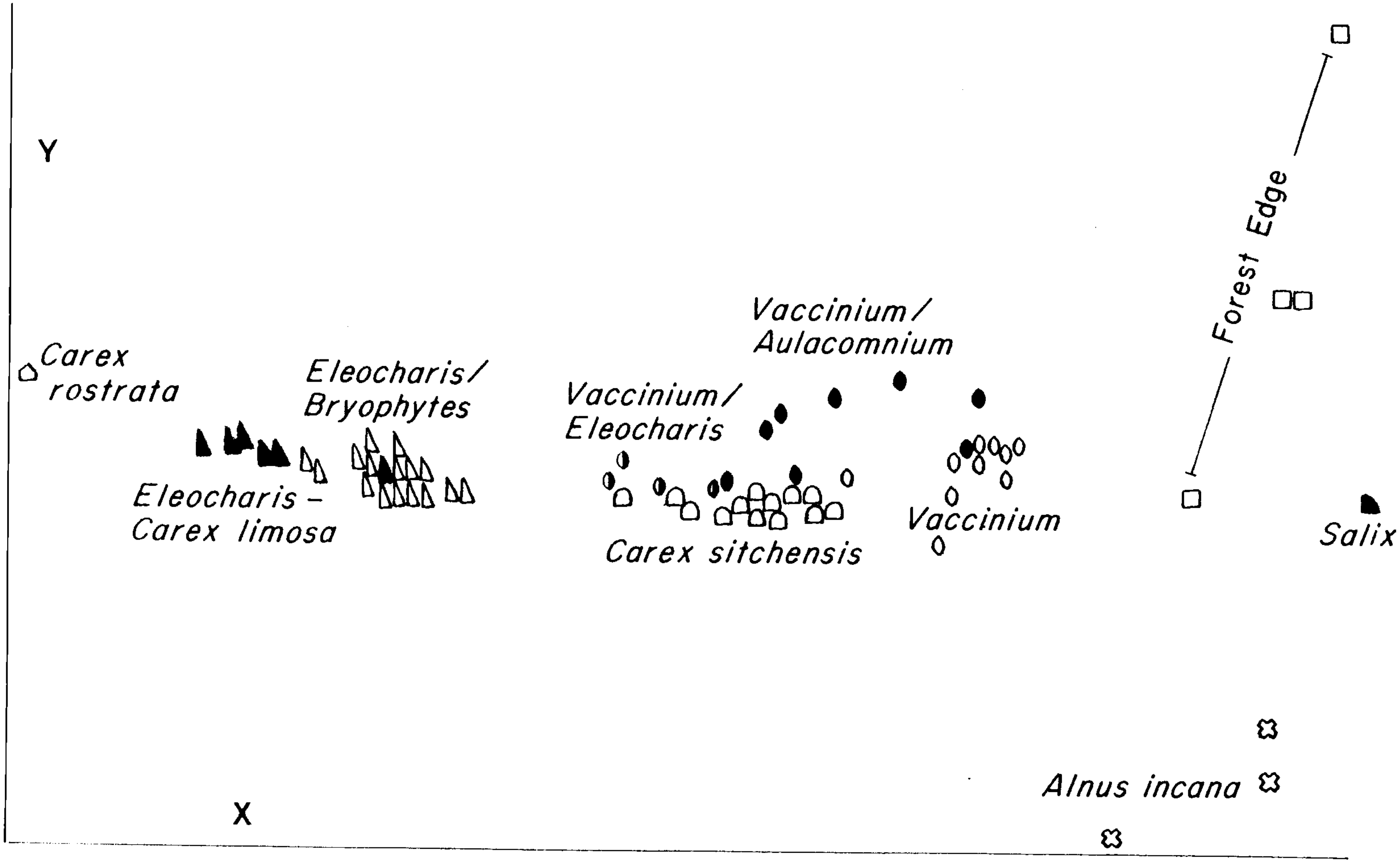


Figure 6. Two-dimensional reciprocal averaging ordination of the 67 stands. Symbols denote community type as determined from tabular analysis.

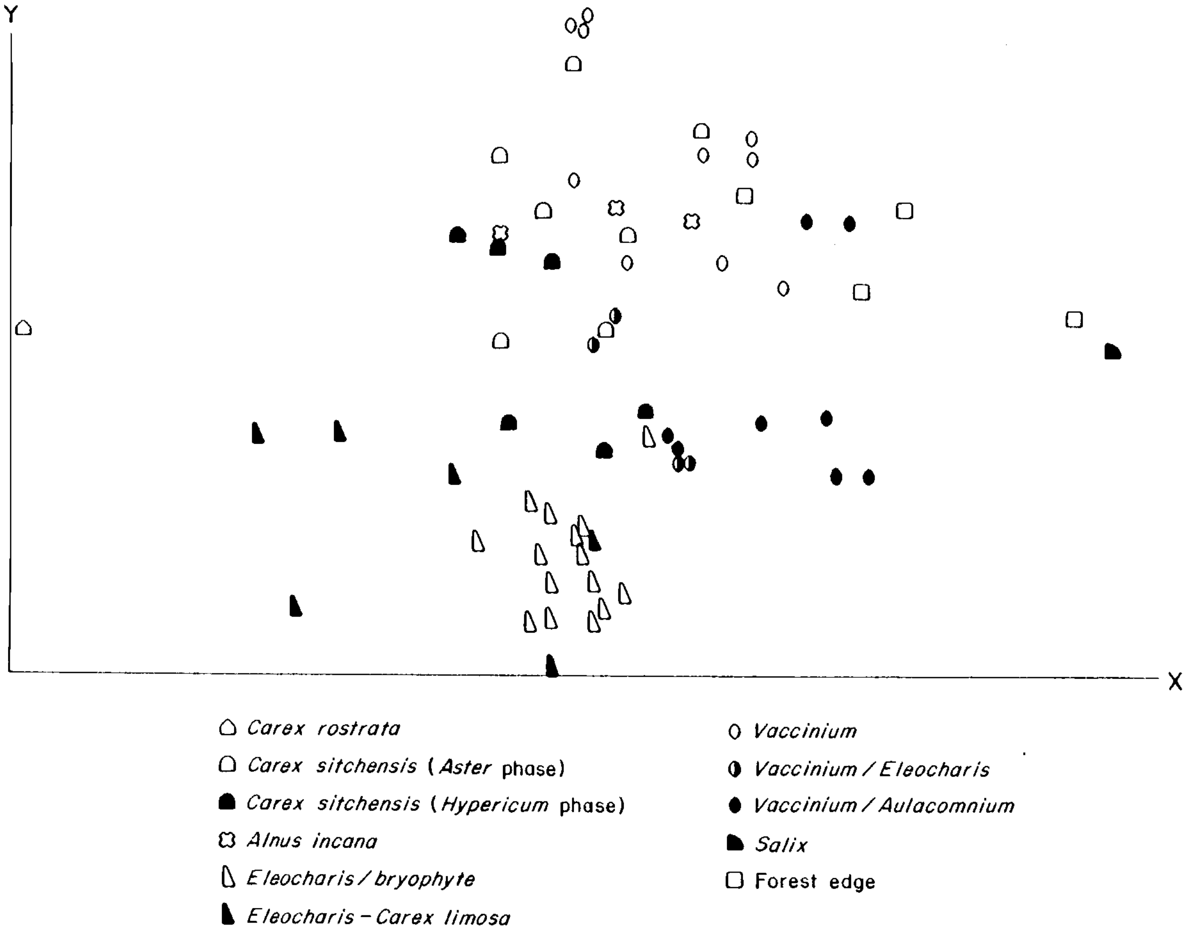


Figure 7. Two-dimensional Bray-Curtis ordination of the 67 stands. Symbols denote community type as determined from tabular analysis.

the center quite well. However, when the stands were labelled according to community type, determined by the Braun-Blanquet classification, considerable overlapping of the communities was evident.

In general, ordering on the abscissa was much like that for reciprocal averaging. The ordinant places the *Eleocharis* communities at one end, the *Hypericum* stage of the *Carex sitchensis* community , dwarf shrub and transitional low sedge-shrub thicket types in the center, with the *Aster* phase of the *Carex sitchensis* community and shrub thickets at the opposite end.

There are several problems with the polar ordination. It emphasizes the extreme nature of the endstands of the X axis, and gives a poorer separation for the stands on this axis. An obvious distortion is also apparent in that one of the extreme communities, *Alnus incana*, placed near the forest edge end stand in the reciprocal averaging, is thrown into the center of the coordinant system. Therefore, it appears that for this type of vegetation, the reciprocal averaging alone gives the better ordination. However, examination of both ordinations is useful, for interpretation of the environmental gradients acting across this mire system, as long as their respective weaknesses are understood.

Environment

Introduction

Various investigators have demonstrated that a variety of environmental factors are important in determining species distributions and vegetative patterns, both within and between different mire systems. Commonly investigated environmental gradients include: a) moisture regime (Jeglum, 1971; Heinselman, 1963; Damman, n.d.; Campbell, 1973; Proctor, 1974; Vitt, et al., 1975; Malmer, 1965; Vitt and Slack, 1975; Kuramoto and Bliss, 1970; Daniels, 1978); b) nutrient regime (Proctor, 1974; Sjörs, 1959, 1963, 1950; Heinselman, 1963, 1970; McVean and Ratcliffe, 1962; Dobson, 1975; Haslam, 1963; Persson, 1965; Sjörs, et al., 1965; Vitt and Slack, 1975; Malmer, 1965; Vitt, et al., 1975; Romanov, 1968; Damman, n.d.; Gorham, 1957; Stanek and Jeglum, 1977; Moore and Bellamy, 1974); c) pH, of the water, or peat, in the mire (Proctor, 1974; Heinselman, 1963, 1970: Daniels, 1978; Persson, 1965; Vitt and Slack, 1975; Gorham, 1957; Sjörs, 1950, 1963; Sparling, 1966; Jeglum, 1971); d) water movement through the system and/or aeration (Burrows and Dobson, 1972; Vitt, et al., 1975; Dobson, 1975; Armstrong and Boatman, 1967; Sjörs, 1963; Haslam, 1965; Heinselman, 1963, 1970: Sparling, 1966); e) topography (Kuramoto and Bliss, 1970; Romanov, 1968; Heinselman, 1970; Sjörs, et al., 1965); f) amount of insolation (Vitt and Slack, 1975; Campbell, 1973); and g) temperature regimes (Fitzergerald, 1966; Kuramoto and Bliss; 1970; Dobson, 1975). In certain cases of hydric communities in the subalpine zone, depth and duration of the snowlie have also been shown to be determining environmental factors (Campbell, 1973; Kuramoto and Bliss, 1970). Snowpack both limits length of the growing season and influences water regime, and may even affect fertility regime (Romanov, 1968). Appropriate topography and a copious water supply are two primary variables differentiating mires from surrounding terrestrial communities. The concentration of drainage flow in small basins, channels, or on gentle slopes is a prerequisite to formation of peat, that results from the poor aeration and poor base status in the slowly moving water (McVean and Ratcliffe, 1962 (from Brooke, 1970). Topography within the mire affects the rate and direction of the flow, in turn affecting aeration of the peat and nutrient availability. Adsorption of certain cations as the water moves through the system, may in part account for a lower nutrient status of zones some distance downslope from the mineral soil-influenced water's source (Heinselman, 1970). Nutrient status is also affected by location of the water table, at least in raised bogs. Certain elements are conserved, whereas others are removed before entering the permanently anaerobic zone (Damman, n.d.). In sluggish or stagnant waters, nutrients are also less available (Sjörs, 1963). The acidity and low base content of such areas are maintained, because there is no rapid influx of fresh water containing cations to replace hydrogen ions on the exchange sites (Sparling, 1966). In topographically raised bogs, with substantial accumulations of peat such that the vegetation root zone is elevated above, and isolated from mineral ground water, the greatest degrees of acidity and mineral deficiency occur.

Apparently, the overriding direction of variation is the gradient related to acidity and base content. The series of mire types, from bog and poor fen, through intermediate and transitional fens, to rich and very rich fens, correlates directly with this gradient. Generally, pH and salt content are quite low in bogs and poor fens. Both properties gradually increase through the series. Rich fens have circumneutral waters and non-deficient salt concentrations.

A second gradient, often measured within mires, is the degree of wetness (Malmer, 1965; Daniels, 1978). Jeglum (1971) stated that moist-peat pH and depth to water table are the most frequently recorded measurements in peatland studies. The current literature suggests that these measures are simple, representative indicators of moisture and fertility regime factor complexes, major factors controlling vegetative patterns and species distributions in bogs (Jeglum, 1971). Various ionic concentrations, particularly calcium, have also been found to be extremely useful in distinguishing mire communities (Heinselman, 1970; Proctor, 1974; Stanek and Jeglum, 1977).

Topography

General. Topographic surveying was restricted to the open areas of Sphagnum Bog. Elevation measurements were taken along a series of intersecting transects at predetermined intervals, and also at points of obvious community changes. Due to the difficulty of sighting through the forest, and the impracticality of clearing trees along the desired sighting lines, the surveying did not extend into the surrounding forest, or through the forested areas between the east and west arms of the bog. Therefore, a general, large-scale contour map of the entire area could not be constructed from this data, as measurements from the two halves could not be related. A smaller-scale, 1:62,500 topographic map is available from U.S. Geologic Survey, the Crater Lake National Park and Vicinity, Oregon map (Fig. 8).

Examination of this map suggests that the mire originated in a rather broad, gently sloping basin at the head of Crater Creek. Numerous springs in the area, including two very large springs directly feeding Crater Creek, provided a water source. Lava dams or buried glacial moraines are common in this portion of the park (Williams, 1942; Diller and Patton, 1902). Such a structural feature might have impeded the downslope movement of subterranean water, thereby creating the high water table necessary for peat development, and hence, for the mire system's inception.

Elevation profiles were constructed along the five vegetation sampling transects, using the levelling data (Fig. 9 & 10). The vertical axis is exaggerated by a factor of ten, a practice commonly used by mire researchers for more effectively illustrating the topographic features of a mire (Moore and Bellamy, 1974). Peat samples were taken from the different community types at nine locations along one transect, and along a portion of a second. With the addition of information concerning depths to the subsurface pumice, a very general idea of the subsurface topography was inferred.

Although surveying only extended into the forest for very short

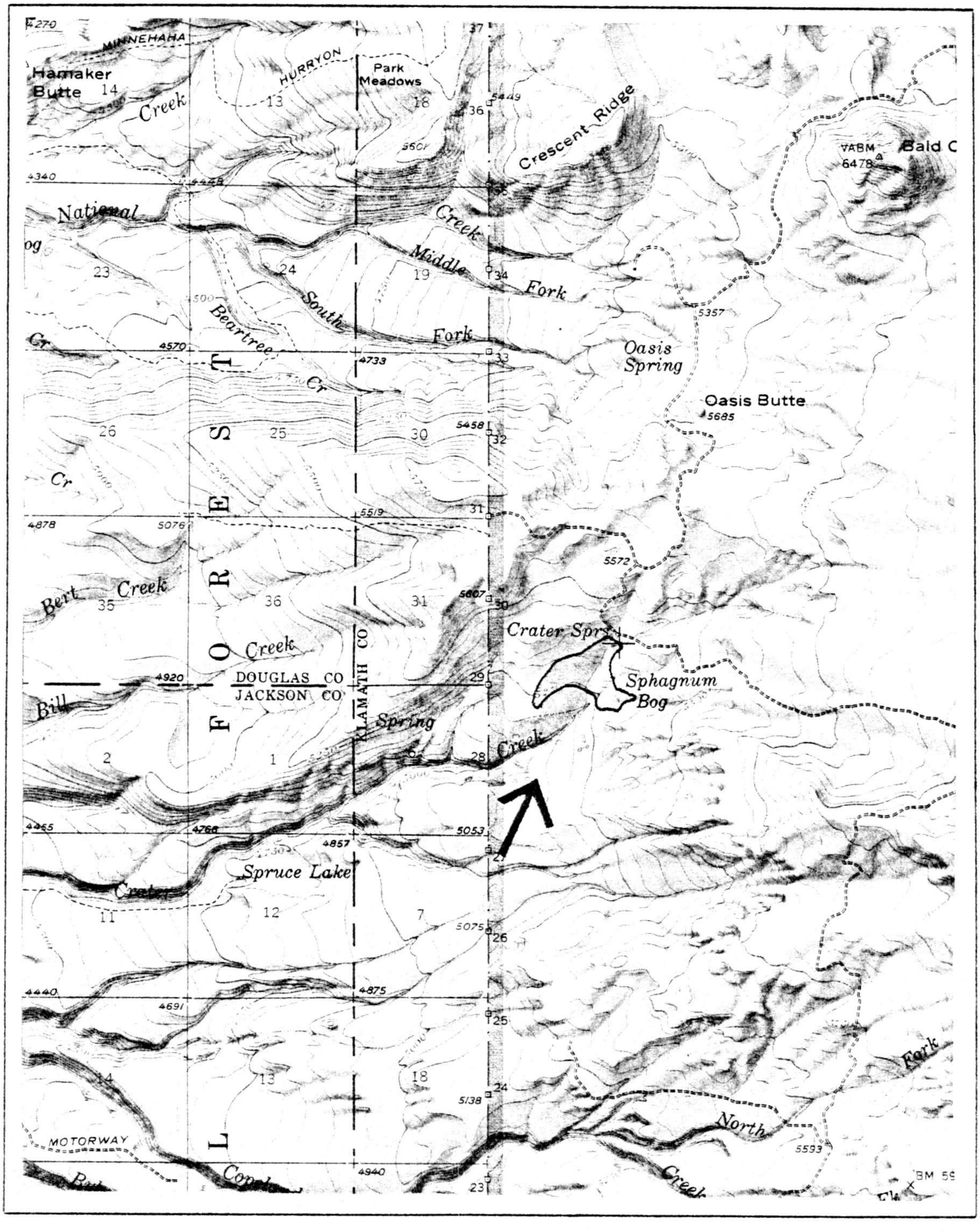


Figure 8. U.S.G.S. map, Crater Lake Park and Vicinity, Oregon.
Scale is 1:125, 000.

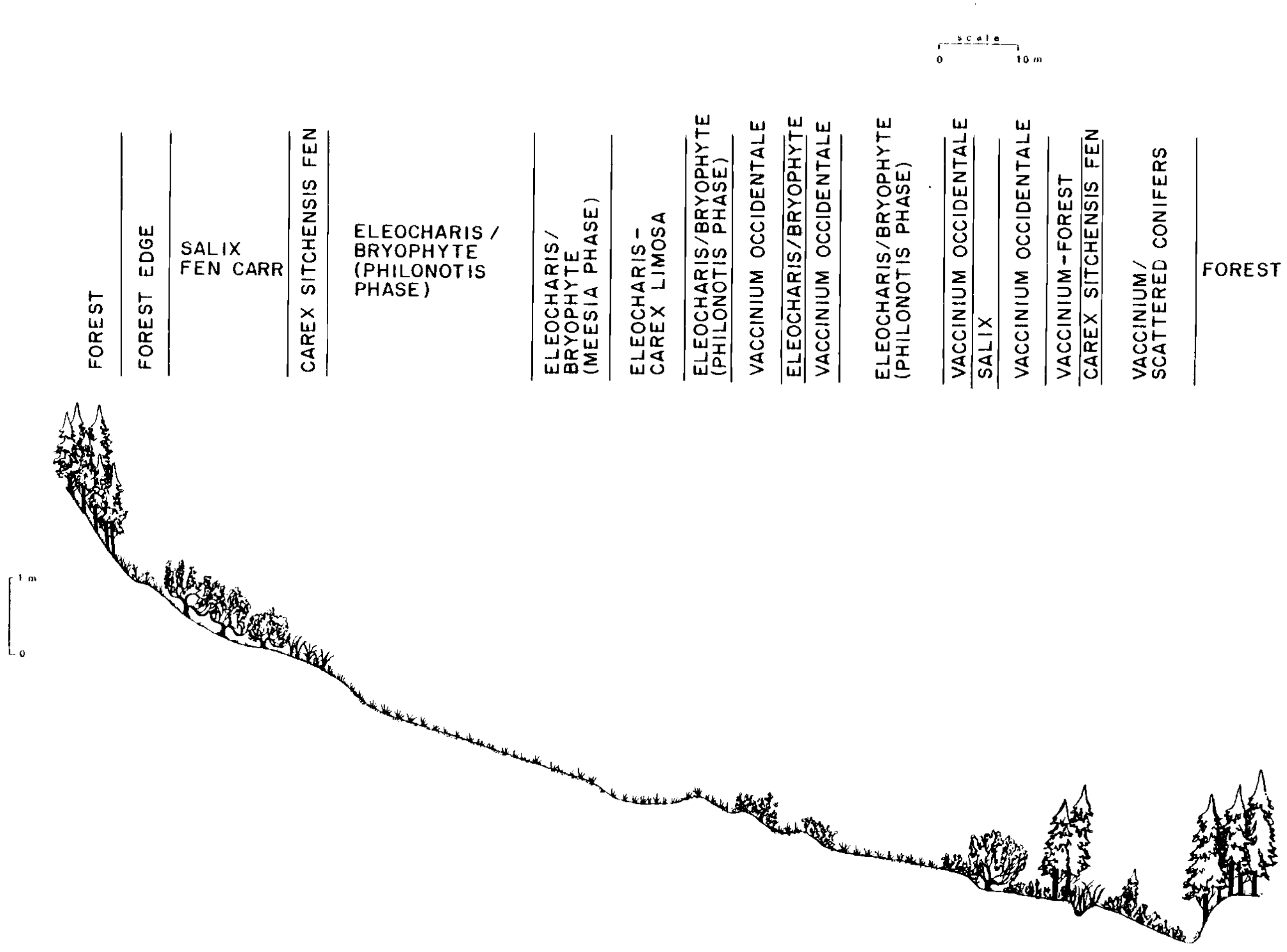


Figure 9. Profile illustrating relationship of communities to topographic position along Transect E. Vertical dimension exaggerated by a factor of 10.

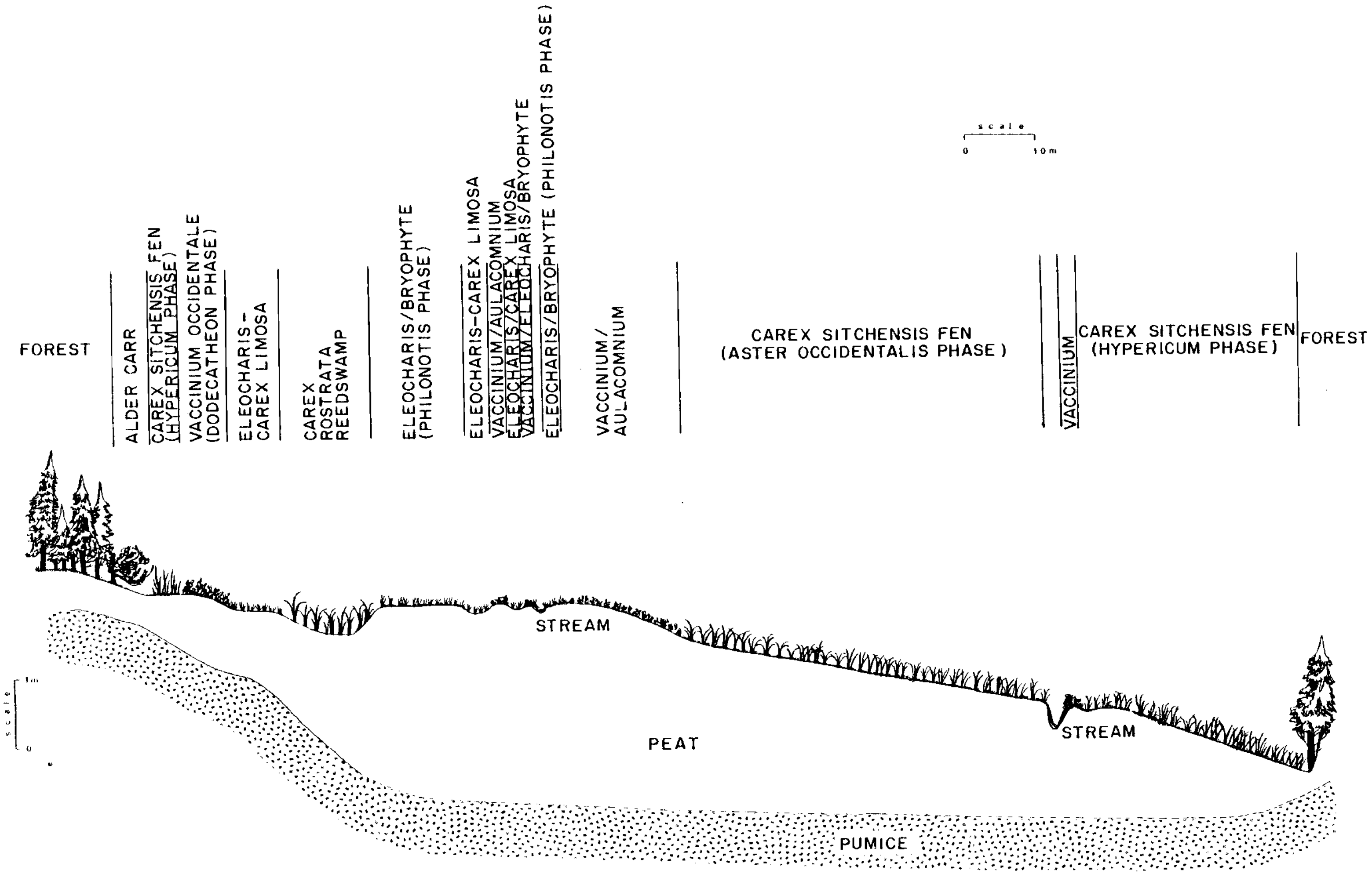


Figure 10. Profile illustrating relationship of communities to topographic position, and to underlying pumice deposits, along Transect A. Vertical dimension exaggerated by a factor of 10.

short distances at the edges of the transects, from these measurements, and from general observations, it appears that the slope gradient is less in the mire than in surrounding forested lands, except at the upper ends of the transects bordering the forest, where the slope is dramatically greater.

From this limited data, one may speculate that mire formation began on the low, relatively flat areas in the basin at the head of Crater Creek. In these areas, impeded drainage might have caused water to accumulate to the extent that hydric communities developed, and peat accumulated under the resultant anaerobic conditions. The shallower peat at the upper end of transect A (Fig. 10) suggests that this portion, with the steeper subsurface slope, is younger. This may represent paludification, a process whereby the water table is raised during the accruement of peat, allowing the expansion of the mire out of the original basin and up onto the steeper forestlands (Heinselman, 1963). Another possibility, however, is that conditions for peat formation were less favorable on the steeper slopes, and hence the layers accumulated more slowly.

Microtopography in the mire. Microtopographic relations in the mire were investigated by superimposing vegetation types onto the elevation profiles. Transects A and E, (Fig. 2) from the lower third of the west arm of the mire, and the upper half of the east arm, respectively, are illustrated (Fig. 9 & 10).

The Carex rostrata reedswamp community is restricted to the deepest depression of the mire's surface, where the water table is above the peat's-surface throughout the year. This corresponds to the typical characterization of Carex rostrata communities as occurring in fairly deep standing water, including reports by other investigators in Oregon (Roach, 1952; Campbell, 1972), Scandinavia (Persson, 1965), and the British Isles (Proctor, 1974).

The Eleocharis pauciflora-Carex limosa community occurs in shallow, slightly concave depressions, or in flat, low areas near the deeper reedswamp. The species composition is similar to that of flarks described by Sjörs (1965) in northern Sweden, and by Vitt, et al. (1975) and Sjörs (1963) in northern Alberta and Ontario. Like the flarks, this community occupies low concavities. However, these areas probably do not constitute true flarks, as they are not consistently elongated at right angles to the slope. True flarks are well developed only farther north in the boreal zone (Moore and Bellamy, 1974). The Eleocharis/bryophyte community appears to occupy a relatively higher position, often occurring at the upper edge of the Eleocharis-Carex limosa depression. The Philonotis phase seems to be a higher and drier phase than the Meesia phase, which is generally in relatively low spots of the mire, that are flat or sloping, but not concave. Descriptions of Eleocharis communities elsewhere in Oregon, as occurring in shallow, stagnant, standing water, imply a similar topographic position (Campbell, 1973). Carex sitchensis fens occupy intermediate positions, that are usually sloping, but neither concave nor convex.

The extensive stands of Vaccinium occidentale thickets appear to be on moderate slopes, often rather near the edges of the mire, close to the forest and mineral soil. But in the central parts of the mire, small Vaccinium thickets, particularly the low Vaccinium types, form small raised hummocks, above the Eleocharis types, that lie in hollows between. The carr communities are usually restricted to the forest margins, particularly the higher edges. Smaller, less mature carr patches occur sporadically along the lower forest-mire border. The occupancy of a marginal transition zone seems to be a prevalent trait of carrs throughout the world; in Sweden willow communities with some of the same bryophyte species, are described as characteristic of mire margins (Persson, 1965), in New Zealand, narrow bands of shrubs pass directly into forest, where the transition from peat to mineral soil is abrupt, and in eastern North America, alders are described as occupying the transitional belt between forest and bog (Dansereau and Segadas-Vianna, 1952). Data is quite limited, but the profiles suggest that the willow carr occupies gentler slopes than the alder carr, or even flat to slightly concave positions. This supposition is confirmed by reports from the literature in the British Isles that whereas willow carrs, or sallows, characteristically occur in badly-drained, fairly wet valley fens, alder carrs generally occupy well-drained, head-water fens, and the occasional dry or well-drained valley fen.

Water Table Variations

The preceding discussion suggests microtopography's importance in explaining the relationship of the communities to the water table. Low spots, concavities, and neglible slopes would tend to accumulate water and have a higher water table than higher areas, or raised sites above concavities. However, the relationship of water table to topography is complicated by scattered upwellings of subsurface water, small rivulets draining from these upwellings, and varying peat layer permeabilities (Niering, pers. comm., 1978; Heinselman, 1970; Malmer, 1965; Dobson, 1975). To investigate more directly the relationship of community distribution to water table level, depth to water table was measured at various sites representative of the different mire communities, across the season. Unfortunately, I was limited by the time and expense of installing pipes; hence, few replicates of either community types or sampled stands were obtained. The data, nonetheless, is useful for suggesting trends.

One of the problems of interpreting the data is readily evident; there are large water table fluctuations over the season in many of the community types. Two other N. American investigators, Jeglum (1971) and Heinselman (1963) evaded this problem by only measuring water table depths once during the year, in early fall, when they anticipated the greatest differences between wet and dry types to be apparent, subsequent to summer droughts. However, it seems equally likely that differences in water table depths at wetter times of the season could be significant. Though drought conditions severely limit productivity and restrict the species that can exist in a area, excessive wetness also exerts a selective influence, restricting occupancy to those species adapted to an aquatic or hydric habitat, and limiting the length of the growing season (Roach, 1952).

Water table fluctuations follow seasonal precipitation patterns. Although water table depth was not measured until 7 July, 1978, I made observations during an early-season collecting trip, June 11, and noted standing water covering much of the mire. Extreme early-season wetness is due primarily to snowmelt, which was almost complete in the area by June. As the summer season progressed, the mire became successively drier, due to evapotranspiration and absence of further snowmelt and precipitation. However, on 11 August, 1978, sporadic rains began, and continued until 25 August, and a second two-week periods of showers began at the end of the month. Those periods of extended precipitation are reflected in the water table depths; many sites showed their highest water table readings on, or near, 15 September, at the end of this second period of rain. With little further precipitation, the mire again became progressively drier (Fig. 11).

Although the relationships of certain communities to the water table are puzzling, it is obvious that some types are consistently wetter than others, and general trends emerge. More data would be needed to really substantiate these trends, however. The *Carex rostrata* community, occupying a shallow pond, remained consistently the wettest community of the mire, throughout the season. The *Eleocharis-Carex limosa* type, occurring in shallow depressions, has standing water following snowmelt, or heavy precipitation, but becomes dry by the end of summer. The *Eleocharis*/bryophyte communities are somewhat drier, but have standing water, or a saturated surface during at least the wetter times of the season. However, in some types that exhibited wide fluctuations, the water table was much lower following prolonged dry periods. According to Malmer (1965), water table fluctuations of these hollow types are due to the damming effect of hummock banks at

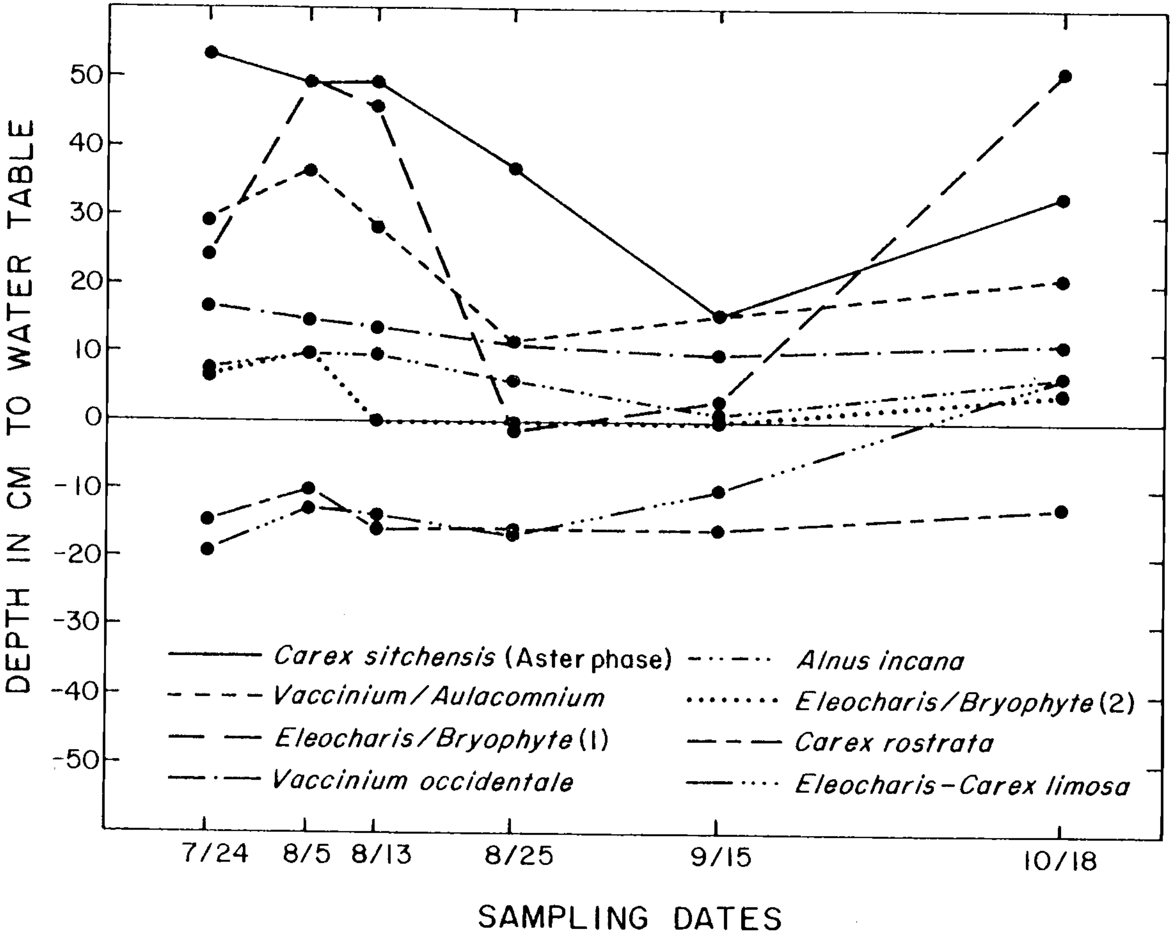


Figure 11. Variation in depths to water table across the summer for different communities. Positive values indicate depth below surface to water table; negative values depth of water standing above surface.

right angles to the slope. When the water level reaches the base of the hummocks, the flow increases strongly until the water level is unable to rise any further. Because of this effect, the hummocks remain above the water table level, and the hollows are inundated only after periods of heavy rains (or snowmelt). Once the water table is lowered into the peat, differing permeabilities and the greater evapotranspirative rate in the more open Eleocharis communities may account for the extreme lowering of the water table in some examples. In the Hypericum phase of the Carex sitchensis community, and the Alnus incana type, the water table level remained less than 10 cm below the surface throughout 1978. The Vaccinium and Salix communities have water table depths generally between 10 and 20 cm below the surface, whereas the low Vaccinium/Aulacomnium community and another example of a Carex sitchensis community (Hypericum phase) are drier. The driest type is the Carex sitchensis community, Aster phase, with water table reaching a maximum depth of 50-75 cm below the surface. Both examples of this phase exhibit come invasion by conifers, mostly Pinus contorta var. murrayana. Conifer invasion is probably very definitely related to water table level. In Scandinavian mires, the water table sinks much deeper during the driest parts of the year in the wooded parts than in non-wooded, reaching a depth of 50 cm below the surface, or more (Malmer, 1965).

It seems obvious that some relationship between the vegetation types and water table exists, but as Proctor (1974) concluded from his data taken in the British Isles, this relationship is not clear-cut. Other factors considered below show a more obvious relationship.

Nutrient Status of Peat

The quantities of the cations, Ca^{++},Mg^{++},K^{+},and Na^{+}, and total P and N, for eight peat samples taken from different community types, are expressed in Table III and Figures 12 and 13. Values are expressed as percent of oven-dry weight. Time and funding limitations precluded the collection of replicate samples within stands or collections of replicates of community types. Results from a mire study in the British Isles indicate considerable variation between data for replicates of at least certain fen community types (Proctor, 1974). In spite of this, Proctor (1974) was able to describe certain broad trends. The data from Sphagnum Bog also suggest trends and gradients. However, with only one sample from each type, rather than mean values, tests of significance were statistically impossible.

Of the nutrients tested, Ca^{++}showed the greatest degree of variation between the different community types, varying by a factor of 10 from the lowest to the highest values. K^{+} and Mg^{++} exhibited the next widest ranges of variation, varying by a factor of 4.5 between the extremes; and for Na^{+}, total N, and total P, the extremes varying only by factors of 3, 1.5, and 1.6 respectively. These results agree with much of the work reported in the literature. In the British Isles, Proctor (1974) found the greatest variation in Ca^{++}, K^{+},and Mg^{++}, whereas $K^{+}$and Na^{+} showed much less inter-community variation. In western Canada, Stanek and Jeglum (1977) in Ontario, and Vitt, et al. (1975) in Alberta both found Ca^{++} to be the single most important element distinguishing mire communities; and Heinselman in Minnesota (1970) and Vitt and Slack in central Canada (1975) found

Table III. Nutrient concentrations expressed as percent dry weight for eight peat samples.

Community types	Ca	Mg	K	Na	N	P
Carex rostrata reedswamp	0.3	0.05	0.04	0.015	1.4	0.1
Eleocharis pauciflora fen (*Philonotis fontana* phase)	0.2	0.04	0.03	0.017	1.9	0.13
Eleocharis pauciflora fen (*Meesia triquetra* phase)	0.7	0.11	0.13	0.022	1.3	0.1
Carex sitchensis /*Deschampsia cespitosa* fen	0.4	0.06	0.05	0.007	1.6	0.15
Carex sitchensis fen	0.6	0.1	0.05	0.011	2.0	0.14
Vaccinium occidentale/*Carex sitchensis* thicket	1.4	0.19	0.08	0.016	2.0	0.14
Alnus incana/*Brachythecium* carr	1.2	0.16	0.12	0.012	2.2	0.1
Salix barclayii carr	2.2	0.15	0.11	0.015	1.8	0.16

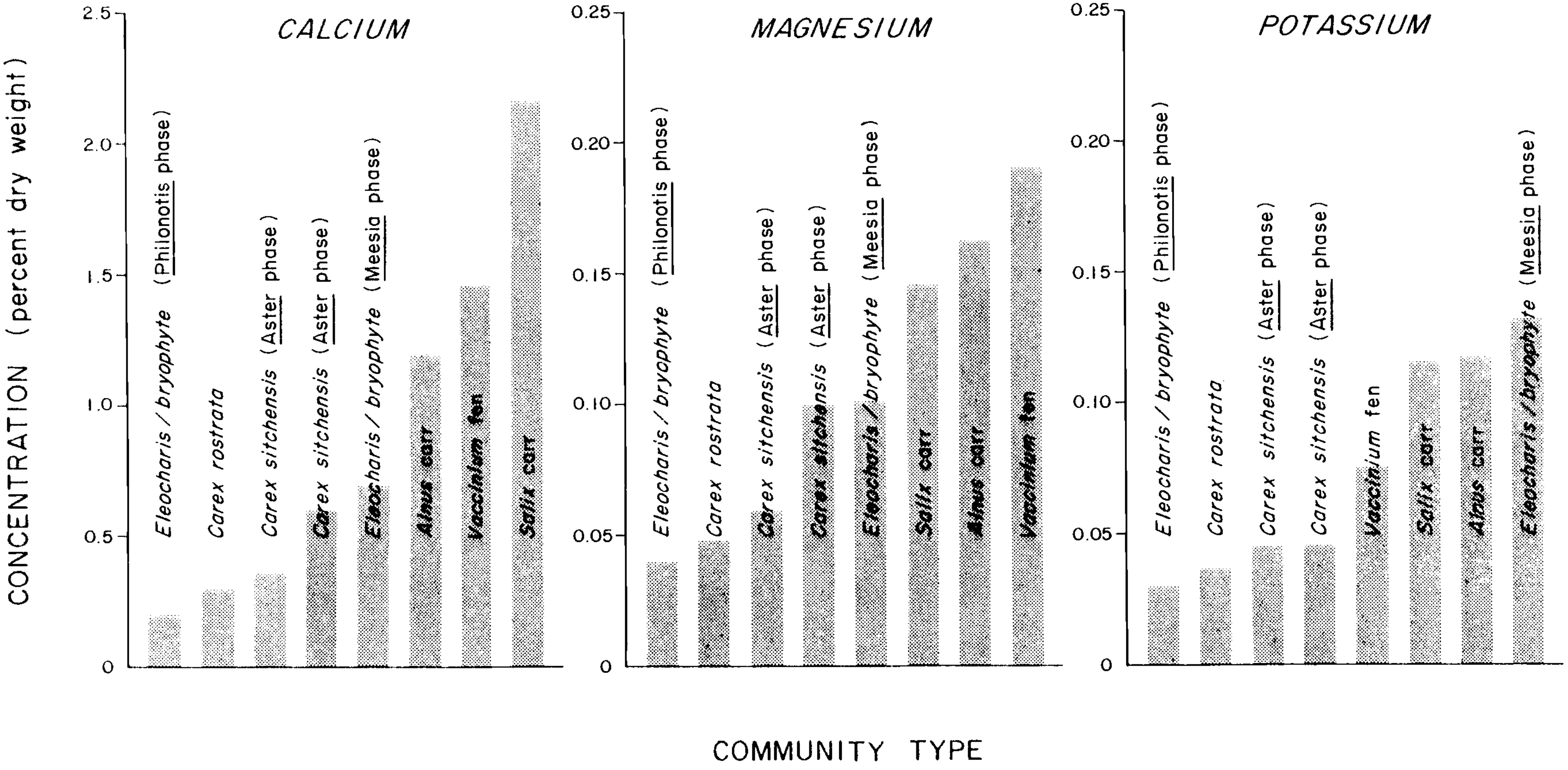


Figure 12. Concentration gradients of calcium, magnesium, and potassium across the different communities. Quantities expressed as percent dry weight of peat sample.

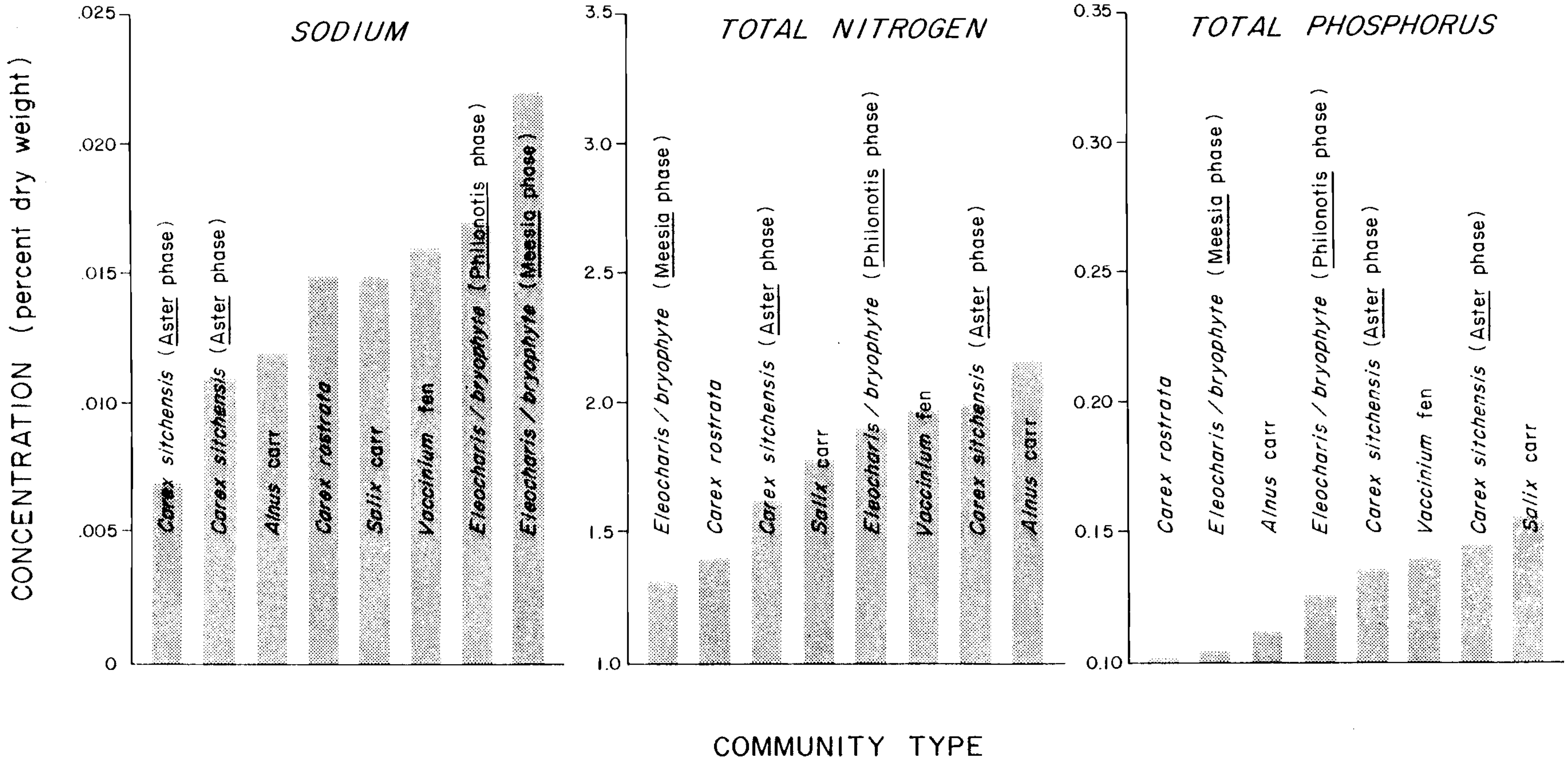


Figure 13. Concentration gradients of sodium, total nitrogen, and total phosphorus across the different communities. Quantities expressed as percent dry weight of peat sample.

both Ca^{++} and Mg^{++} to be major distinguishing nutrients of bogs and fens.

Trends of concentrations between Sphagnum Bog community types tended to vary somewhat for the different ions measured, as is reported in the literature. Ca^{++} increases progressively in the following order: *Eleocharis* community (*Philonotis* phase), reedswamp, tall sedge fen, *Eleocharis* community (*Meesia* phase), alder carr, *Vaccinium* thicket, and finally, willow carr, with the greatest difference occurring between the sedge versus shrub types. Mg^{++} exhibits a comparable pattern to Ca^{++}, showing the greatest variation between the sedge and shrub types. Within the shrub and carr types, there is a change in order, however, the willow carr having a lower value than the alder carr and Vaccinium thicket. K^{+} varies similarly except for one anomaly (the *Meesia* phase of the *Eleocharis* community has the highest concentration, in the same range as the carr communities). There is also a greater separation in the case of K^{+} between shrub and carr communities.

No clear pattern emerges from the Na^{+} data, but the variation is small and irregular, suggesting that this may not represent a gradient, but only random variation. For total N and P, variation is again nearly continuous, with no large, clear breaks. The order is somewhat changed compared to Ca^{+}, Mg^{++}, and K^{+}. However, the overall variation is so low that the trends may not be meaningful. The relatively high value of total N for the alder carr is probably explained by the fact that alders are known to be nitrogen-fixers.

Much work on nutrient regimes reported in the literature summarizes differences between mire types from widely separated locations in general terms, i.e., poor fen, rich fen, and alder carr. Such information, therefore, is of little use for examining gradients displayed within Sphagnum Bog. The communities Proctor (1974) described at Malham Tarn Fen, England are not all comparable to those at Sphagnum Bog, but some of the broader physiognomic types are applicable. He reported that Ca^{++} increases from poor fen to rich fen to fen carr, and, in general, that Mg^{++} exhibited the opposite trend. Data from Sphagnum Bog correspond well as to Ca^{++} concentrations, the carr types having distinctly higher concentrations of Ca^{++} than the sedge types, but the Mg^{++} trend closely parallels that of Ca^{++}. Closer examination of Proctor's data reveals that in fact, there is no inconsistency. The opposite trend he referred to was the higher Mg^{++} level in the raised bogs and poor fens relative to the other fen communities. But in that portion of the range comparable to the community types represented at Sphagnum Bog, the carr elements showed a similarly higher concentration of Mg^{++} than the fen types. Stanek and Jeglum (1977) compared peatland formation types in Northern Ontario where the basic patterns are similar for comparable types.

pH

Bog substrata pH is usually measured directly in situ with a portable pH meter (Jeglum, 1971; Heinselman, 1970), or from frozen samples in the lab, with an electronic pH meter. The pH meter offers the advantages of providing objective readings that are accurate to at least 0.1 of a pH unit. Unfortunately, neither method was available. In lieu of these traditional methods, several other techniques were employed, but the meaningfulness of the results is questionable.

Initially, two simple methods for testing soil pH were used: a Kelway soil tester, that gives a direct reading upon insertion into moist peat or soil, estimated to 0.1 unit pH. Unfortunately, water leaked into the instrument after about eleven readings, and further measurements were not considered satisfactory. A soil pH testing kit was also used, from which estimates to 0.2 pH units were made colorimetrically. Considering the subjectivity involved in matching colors, however, the readings are probably only accurate to about 0.4 or 0.5 pH units. Furthermore, the fine particles in the peat tended to remain in suspension, making accurate visual color determination even more difficult. Therefore, this method was not considered satisfactory for distinguishing communities, and was discontinued. Subsequently, another simple soil testing instrument, the Accutronics tester, was employed on two occasions. Direct readings estimated to 0.1 pH units were taken upon insertion into moist peat. Finally, pH was tested colorimetrically with paper, from which estimates to 0.5 pH units could be made. Accuracy is probably only to one pH unit, however, considering the degree of subjectivity involved in matching colors. Results of the Accutronics measurements are presented in Table IV; all others are in Appendix B.

Table IV. pH measurements from various communities taken on 8/25 and 9/15 with the Accutronics soil tester.

		Accutronics pH data	
Community types and phases		8/25	9/15
Vaccinium occidentale/ *Aulacomnium palustre*		6.0	6.0
Carex rostrata reedswamp	edge ----	6.0 *(5.5)	6.2 (5.7)
	in water-----	6.4 (5.9)	
Carex sitchensis community (*Aster occidentalis* phase)	#1	6.3	6.0
	#2	6.4	6.2
Eleocharis pauciflora community (Meesia triquetra phase)	#1	6.4 - 6.6 (5.9 - 6.1)	6.8 (6.3)
	#2	6.9 (6.4)	6.8 (6.3)
Salix barcalyi carr		6.5 - 6.6	6.5
Vaccinium occidentale/*Carex sitchensis* thicket	#1	6.6	6.2
	#2	6.6	6.5
Alnus incana/*Brachythecium* carr		6.6	6.2
Eleocharis pauciflora - *Carex limosa* community		6.7 (6.2)	6.1 (5.6)
Carex sitchensis community (*Hypericum anagalloides* phase)	#1	6.75	6.4
	#2		6.8 (6.3)
Eleocharis pauciflora community (*Philonotis fontana* phase)	#1	6.9 (6.4)	6.8
	#2	7.1 (6.6)	6.8

*Corrected values in parentheses for samples measured with free water present (Jeglum, 1971)

The various methods suggest interesting trends, but they are not consistent with each other. One problem is too little data; another is the complicating factor of the influence of weather fluctuations. Heinselman (1970) pointed out that changes in pH, as well as salt content (Fitzergerald, 1966; Sjörs, 1950), may be induced by both diurnal and seasonal weather fluctuations, and that the most serious problem in measuring pH is that of comparison of data from very wet with very dry periods. Furthermore, pH is known to vary considerably between free water and that pressed form peat (Fitzergerald, 1960; Sjörs, 1950; Jeglum, 1971) and (Malmer and Sjörs, 1955; Malmer, 1962; and Persson, 1962 (in Jeglum, 1971)). Jeglum reported that moist peat averaged 0.5 units lower than free bog water in the same stand. He suggested subtracting 0.5 units from free water ph values to produce comparable readings. Therefore, seasonal differences in mire wetness may explain, at least in part, differences in the trends exhibited. Corrected values for samples in which there was standing water, or where the water table was within a few centimeters of the surface, are presented in parentheses following the original data in Table IV.

On both of these dates, the corrected Accutronics data show the *Carex rostrata* reedswamp, the low *Vaccinium*/*Aulacomnium* hummocks, and *Eleocharis*-*Carex limosa* communities at the lower end of the pH gradient; and the *Vaccinium* community, *Salix* carr, and *Carex sitchensis*-*Hypericum anagalloides* fen near the upper end. Intermediate types are the *Eleocharis* communities, *Carex sitchensis*-*Aster occidentalis* communities, and the alder carr.

Proctor (1974) suggested that there should be a close relationship between pH and calcium concentration in mires. The relationships of vegetation to Ca^{++} and to pH are similar at Sphagnum Bog. There are several reasons, however, that the correlations between these two environmental factors, pH and Ca^{++}, may not be so readily evident from the data as collected. When the Accutronics pH measurements were taken, the water table was generally higher than when peat samples for nutrient analyses were collected on 18 October (Fig. 11). Furthermore, nutrient analyses were not conducted for the same number of vegetation types as were pH measurements. Thus, certain portions of the pH gradient, particularlu the Hypericum phase of the Carex sitchensis community, and the low Vaccinium/Aulacomnium palustre community, have no direct counterparts on the Ca^{++} gradient.

The pH of the Carex rostrata community (Table IV) at Sphagnum Bog falls within the range, 6.3-7.2, reported by Bernard (1976) as typical of such communities during the growing season in New York; and is comparable to data by Jeglum (1971), who reported that it grows in Alberta across a fairly broad range, but has an optimum pH range of 6.0 to 6.9. The relatively low pH values of the low Vaccinium/Aulacomnium hummocks correspond to the slightly more acidic conditions found by Dobson (1975) in mire hummocks in New Zealand. He suggested that the aeration of the hummocks probably increases humification, and hence, acidity. Species typical of ombrotrophic conditions, such as Kalmia polifolia (syn. with K. microphylla), Eriophorum sp. (Heinselman, 1970), and Carex limosa (Sjörs, 1963), occur rather prominently in either the hummocks or the in the intervenient Eleocharis-Carex limosa communities, which also display a relatively low pH. A dominant species of the community, Aulacomnium palustre, is described as having a wide range of tolerances, but capable of modifying the microenvironment towards more acidic conditions, the optimum being 4.4 (Conway, 1949).

In general, however, it appears that pH is not as useful in distinguishing the communities within a mire (Dobson, 1975; Heinselman, 1970), as it is for classifying the mire as a whole. Using corrected values, the pH of Sphagnum Bog varied between 5.5 and 6.75.

Relationships of Vegetation Gradients to Environmental Data

Correlations were performed between the stands' ordination scores along the reciprocal averaging and polar ordination axes, and the environmental data sets, using the latter as independent variables. The small number of samples and lack of replication in the measurement of environmental variables, make an assessment of statistical significance impossible. Interesting trends are suggested, however, that are useful for interpreting environmental gradients which might underly the vegetational gradients (Austin, 1971).

Correlations between the data sets, listed as R^2 values, are presented in Table V. The best correlations with vegetation patterns, overall, are with the concentration gradients of the cations Ca^{++}, Mg^{++}, K^+, and, in one case, total phosphorus. Moderate correlation is exhibited for pH readings taken on 15 September. Water table measurements, in general, did not correlate well with the vegetation gradients, but the readings taken on 24 July, 25 August, and 15 September, as well as the average of water table depths and average of the higher water table readings, exhibit low but obvious correlation. These three sampling dates reflected relatively high water table periods for the summer season; on 24 July, snowmelt still had a marked influence, and 25 August and 15 September both followed periods of extended precipitation.

From examination of its correlations, the reciprocal averaging x-axis appears to represent a complex gradient, dominated by calcium,

Table V. Correlations between vegetation gradients, as represented by ordination axes, and environmental data sets, expressed as R^2.

Environmental variables:	Reciprocal averaging x axis	Reciprocal averaging y axis	Polar ordination x axis	Polar ordination y axis
Nutrient concentrations:				
Calcium	.710	.193	.753	.139
Magnesium	.616	.206	.504	.158
Potassium	.705	.680	.494	.008
Sodium	.033	.099	.023	.121
total nitrogen	.386	.466	.100	.00003
total phosphorus	.466	.019	.678	.119
Water table depths, measured on the following dates:				
7/24	.314	.004	.135	.163
8/5	.125	.183	.008	.048
8/13	.154	.012	.016	.076
8/25	.287	.029	.130	.263
9/15	.359	.006	.251	.055
10/18	.036	.003	.00005	.006
Average water table depth across season:	.295	.013	.120	.171
Average of values during drier times:	.038	.001	.0002	.077
Average of values during wetter times:	.080	.048	.017	.291
Range of averages:	.016	.0005	.089	.0007
Range of total variation:	.0003	.006	.029	.042
pH				
Kelway soil tester 8/13	.133	.006	.081	.061
Soil pH testing kit 8/13	.169	.0002	.016	.0009
* Accutronics soil tester 8/25	.005	.053	.008	.178
* Accutronics soil tester 9/15	.061	.003	.012	.463
** Accutronics soil tester 8/25	.130	.001	.169	.033
** Accutronics soil tester 9/15	.112	.056	.470	.032

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* Uncorrected for differences between free bog water and moist peat

** Corrected for differences between free bog water and moist peat, by subtracting 0.5 pH units from measurements taken in free water.

magnesium, and potassium concentrations, but explained in part by total nitrogen and phosphorus, differences in average water depths, or differences on the wetter days. Although the reciprocal averaging y-axis does little to distinguish community types, it correlates fairly well with potassium and total nitrogen concentrations.

The polar ordination x-axis displays relationships similar to those of the reciprocal averaging x axis. Concentration gradients of calcium, magnesium, potassium, and total phosphorus explain much of the variation on this axis. Water table depths have only very poor correlations with this axis, and moderate correlation is exhibited for pH data, using corrected values from 15 September. Few good correlations are displayed for the y axis of the polar ordination; uncorrected pH data from 15 September correlates moderately well, and poor correlations are shown with water table depths during a wet period, on 25 August, and for the average of the high water tables.

The most obvious conclusion to be drawn from these results is that there is no single overriding environmental gradient in this mire, but a variety of interacting ecological factors. The mosaic of vegetation types in any mire, and site-to-site variability in composition and structure reflect this complex of controlling and interacting environmental variables (Dahl, 1956; Sjörs, 1965; Burrows and Dobson, 1972). Furthermore, there is a marked "reciprocity of relation between habitat and vegetation in a mire" (Sjörs, 1965).

The major factors correlating with the variation in vegetation at Sphagnum Bog have also been designated as effective gradients at other mires, particularly minerotrophic ones. Of the tested nutrients, Heinselman (1970) found calcium the single most important indicator of peatland type in northern Minnesota, but that magnesium concentration was also useful in distinguishing intermediate types. Proctor (1974), in investigations of natural fen vegetation in the British Isles, found the calcium gradient one of the most important in relation to vegetation, and Stanek and Jeglum (1977), in Ontario, determined calcium the single most important element in distinguishing broad peatland types, but also found nitrogen concentration useful in distinguishing certain types. Concentration gradients of calcium and, to a lesser degree, of magnesium, corresponded with segregation of communities for bogs in Michigan and fens in Alberta (Vitt and Slack, 1975; Vitt, et al., 1975). Calcium gradients have been previously exhibited within a particular system, as well as from site-to-site; Vitt, et al. (1975) demonstrated a depletion of calcium along a flark-string series, and in the central pools of the system.

Proctor (1974) interpreted his nutrient data as representing two trends: the calcium gradient, representing the variation from ombrogenous to soligenous conditions, and potassium and magnesium gradients representing the oligotrophic to eutrophic variation in more calcareous regions. Variations in phosphorus also occured between the nutritionally poorer groups and more minerotrophic groups. Haslam (1965) reported a direct relationships between phosphate or potassium and the vegetation. According to Damman (n. d.), there should be a good association between the nature of the plants forming the peat, and the microelement content; sedge peats are said to contain more phosphorus than other peats due to the presence of the mineral vivianite ($Fe_3(PO_4)_2 \cdot 8H_2O$ (P'Yavchenko, 1964 (in Fitzgerald, 1966). Figure 13 indicates all of the Sphagnum Bog communities with relatively high phosphorus contents, except the Salix carr, are strongly dominated by Carex sitchenisis. The higher phosphorus content there may be accounted for by its close proximity to mineral soil.

Numerous investigators have used pH and depth to water tables as distinguishing variables for peatland types; Jeglum (1971), Vitt and Slack (1975), and Proctor (1974) concluded that these were among the major variables affecting vegetational gradients. Heinselman (1970) concluded, however, that pH was mainly useful in distinguishing ombrotrophic mires from minerotrophic, but not for distinguishing other types. The Scandinavians (Sjörs, 1963, Nordqvist, 1965; Malmer, 1965) typically divide mires into various poor and rich types, characterized by indicator species, pH and mineral concentrations, particularly calcium, and discuss wetness gradients within these.

Environmental factors are often interrelated in mire ecosystems. Heinselman (1963) discussed ideas by Wilde (1954), and Lucas and Davis (1961) that very acidic conditions might impair the availability of certain nutrients (calcium, phosphorus and nitrogen), even if these are present in fairly high concentrations. Another factor not investigated in this study, but known to have substantial influences on both vegetation and physical conditions in mires, is the mobility of the groundwater. Acidity is related to rate of flow in the following manner: flowing, nutrient-rich ground water neutralizes the acidic substances produced by roots and microbes as byproducts, and flushes them out of the area; but if the flow is reduced, the acidic products accumulate (Sparling, 1966). The nutrient flux through the peat and greater acration of flushed sites, therefore, increase fertility and nutrient availability (Dobson, 1975; Sjörs, 1963; Vitt, et al., 1975). Furthermore, as minerotrophic water moves farther from contact with mineral soil in a peatland, the minerals it carries are depleted. In a minerotrophic mire, therefore, one would expect the central stagnant pools and surrounding low, flat areas to be among the more nutrient-poor areas of the mires, due to both distance from a nutrient source, and stagnant conditions, accompanied by a lack of nutrient flux and greater acidity, leading to reduced nutrient availability. Armstrong and Boatman (1967) found the most striking difference between flushed and stagnant sites in British mires to be a deficiency of phosphorus in the plants of the stagnant areas. At Sphagnum Bog the _Carex rostrata_ reedswamp may very well represent one of the most stagnant areas, lying in large, deep depression (fig. 10). This may explain the relatively low phosphorus content of the sedge peat here.

PH may additionally be affected by water table levels. It has been suggested that pH is lower in hummocks than hollows because the seasonal lowering and drying of these types could lead to a decrease of pH (Moore and Bellamy, 1974). Dobson (1975) observed these conditions in New Zealand and suggested that aeration of hummocks elevated above the water table accelerated humification, and hence, greater acidity. Godwin, et al. (1974) also postulated acidification accompanying drying of peat. this hypothesis appears to be borne out by the pH data, presuming that the different methods are comparable. The first pH sampling date, 13 August, fell during one of the drier periods of summer, 1978, but the next two sampling dates, following extended periods of precipitation, were among the wettest, and generally highest water tables of the season (fig. 11). In the Eleocharis community (Philonotis) phase), pH was relatively low, 5.7, following drying out, on 13 August, but with renewed moisture, pH increased greatly to approximately 6.3-7.1 (6.3 is the pH reading after a correction factor of 0.5 has been subtracted for differences between free water and moist peat pH). The Vaccinium/Aulacomnium hummocks are also relatively acidic in drier parts of the season, with a pH of 5.6.

In summary, the major environmental gradients controlling distribution of the vegetation at Sphagnum Bog, as at many other mires of the world, are nutrient concentrations and availability. Other factors, such as water table depths and fluctuations, mobility of ground waters, acidity, proximity and topographic position may in some cases affect the vegetation directly, but generally are more important for how they affect nutrient status. The carr elements, alder and willow belts, occur at the mire margins in zones of contact with forest soils, where nutrient status is high, as reported by Dansereau and Segadas-Vianna in eastern North America (1952) and by

Dobson (1952) in New Zealand. As the water moves downslope through the system, and through streams, nutrient status probably decreases as the cations are adsorbed (Heinselman, 1970; Vitt, et al., 1975). Nutrient status is lowest in central, stagnant *Eleocharis* fens and *Carex rostrata* reedswamps.

Autecological Considerations of Selected Mire Species

Species occupying habitats that pose distinct problems are generally successful because they have adapted special menas of surviving these stresses, through genetic variation and natural selection. Examples of adaptation to life in areas of poor aeration, and of low nutrient status are found in the literature.

One of the problems associated with water-logging is the accumulation of reduced forms of ions and compounds that are toxic to the plants (Rutter, 1955). *Menyanthes trifoliata*, found in the reedswamp at Sphagnum Bog, is a species typical of stagnant waters. Armstrong and Boatman (1967) found that it can tolerate the hydrogen sulfide that accumulates because it has a greater diffusion rate from its roots, thereby oxidizing the sulfide. In its reduced state, hydrogen sulfide can enter and damage the root, causing root rot in *Carex rostrata*, which appeared to be happening at Sphagnum Bog at the edges of the reedswamp. This method of creating an aerobic micro-environment may explain how these species deal with other toxic substances (Moore and Bellamy, 1974).

Another problem associated with waterlogging is the toxic build-up of ethanol that results from accelerated glycolysis. In species tolerant of water-logging, it has been proposed from experimental findings that there is a diversion of glycolysis via an alternate pathway to produce malate (Crawford, 1969; Mcmanmom and Crawford, 1971 (from Moore and Bellamy, 1974)). Such an accumulation of malate is not toxic, and it involves only a partial blockage of normal respiration. This has not yet been proven in acidic mire plants, however (Moore and Bellamy, 1974). Another adaptation to anaerobic conditions is the diffusion of O_2 from parent plants of Carex rostrata to young growing shoots via attachments of the rhizomes (Armstrong and Boatman, 1967). It has also been demonstrated that Menyanthes trifoliata can reduce its O_2 demand under anaerobic conditions with a reduction in respiration rates (Coult and Vallance, 1950 (from Moore and Bellamy, 1974)).

Various adaptations to a low nutrient status are possible: greater uptake, storage, or procural form outside sources. The root systems of sedges and rushes illustrate the first means; extremely fine root systems suitable for phosphorus uptake in very infertile soils have evolved in these graminoids. Mycorrhizae serving this function in other species are unnecessary and not found associated with rush and sedge roots (Powell, 1975). Eriophorum vaginatum, another typical bog species, concentrates and stores essential ions that are in low supply, mobilizing these reserves in autumn (Goodman and Perkins, 1959 (from Moore and Bellamy, 1974)). Alnus incana, through microbial association in root nodules, is capable of symbiotic nitrogen fixation (Moore and Bellamy, 1974), which explains the relatively high nitrogen content of this community at Sphagnum Bog.

Nutrients may be supplemented through carnivory. The carnivorous plants at Sphagnum Bog, two species of *Drosera*, and three species of *Utricularia*, are capable of absorbing nitrogen and phosphorus form insects they digest. In extremely poor environments, these additional sources may increase growth (Chandler, 1976) and the derived organic compounds may be essential for flowering (Pringsheim and Pringsheim, 1962). *Utricularia intermedia* and *U. minor* are prominent in habitats of the Sphagnum Bog complex that have the lowest concentrations of nitrogen and phosphorus of the areas sampled-- the *Carex rostrata* reedswamp and *Eleocharis* (*Meesia* phase) fen. *Drosera anglica* and *D. rotundifolia* are restricted to the *Eleocharis* (*Meesia* phase) fens, *Eleocharis*-*Carex limosa* fens, and *Vaccinium*/*Aulacomnium* hummocks. There is no nutrient data on the latter two types, though they correspond to types in the literature with low nutrient status.

Dynamics of the Mire System

General

Peat-forming ecosystems, unlike other systems, retain a record of past vegetational stages from inception to present. Peats generally contain recognizable fragments of the vegetation that formed them, both macro- and micro- pseudofossils. The micropseudofossils, comprised mainly of pollen, are often blown or washed in from surrounding upland forests. Although this component is useful in studying past climatic and general vegetational change, it is only indirectly useful in understanding succession within the mire itself. The macropseudofossils are generally dominated by the underground plant parts, particularly roots and rhizomes, but also include occasional leaves and seeds. These are mostly deposited in situ, and remain stratified in the order of their deposition (Moore and Bellamy, 1974). A study of peat stratigraphy is, thus, the best means of elucidating past development history of any mire (Vitt, et al., 1975; Moore and Bellamy, 1974). Horizontal zonation of vegetation into bands may also suggest seres, but the correspondence between succession and zonation is only partial in highly complex systems (Proctor, 1974).

Predicting future stages of the ecosystem at Sphagnum Bog is difficult. The literature on comparable subalpine, spring-fed, sloping mires is minimal, in contrast with the great mass of information on typical sphagnum bogs. Permanent vegetation transects were established during the second field season, in 1978, as an attempt to document future vegetation changes. Periodic monitoring of these transects should provide useful infromation towards construction of a model of typical subalpine Cascade mire succession. Peat cores were taken in the various community types along one and one half transects, and examined in the field. Lack of time precluded a more extensive study. Many questions and details concerning succession at Sphagnum Bog, therefore, must remain unanswered for the present, but some very basic conclusions are possible, and interesting speculations can be made.

General trends of mire succession have been described in the literature. The early literature was basically concerned with hydrarch succession--basin-filling sequences in which the accumulation of peat resulted in a "bio-automatic progression toward mesophytism" (Moore and Bellamy, 1974). More recent investigations, however, suggest that although this pattern occurs under certain circumstances, there is no such general, uniform direction of succession in mires. Heinselman (1970), in the Lake Agassiz region of northern Minnesota, found the more general trend to be a water table rise, concurrent with sedimentation, resulting in a general swamping of the landscape, deterioration of tree growth and diversification of the landscape. Sequences from fen, to marsh or carr, through swamp forest, to either ombrotrophic bog forest or moss heath, or string bog and fen complex are typical. Such a successional trend, characterized by increasingly impaired drainage, as a cause as well as effect of peat accumulation, is termed paludification (Sjörs, 1963; Dahl, 1956; Heinselman, 1970). Paludification is characteristic of the cool, oceanic, boreal and subarctic regions, where peatlands are extensive (Sjörs, 1963).

Climate and physiography, in general, determine the limits to peat accumulation, in conjunction with the relation of water supply to peat. Permeability of peats and steepness of water slopes, are also important controls. Therefore, successional trends are probably not particularly applicable from distinctly different climatic and physiographic regions. Studies in montane regions in Scandinavia and here in the Pacific Northwest are among the most relevant. Investigators of subalpine and alpine mires in Scandinavia suggest that such fens do _not_ progress to the ombrotrophic bog stage, nor to the terrestrial stage (Dahl, 1956). Peat accumulation continues until an equilibrium point with destruction by oxidation is reached. Dry summer oxidation there slows peat accumulation at moderate thicknesses of one to two meters. In montane meadows in the Pacific Northwest, Van Vechten (1960) hypothesized that the late persisting snowbanks, keeping the meadows wet in early summer, through seepage, acted to maintain the meadows and inhibit tree invasion.

Cyclic succession, involving interchange of hummocks and hollows, was another successional trend prominent in the earlier literature. However, recent studies suggest that strict alternation is not always the case (Moore and Bellamy, 1974; Dahl, 1956). In minerotrophic peatlands, cyclic succession occurs only in very special, or local cases (Sjörs, 1963).

Hydric Communities

Floristic composition and stratigraphy of peat cores indicate that many of the hydric communities represent initial pioneer communities or early seral stages. Much of the diversity appears to be related to differences along gradients within the system, rather than differences in successional advancement. The *Carex rostrata* reedswamp and closely adjacent areas probably represent what was initially a shallow pond (Niering, pers. comm., 1978). Of the cores taken, this area showed the greatest layer of muck or limnic peat at the bottom, indicating an initial aquatic community (Moore and Bellamy, 1974). Campbell (1973) concluded that *Carex rostrata* was often a pioneer species, growing alone in water at the lowest end of a seepage area, where the ionic content might be low, in subalpine meadows in Oregon's High Cascades. Although it was difficult to distinguish the particular species of *Carex* comprising a layer of peat in the field, a layer containing *Eleocharis pauciflora* was readily distinguished by bright red roots. On this basis, I concluded that invasion by the *Eleocharis-Carex limosa* community had taken place at the edges of the reedswamp. In N. central Alberta, Vitt, et al. (1975), hypothesized that flark communities in deep standing water were filled in and dominated by a *Carex limosa* community. These flark communities, in large, deep pools, are probably comparable to the reedswamp, including *Menyanthes trifoliata*, a reedswamp species, as dominant. However, they did not believe that such simple hydrarch succession was always the case, and recommended a complex peat coring study to answer questions of past history of a mire.

Eleocharis/bryophyte communities in other parts of Sphagnum Bog, proved upon coring to have dominated the site since its inception. In other subalpine meadows and bogs in Oregon, Campbell (1973) found

Eleocharis to be a pioneer in areas of shallow, stagnant water, or surface-saturated conditions. The site at Sphagnum Bog may have originally been a seepage area, or area of impeded drainage with very shallow water, but the fact that it is slightly sloping, and the presence of *Eleocharis* peat at the bottom of the core, suggest that it probably was never a pond. The horizontal zonation of the different phases of the *Eleocharis* community, and gleanings from the literature concerning similar types, suggest that these represent different successional stages, in part, but also different tolerances to certain physical gradients. Vitt, et al. (1975), proposed the following successional sequence for characteristic bryophytes in poor fens in northern Alberta: *Drepanocladus exannulatus* → *Sphagnum subsecundum* → *Aulacomnium palustre*. According to observations at Sphagnum Bog, *Drepanocladus* often dominates the deepest water in *Eleocharis* communities, whereas *Meesia triquetra*, *Philonotis fontana*, or *Sphagnum subsecundum*, were seldom submersed. *Aulacomnium* is abundant only on considerably drier sites. Thus, in part, Vitt's scheme appears applicable to Sphagnum Bog. The *Philonotis* phases of the *Eleocharis* communities might also be responding to a physical gradient. According to Dahl (1956), *Philonotis fontana* and *Drepanocladus exannulatus* are separated by a temperature gradient, in Scandinavian mires, *P. fontana* occurring closer to the center of a cold spring than *D. exannulatus*. Campbell (1973) concluded that *Philonotis fontana*, along with *Epilobium alpinum*, distinguishes late snowfree areas, or invaded streambanks. The temperature gradient may play a role in either of these cases.

Conditions in the communities with shallow standing water may be comparable to those in flarks of patterned fens, or hollows in mires. Species composition is quite similar. There is considerable controversy as to the formation and maintenance of such hollows. It is generally believed that peat must be formed more slowly in the hollows. Sjörs (1963) suggested that the microalgae have a competetive ability to outcrowd the mosses. These dominant microalgae cause an almost corrosive type of oxidation at the surface of the hollows, thereby inhibiting peat deposition. Observations and collections at Sphagnum Bog demonstrated that the algal flora was, indeed, rich and abundant in the hollows and pools. Sjörs (1963) also proposed that the peat under the hummocks was less permeable than under the hollows, and that the hummock banks might act as dams to retain water in the pools. Boatman and Tomlinson (1977), however, found that the water level in the pools behaved in a similar manner to that beneath continuous surfaces. They suggested instead, that in pools, with species growing under suboptimal conditions, the growth rate is lower, and this lowered rate of production maintains a lower surface where water will accumulate. Moore and Bellamy (1974) suggested that the pools and hollows expand and contract periodically, but that the hollows remain constant.

Too few peat cores were taken in the various types of Eleocharis communities to sort out the different successional and environmental gradients differentiating the types. Future monitoring of vegetation in these community types and/or extensive peat sampling would be required to unravel these complex relationships.

Although Carex sitchensis is often a component of the Eleocharis communities, the *C. sitchensis*-dominated communities probably are not successionally related to the *Eleocharis* communities. Sedge peat continues to the bottoms of cores taken in such communities, with some banded sediments interspersed near the bottom, suggesting that this community was a pioneer here, and that succession has not continued significantly beyond this stage. Brooke, et al. (1970), report that *Carex aquatilis* (a species closely related to *C.sitchensis* (Hitchcock, 1976)), with *Drepanocladus exannulatus*, characterizes an initial successional stage onto a slope with greatly impeded drainage, or in stagnant open water, in subalpine zones in British Columbia.

Shrub Communities

The *Vaccinium occidentale* communities exhibit many floristic similarities to the *Carex sitchensis* communities, and successional relationships between the two are not clear. Niering (pers. comm., 1978) suggested that in some cases the absence of one dominant or the other may be simply fortuitous, allowing one species to become established first and them gaining a competitive advantage. In other cases, some physical gradient is probably responsible for the distinction.

The dwarf *Vaccinium/Aulacomnium* community may represent a hummock community that has maintained a faster peat deposition rate, thereby remaining higher than the surrounding *Eleocharis* communities. Vertical zonation of peat cores, and the bryophyte sequence suggested by Vitt et al. (1975), suggest that these hummocks may represent former *Eleocharis* communities invaded by *Vaccinium* that has maintained the site since. Observation of occasional, very small Vaccinium individuals, often accompanied by Aulacomnium palustre, and already building up a slightly higher base, in Eleocharis/bryophyte communities, substantiate this conclusion.

Carrs

There is some evidence that the willow carrs might be expanding, but very little to suggest that the alder carrs are. According to Dansereau and Segadas-Vianna (1952), alders exist only on contact zones with the adjacent forest, forming a transitional belt. In general, this is true at Sphagnum Bog. One small alder, however, was observed growing near the main stream running through the lower part of the west arm of the mire. Perhaps there is a stronger ionic concentration near the stream, due to sedimentation satisfying requirements of Alnus incana. Moreover, this site is still relatively close to the forest border. Otherwise, no alders were seen in the open, central parts of the mire. Haslam (1965) further states that alder carr differs from willow carr in not growing in poorly drained, wet areas. It is unlikely, therefore, that alder would ever replace a willow carr, or that they would co-dominate a site.

Roach (1952) in his study of succession at Nash Crater mire, in the Cascades in central Oregon, concluded that the position of the willow band was fixed by the depth of the substrate, and as the bog was filled in, willows would advance over it. There is little evidence at present for this, at Sphagnum Bog. Salix, like alder, occupies marginal, though wetter positions. How much it will expand is of interest. The effect of heavy elk grazing on the willow, and whether such grazing has the effect of stimulating growth, or of reducing overall volume, is unknown. Observations over two summers suggest that the amount of grazing presently received by the willow stimulates production. Only monitoring of future changes along the permanent transects will elucidate the role of the *Salix* carr in the succession of this mire.

Conifer Invasion

Invasion by conifers is apparent, to at least a limited extent, over much of the mire. As stated previously, the commonly accepted idea of bog succession is that with time, the bog will fill in and be succeeded by a forest community typical of the area. Rigg (1922), found stunted conifers in many of the bogs he visited in the Pacific Northwest, and on the coast, in an example of a sphagnum bog that had been completely succeeded by a *Pinus contorta* community; however, in the latter case, he conceded that artificial drainage and clearing of the area had hastened the successional process. Roach (1952), concluded that at Nash Crater bog in the Oregon Cascades, the lack of succession to forest indicated the youth of the system, and he expected the forest to encroach over the peat as the bog filled in. For certain systems, at least, there is presently some disagreement with this general scheme. Dahl (1956) proposed that subalpine and alpine mires in Scandinavia would not progress to the mesic forest stage. Campbell (1973) stated that succession is quite slow in subalpine habitats in the Pacific Northwest Cascades. Hickman (1976), suggested that only on certain sites are Cascade conifers able to colonize bog soils in the Oregon Cascades, that generally are inappropriate for colonization.

Two types of data were collected to analyze conifer invasion. Table VI illustrates results of a collection of cores taken from selected large trees established in the mire at various locations. Tables VII and VIII present data from an areal plot, clarifying structure, density, and dominance relationships in a meadow-like portion of the mire abutting the forest edge. Five conifer

Table VI. Tree species, mire community types invaded, and average ages of the oldest trees in Sphagnum Bog.

	Mire Community Type Invaded		
Species	*Vaccinium occidentale/ Carex sitchensis*	*Carex sitchensis*	*Carex sitchensis-Aster occidentalis*
Pinus contorta			
No. of samples	12	5	7 *(6)
Ave. age (rings)	48.2	34.0	39.0 *(27.6)
Std. dev.	15.6	9.9	18.9 *(8.1
Ave. dbh (cm)	14.9	no data	22.4 for 5 of the 7
Picea engelmannii			
No. of samples	2		
Ave. age	126		1
			51
Pinus monticola			
No. of samples	1		
Ave. age	47		
dbh (cm)	11.3		

* omitting one very old, large specimen so that a more homogeneous group results

Table VII. Stand structure of area of conifer invasion, illustrating numbers of individuals of particular species in the different size classes.

	Number of individuals of species						
Size classes (range of diameter at breast height, in cm)	*Pinus contorta*	*Picea engelmannii*	*Abies lasiocarpa*	*Pinus monticola*	*Tsuga mertensia*	dead trees	Totals
seedlings (<.76m in height)[1]	3	11	5	1	3		
saplings (<1.82 m in height)	34	32	28	4	21		
1-2.5	5	3	1	1			
2.5-7.5	15	11	8	2	3		
7.5-12.5	12	8	3	3			
12.5-17.5	4	5					
17.5-22.5	3	1					
22.5-27.5	1	1					
27.5-32.5				2			
32.5-37.5		1					
Totals--no. in 2601.2 m^2 plot							
(<1 cm dbh)	37	43	33	5	24		142
(>1 cm dbh)	40	29	12	8	3	23	115
Total	77	72	45	13	27	23	257
Totals per hectare							
(<1 cm dbh)	142.31	165.4	126.92	19.23	92.31		546.15
(>1 cm dbh	153.85	111.54	46.15	30.77	11.54	88.46	422.3
Total/hectare	296.15	276.92	173.08	50.00	103.85	88.46	988.46

Table VIII. Dominance relations of tree species invading Sphagnum Bog.

Diameter range class (cm)	Basal area (cm^2)	Number of trees x basal area					
		Pinus contorta	*Picea engelmannii*	*Abies lasiocarpa*	*Pinus monticola*	*Tsuga mertensiana*	Totals
< 1	0.785	29.05	33.75	25.9	3.92	18.84	
1-2.5	3.14	15.7	9.42	3.14	3.14		
2.5-7.5	19.6	294.0	215.6	156.8	39.2	58.8	
7.5-12.5	78.5	942.0	628.0	235.5	235.5		
12.5-17.5	176.7	706.8	883.5				
17.5-22.5	314.2	942.6	314.2				
22.5-27.5	490.9	490.9	490.0				
27.5-32.5	706.9				1413.8		
32.5-37.5	962.1		962.1				
Totals--m^2 in 2601.2m^2 plot							
(all size classes > 1 cm dbh)		0.34	0.350	0.040	0.170	0.0059	0.903
(all size classes)		0.342	0.354	0.042	0.170	0.0078	0.916
Totals---m^2/hectare							
(all size classes > 1 cm dbh)		1.305	1.346	0.152	0.65	0.023	3.473
(all size classes)		1.315	1.361	0.162	0.654	0.03	3.523

species from the adjacent forest community invaded tha area: Pinus contorta, Picea engelmannii, Abies lasiocarpa, Pinus monticola, and Tsuga mertensiana. All but Tsuga mertensiana are listed in the literature as typical mire invaders (Rigg, 1922; Hickman, 1976; Rigg, 1940). According to Hickman (1976), Picea engelmannii and Abies lasiocarpa are able to invade some mires because of their cold- and water-tolerances. Zeigler (1978) stated that Pinus contorta can tolerate saturated soils, as well as high soil temperatures and extremely low air temperatures, better than most associated conifers. According to Fitzergerald's (1966) work in Pacific Northwest coastal bogs, invasion is limited during the establishment rather than the germination phase. Temperature extremes at the surface of the peat, due to the poor heat conductivity of peat, are the probable limiting factors. This wide range in temperature extremes is due partly to the lack of a canopy, as well as the lack of buffering action from a large body of water, and poor heat conductivity of peat (Fitzgerald, 1966).

In Tables VII and VIII, it is seen that Pinus contorta and Picea engelmannii are the most abundantly represented species in all age classes. Basal area data also show their dominance. Abies lasiocarpa has low numbers of older trees, but abundant seedlings, indicating, perhaps, that the area is becoming more favorable for later seral species.

Age data show that invasion has been rather recent, and is quite slow. Initial, and peak invasion appears to have occurred between 34 and 50 years ago. This time period agrees with that reported in Franklin, et al.(1971), Campbell (1973), and other Pacific Northwest investigators' studies of recent meadow invasion, where invasion is attributed to a warmer, drier climate lasting from the late 1800's to the mid-1940's. Since the mid-1940's, however, the climate has been cooler and moister, accompanied by a drastic decline in tree invasion in most areas. The data in Table VII suggest two invasion periods; one for the combined 2.5-7.5 and 7.5-12.5 cm dbh classes, and one corresponding to the establishment of the younger, sapling-sized trees. Contrary to other investigators, Henderson (1973) found invasion to be continuing at Mt. Rainier. He decided that a good seed year, followed by a summer of normal precipitation and temperature is a further requirement for conifer invasion in addition to climate. The largest trees in the mire were selected for age-sampling, to give some idea of how long ago trees began invasion. Thus, many of the established trees may average much younger than 34 to 46 years, the average age of the oldest invaders. If so, the average age may correspond rather closely with the average of 20 years found for Pinus contorta invading the Pumice Desert, just north of Crater Lake (Horn, 1968).

There has been a decline in the numbers of small seedlings in recent years, and numerous dead seedlings were observed, resulting, possibly, from deeper snowpacks and shorter growing seasons during 1971 and 1972. It seems apparent from these observations that there has been no current episode of invasion occurring at Sphagnum Bog during the last few years.

Prediction of future changes at Sphagnum Bog are difficult. With increase in size of the already established trees, the understory vegetation may be affected. Such was the case under a large Picea engelmannii, approximately 200 years old, that had an understory more typical of moist forests in the surrounding uplands, including such characteristic species as Vaccinium scoparium and Rubus lasiococcus. Under a stand of fairly large Pinus contorta, the older individuals averaging about 39 years of age or older, leaf litter had accumulated somewhat, and the understory is very sparse, in contrast to the surrounding dense mire vegetation.

Whatever the course of conifer succession, invasion will probably be restricted to two of the mire types: the Vaccinium occidentale/ Carex sitchensis type, and to the drier, Aster occidentalis phase of the Carex sitchensis type, although to a more limited extent in this community. This conclusion is based on observations of stunted conifers in both community types, and a distinct lack of conifers in carrs or other fen types at Sphagnum Bog. As would be expected, transitional meadow types also typically included conifers.

Disturbances and succession

The role of cattle impact in succession is not clear. In one of the dry Carex sitchensis-Aster occidentalis stands, with abundant Deschampsia cespitosa, invasion was quite evident, with numerous small Pinus contorta saplings, in addition to a fair number of larger trees. It is abvious from the numerous cowdroppings that cows spent a good deal of time here. Soil compaction and drying are known effects of grazing and trampling (Liddle, 1975), and may have been factors in the establishment of the young conifers. Community structural changes, e.g., formation of openings in a denser community, may also have given seedling conifers the competitive advantage necessary for invasion. However, relatively extensive cattle use in the *Eleocharis pauciflora*/*Philonotis* type was apparently not accompanied by conifer invasion. Furthermore, conifer establishment was evident, though not to the same extent, in another, apparently unused *Carex sitchensis*-*Aster occidentalis* stand. In conclusion, although grazing may have accentuated the dryness or suitability of a stand, observations of invasion in similar, but unaffected stands, reveal that any effect is only secondary.

Fire has probably not played any important role in the past history of this mire. No evidence of charcoal was found in the sampled peat cores. At present, it appears that conditions are too wet, and that there is an insufficient fuel load to carry a fire through this area.

Geographic Considerations of the Oregon Cascade Mire Communities

The intensive study at Sphagnum Bog was confined to a very limited geographic area. Assuming that similar communities may exist under similar conditions, one might expect to find some replication of the communities described here. Little work has been done previously on mires in the Pacific Northwest. For purposes of comparison, I did brief reconnaissance sampling of the vegetation at five other Cascade mires in central Oregon near the end of the second field season, spending one-half to a full day at each. A list of representative species from each mire was compiled, and unknown species were collected. Various communities were described in terms of dominants, with estimates of their height and cover, plus a list of certain key associated species. Rough estimates of the extent of the different communities were made. Summaries of the information collection at each of these other mires is contained in Appendix C.

A comparison of the distribution of various community types represented at the five surveyed mires, Sphagnum Bog, and three other similar, previously investigated areas (Campbell, 1973; Roach, 1952; Beguin and Major, 1975 (from Major and Taylor, 1977)) is presented in Table IX. A study by Hickman (1976) identified a Caltha biflora/Carex sitchensis/Dodecatheon jeffreyii Bog association, with many of the same species found at Sphagnum Bog, but is not comparable because Hickman's communities are not defined quantitatively, and are recognized on a broader scale.

Form Table IX, it is evident that all of the communities

Table IX. Occurrence of mire community types at different western mire sites.

MIRE SITES COMMUNITIES	Surveyed Sphagnum Bog	 Gold Lake Bog	 Little Cultus Lake Bog	 Thousand Springs Bog	 Crescent Lake Junction Bog	 Bybee Creek Bog	Literature Hunt's Cove (Campbell, 1973)	 Grass Lake--(Beguin, 1975)	 Nash Craters (Roach, 1952)
AQUATICS AND REEDSWAMPS									
<u>Potentilla</u> <u>palustris</u>								x	
<u>Puccinellia</u> <u>pauciflora</u>								x	
<u>Carex</u> <u>rostrata</u> reedswamp	x	x						x	x
LOW SEDGE/NO MOSS FENS									
<u>Eleocharis</u>-<u>Carex</u> <u>limosa</u> fens	x	x	x					x	
LOW SEDGE or HERBS/MOSS FENS									
<u>Eleocharis</u>/bryophyte									
<u>Philonotis</u> phase	x		x			x			
<u>Meesia</u> phase	x		x						
<u>Drepanocladus</u> phase		x	x		x				
<u>Carex</u> <u>rostrata</u>/<u>Sphagnum</u> <u>squarrosum</u>							x		
<u>Eleocharis</u>/<u>Aulacomnium</u> <u>palustre</u>							x		
herbs-low sedges/bryophytes									
<u>Philonotis</u> phase				x					
<u>Helodium</u> phase				x					
<u>Tomenthypnum</u> phase			x	x	x				
TALL SEDGE/NO MOSS FENS							x		
<u>Carex</u> <u>sitchensis</u> fens				x					
<u>Hypericum</u> phase	x		x						x
<u>Aster</u> phase	x	x				x			
rush-sedge fens		x							
LOW SEDGE--SHRUB/MOSS TRANSITION									
<u>Vaccinium</u>--<u>Eleocharis</u>/<u>Meesia</u> transition	x	x							
DWARF SHRUB/MOSS THICKETS									
<u>Vaccinium</u>/<u>Aulacomnium</u> hummocks	x				x				x
mixed shrub/moss hummocks		x	x						
SHRUB/INVADING CONIFER THICKET									
<u>Vaccinium</u>/<u>Carex</u> <u>sitchensis</u>/<u>Pinus</u> <u>contorta</u>	x					x			
mixed shrubs/<u>Pinus</u> <u>contorta</u>		x	x						
SHRUB THICKET									
low willow thickets						x			
TALL SHRUB THICKETS									
<u>Betula</u> <u>glandulosa</u> carr		x	x		x				
<u>Alnus</u> <u>incana</u> carr	x			x					
<u>Salix</u> sp carr	x	x	x	x	x			x	
SPECIALIZED SMALL SPRING BOGS				x					

identified at Sphagnum Bog, or equivalent types are repeatable units. Certain communities, of course, are more widespread than others. The Carex rostrata reedswamp is present only at Sphagnum Bog, Gold Lake Bog, and Nash Craters. Characterizations of reedswamp communities in the literature and observations of physical conditions at the sites suggest that reedswamps are restricted to lake edges or shallow ponds with stagnant or slow-moving water. Such a requirement limits the distribution of this community type to areas with specialized topographic features where large amounts of water can accumulate. Crescent Lake Junction Bog was too flat and dry, Little Cultus Lake lacked any large depressions, and the slopes at Thousand Springs Bog were too great. The Eleocharis-Carex limosa fen is also typical of depressions, but shallower, smaller pools serve as appropriate habitat. Such features are common; this type, therefore, is more widely distributed.

Communities with a continuous moss mat are rather variable, but this same physiognomic type was present at all the mires visited by the author, as well as at Hunt's Cove. (From the available literature, it was not possible to determine if such a community occurred at Grass Lake or at Nash Craters.) These seem to be characteristic of areas of saturated, organic soils. Bybee Creek, which was not as wet, had small patches of Philonotis fontana, only near springs or small rivulets. Carex sitchensis fens and Vaccinium occidentale thickets often occur, but were notably absent from the more strongly sloping mire at Thousand Springs. These types are widely distributed, and probably occur in areas too dry to support a moss-mat community.

Mire margin communities, or carrs, occur at all of the areas visited except Bybee Creek Bog. Different species or groups of species were dominant in different areas, however. *Betula glandulosa* var. *glandulosa*, had been listed on the "1977 Provisional List of Rare, Threatened, and Endangered Plants in Oregon", prepared by Siddall and Chambers, as rare in Oregon, but more abundant elsewhere, but was deleted in 1979. It apparently is reasonably abundant in appropriate mire habitats. Alder carrs are absent from several of the mires. Haslam (1965) concluded that willow carrs could invade badly-drained sites, but alder woodland required will-drained sites. Therefore, although all of the mires except Bybee Creek have wet margin habitats appropriate for willows, topographic or substrate hydrology features preclude the growth of alder in several areas.

The diversity of types found at Sphagnum Bog is a common feature of most of the other mires inventoried. Only the small, drier mires Crescent Lake Junction Bog and Bybee Creek Bog were relatively uniform. Other investigators have concluded that any large mire will consist of a mosaic of different vegetation types due to the complexity of the environmental relations, with so many different factors affecting the distribution of species and species groupings (Dahl, 1956).

Classification of Sphagnum Bog and other Cascade Mires along the Rich-to-Poor Gradient

Certain mire species are known to be exclusive to distinctive types of mires. Distributional boundaries of some of these species so closely approximate the limits of influence of mineral water where a fen and bog are adjoining, that the concepts of "Mineralbodenwasserzeigengrenze" or "fen plant limit" were proposed (DuRietz, 1954; Sjörs, 1948 (from Malmer, 1965)). Other species have been defined as corresponding to a calcareous or lime water limit, or extremely rich type of fen vegetation (Dahl, 1956). Certain species are characteristic of ombrotrophic situations, or true bogs, especially Sphagnum spp. However, according to Dahl (1956), bog species are not obligate. Any ombrotrophic area should be evident by its lack of any exclusive fen species (Sjörs, 1959; Malmer, 1965). Since many of the mire species and aquatic species are circumboreal, it should be possible, according to this concept of indicator species, to determine the type of mire at Sphagnum Bog and the other Cascade mires visited by floristic comparisons with previously classified mire vegetation associations elsewhere in the world. An inherent difficulty with such a classification method, brought out by Persson (1965), is that the field-layer species of many of the wetter mires are capable of growing in such extremely wet habitats that they are more or less indifferent to other ecological gradients.

Sphagnum Bog includes some species designated by Sjörs (1963) as typical of bogs: Kalmia polifolia (an old name synonamous with

K. microphylla), *Carex limosa*, *Drosera anglica*, and *D. rotundifolia*, and *Scheuzeria palustris* also appears at Little Cultus Lake Bog and Gold Lake Bog (Franklin, et al., 1972). However, even in portions where these bog species are concentrated, certain species known to require mineral water are found: *Carex rostrata*, *Menyanthes trifoliata* (Dahl, 1956; Sjörs, 1965; Malmer, 1965), *Utricularia* spp. (Sjörs, 1963; Heinselman, 1970), and *Betula glandulosa* (Sjörs, 1959). Furthermore, the dominance by brown mosses, i.e., mosses usually brownish in color as *Tomenthypnum nitens* or *Drepanocladus vernicosus*, and sedges, rather than a *Sphagnum*-dominated system indicates that the area is influenced by mineral ground water, rather than acidic water (Vitt, et al., 1975; Sjörs, 1963).

Several species comprising part of these bogs' floras are further listed as indicators of rich fens: *Tofieldia glutinosa* (Sjörs, 1963), and the bryophytes *Tomenthypnum nitens* and *Meesia triquetra* (Dahl, 1956); or as typical of rich fen pools: *Carex limosa*, *Menyanthes trifoliata*, *Eriophorum* sp., *Drosera anglica*, *Sparganium*, and *Utricularia* (Sjörs, 1963).

None of the species listed by Sjörs (1959) and Vitt, et al.(1975) as indicative of extremely rich fens occur in any of these Oregon Cascade mires.

Bryophytes are particularly useful in distinguishing different types of mires and have long been used for this purpose by European investigators. Examination of Table X which compares bryophytic floras of Sphagnum Bog and the five other Cascade mires indicates that the three mosses, Philonotis fontana, Aulacomnium palustre and Meesia triquetra, important members of the Eleocharis/ bryophyte or shrub hummock communities, are universally present.

Philonotis fontana is a species that prefers spring vegetation (Persson, 1965). Although Sjörs includes spring vegetation as part of the fen series, other consider it separately. Spring vegetation has been described in Scotland (Ratcliffe, 1964), Sweden (Malmer, 1965; Persson, 1965), southern Africa (van Zinderen-Bakker and Werger, 1974) elsewhere, as vegetation dominated by one or more bryophytes, with a vascular species component, that develops around a concentrated outflow of subsoil water or in a regular seepage or flow, on slopes. Excess water courses through small stream channels, or may develop into a sheet flow during periods of heavy inundation (van Zinderen-Bakker and Werger, 1974). Such a sheet flow was evident in early summer at Sphagnum Bog following extensive melting of snow; and Niering (pers. comm., 1978) interpreted the numerous deep holes at Sphagnum Bog as upwellings of spring water, surrounded by built-up layers of peat. The abundance of small channels may represent erosional activity resulting from drainage of the excess ground water to lower levels (van Zinderen-Bakker and Werger, 1974). As with other fens, there is some correspondence between the mineral content of the water and the prominence of certain bryophytes (Ratcliffe, 1964), but Dahl (1956) suggests that temperature gradients may also be extremely important. If there is a constant supply of subsoil water that has been influenced by more mineral-rich soils or deposits, moderately rich or transitionally rich mire vegetation may be encountered even in areas with

Table X. Distribution of bryophytes at inventoried Oregon Cascade mire sites.

Bryophytes: / Mires:	Bybee Creek Bog	Crescent Lake Junction Bog	Thousand Springs Bog	Little Cultus Lake Bog	Gold Lake Bog	Sphagnum Bog
Mosses:						
Amblystegium serpens					×	×
Aulacomnium palustre	×	×	×	×	×	×
Brachythecium frigidum			×		×	×
Brachythecium salebrosum						×
Brachythecium sp.		×		×	×	×
Bryum creberrimum						×
Bryum pallescens		×			×	×
Bryum pseudotriquetrum	×	×		×		×
☆ *Bryum weigelii*						×
Campylium polygamum	×					
Drepanocladus aduncus	×		×			×
Drepanocladus exannulatus				×	×	×
Drepanocladus fluitans						×
Drepanocladus sendtneri		×				
☆ *Drepanocladus vernicosus*				×	×	×
Fontinalis antipyretica				×	×	×
☆ *Helodium blandowii*			×	×		×
Hygrohypnum bestii						×
Meesia triquetra	×	×	×	×	×	×
Mnium punctatum var. *elatum*			×	×		×
Mnium rugicum			×	×		×
Philonotis fontana	×	×	×	×	×	×
Plagiothecium denticulatum						×
Sphagnum capillaceum			×		×	
Sphagnum fuscum		×	×			
Sphagnum squarrosum			×			×
Sphagnum subsecundum				×		×
☆ *Tomenthypnum nitens*		×	×	×	×	
Liverworts:						
Chiloscyphus polyanthus			×		×	×
Lophocolia heterophylla						×
Marchantia polymorpha			×		×	×

☆ new Oregon records

gnerally poor soils (Malmer, 1965; Moore and Bellamy, 1974). In the Crater Lake area, though Steiger soils of Mazama pumice origin are known to be nutritionally poor, especially in nitrogen, underground water may have been influenced by deeper basaltic dactie deposits. Species composition in the Cascade spring-mires overlaps with several of the types described by the Europeans. These have been equated with the rich-to-poor fen series. On this basis, Sphagnum Bog and the others correspond best with Philonotis springs or moderately rich fens, characterized by Eleocharis pauciflora, Drepanocladus aduncus, Sphagnum subsecundum, Menyanthes trifoliata, and Bryum weigelii, as well as other species not common to all the areas (Persson, 1965; Malmer, 1965; Ratcliffe, 1964). The annual inundation by snowmelt from surrounding terrestrial uplands also provides a continued source of enrichment to the mire early each summer (Romanov, 1968).

On the basis of the overall pH range at Sphagnum Bog, a similar conclusion as to the type of mire represented by Cascade peatlands is reached. PH varies between different mire types as follows: a) ombrotrophic bogs in inventories from mires in Scandinavia, Canada, and the northern United States, are characterized by low pH readings, ranging from (3) 3.5 to 4.5 (5) (Heinselman,1970); DuRietz (in Moore and Bellamy, 1974); Sjörs, 1963; Persson, 1965); b) poor fens range between 4.0 and 5.4 (Persson, 1965; Malmer, 1965; Sjörs, 1963; Vitt, et al., 1975); c) rich fens range from 5.8 to 7.4 (Sjörs, 1963), and these can be subdivided into moderately rich fens and Philonotis springs, ranging from 6.0-7.0 (Persson, 1965), and extremely rich fens and Cratoneuron springs, ranging from 6.5-8.0, or greater than 6.8

which was defined by Heinselman as the calcareous water limit. The range of 5.5 to 6.75 at Sphagnum Bog corresponds closely with the moderately rich fen and Philonotis-Pohlia albicans spring types. PH of this type overlaps with the intermediate fens and Scapania uliginosa springs, somewhat, as does species composition.

Macronutrient contents of different peat types at Sphagnum Bog were expressed as percent of dry weight of the peat samples. Unfortunately, many of the earlier investigations into nutrient regimes measured nutrient contents in the mire waters, or expressed the values in units that are not comparable. An investigation of nutrient status relationships between different peatland types in northern Ontario also expressed values as percent dry weight, and includes results from an older European study by Bruene in 1948 in the same units. Stanek and Jeglum's bog peat pH values are not consistently as low as Bruene's, since they include weakly minerotrophic transitional mires under the heading of bog. Comparison of nutrient data from Sphagnum Bog with Stanek and Jeglum' shows that a wide range of variation is present at the study area, but that at least substantial portions of the open parts of the mire correspond to one of the fen types. For calcium and magnesium, the Vaccinium and Carex sitchensis communities' readings fall into the broad range of graminoid fens and shrub fens (Stanek and Jeglum, 1977).

SUMMARY AND CONCLUSIONS

1) The vegetation pattern at Sphagnum Bog consists of a complex mosaic of species associations, with only the extreme groups sharply distinguished from the rest. Gradual variation of species composition and structure is evident for the intermediate types.

2) The species associations, defined as communities and phases, were classed into four physiognomic types: reedswamp, sedge fen, deciduous shrub thicket, and deciduous fen carr. The *Carex rostrata* community corresponds to reedswamp; *Eleocharis-Carex limosa* to a low sedge fen with no moss layer; *Eleocharis pauciflora*/bryophyte with *Philonotis fontana* and *Meesia triquetra* phases to low sedge fens with a more or less continuous moss layer; *Carex sitchensis* community, with *Hypericum anagalloides* and *Aster occidentalis* phases to tall sedge fens lacking a moss carpet; *Vaccinium occidentale*/*Aulacomnium palustre* community to a dwarf shrub thicket with a dense moss ground layer; *Vaccinium occidentale*/*Carex sitchensis* to a shrub thicket, with no moss ground layer; and the *Alnus incana*/*Brachythecium* sp. community and *Salix barclayi* community correspond to deciduous fen carr types. A transitional type, intermediate between shrub thickets and low sedge/moss fens was also defined, the *Vaccinium*--*Eleocharis*/bryophyte type.

3) One strong vegetation gradient was displayed by these community types when the stands were ordinated by reciprocal averaging. Stands were arrayed such that the wettest communities, i.e.,

reedswamp and low sedge fens lay at one end, the marginal carr types at the other, and sedge and shrub thickets in the center.

4) The vegetation gradient was most closely paralleled by nutrient concentrations: calcium, magnesium, potassium, and total phosphorus, with R^2 values ranging between 0.6 and 0.7. Peat chemistry is probably the single most important determinant of vegetation patterns at Sphagnum Bog.

5) Importance of other environmental factors, as they relate to vegetation and species distributions and nutrient status was illustrated. The distribution of carr communities on the vegetation map indicates the importance of proximity to mineral soil. Topographic profiles indicate a general correspondence between vegetation types and topographic position, determining, in part, the wetness of the habitat, its relative aeration, and supply of flowing water. The pH did not vary widely across the system, and was not very useful for distinguishing communities within the system, but rather for characterizing the area as a whole.

6) The environmental gradient underlying the vegetation pattern is complex, involving nutrient status, and probably also the related and interacting factors of wetness regimes, water flow rates and patterns, and distance from mineral soil.

7) The vegetation units defined at Sphagnum Bog are repeated, often with similar species, and with similar structure and physiognomy, at other sites in the Cascades of central Oregon, where there is appropriate habitat.

8) Based on considerations of topography and hydrology, floristic affinities, nutrient status, and acidity, Sphagnum Bog and other similar areas in the central and southern Cascades of Oregon, do not represent bogs, i.e., ombrotrophic mires, but moderately rich, spring-fed fens, fed by mineral-influenced water via springs. Elevation measurements showed that the peat did not form a convex surface above the water table; the pH range of 5.5 to 6.75 is higher than the average for ombrotrophic bogs; the Cascade mire vegetation is dominated by brown mosses and sedges and shrubs, characteristic of minerotrophic fens, rather than by Sphagnum-dominated, species-poor vegetation typical of truly ombrotrophic mires; and the nutrient contents are too high to fit the definition of a nutrient-poor bog.

9) Succession has not progressed significantly at Sphagnum Bog. Peat production probably began on a gentle slope fen by springs where drainage was extremely poor, and water accumulated in irregularities of the surface. Various sedge communities acted as invaders in the wetter habitats, and Vaccinium thickets probably became established around the edges. Dwarf Vaccinium was observed invading low sedge/bryophyte fens. Conifer invasion will probably proceed very slowly, with establishment occurring in isolated periods of unusually favorable climatic conditions coupled with high seed production. Harsh conditions continue to eliminate all but the strongest individuals, such that equilibrium is nearly maintained. Invasion that does proceed

will be limited to the *Vaccinium occidentale*/*Carex sitchensis* and the *Carex sitchensis* (*Aster occidentalis* phase) community.

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APPENDICES

APPENDIX A

VEGETATION STAND DATA

Vegetation data for each community is listed as summaries of the stands representing the community, with average percent species cover per stand for each species listed. A total average percent cover in the community for each species is also listed, as well as relative constancy. The total number of microplots sampled in the community is listed at the bottom, as is average species richness per microplot.

Carex rostrata community

	% Cover
Plot no.	12
Species	
Graminoids:	
Carex limosa	.3
Carex rostrata	28.2
Eleocharis pauciflora	.3
Potamogeton gramineus	2.8
Puccinellia pauciflora var. *microtheca*	12.3
Sparganium minimum	.3
Herbs:	
Bidens cernua	3.6
Utricularia intermedia	1.6
Utricularia minor	2.8
Veronica americana	1.8
Mosses:	
Meesia triquetra	3.0

Total no. of microplots = 12
Species richness/microplot = 4.25

Eleocharis pauciflora-Carex limosa community

	% Cover								
Plot no.	18	8	10	21	49	13	68	Mean Cover	Relative Constancy
Species									
Shrubs:									
Vaccinium occidentale				.3				+	14
Graminoids:									
Agrostis idahoensis							.4	+	14
Agrostis thurberiana				+			.3	+	29
Carex limosa	37.5		15.0	16.5		14.7		12.0	57
Carex muricata						3.1		.4	14
Carex rostrata			9.0			10.6	11.6	3.9	43
Carex simulata							11.0	1.6	14
Carex sitchensis	15.0		7.8	3.0	7.2	10.5	6.0	7.1	86
Carex sp.			1.5		24.0			3.6	29
Eleocharis pauciflora		37.5	32.8	50.9	6.0	49.6	7.8	26.4	86
Equisetum arvense	.5			.3	.1	.7		.2	57
Muhlenbergia filiformis				13.8		17.1	3.3	4.9	43
Herbs:									
Dodecatheon alpinum				5.3		3.0	3.9	1.7	43
Drosera anglica		.5		.7				.2	29
Drosera rotundifolia		3.0		.4				.5	29
Epilobium alpinum var. gracillimum	37.5	15.0		27.2		.6	.1	11.5	72
Hypericum anagalloides				6.5		.7		1.0	29

Eleocharis pauciflora-Carex limosa community

	% Cover								
Plot no.	18	8	10	21	49	13	68	Mean Cover	Relative Constancy
Menyanthes trifoliata						3.6		.5	14
Mimulus primuloides				10.1		3.0		1.9	29
Polygonum bistortoides				+				+	14
Spiranthes romanzoffiana						.6		+	14
Tofieldia glutinosa						.7		.1	14
Utricularia intermedia				+	6.7	16.1		3.3	43
Mosses:									
Aulacomnium palustre				+				+	14
Drepanocladus exannulatus				+	11.1		3.7	2.2	43
Meesia triquetra		.5		15.0	3.0			2.6	43
Philonotis fontana				.6		17.1	.4	2.6	43
Sphagnum squarrosum		.5						+	14
Sphagnum subsecundum							+	+	14

Total no. of microplots = 35

Average species richness/microplot = 6.97

Eleocharis pauciflora/bryophyte community (*Meesia triquetra* phase)

	% Cover									
Plot no.	7	48	60	40	50	52	53	63	Mean Cover	Relative Constancy
Species										
Shrubs:										
Vaccinium occidentale	15.0			.2					1.9	25
Graminoids:										
Agrostis thurberiana				2.2		2.6	.4		.65	38
Carex jonesii						1.9	3.8		.7	25
Carex limosa					11.6	1.9	23.1		4.6	38
Carex muricata		14.7	1.6	.8		.8			2.2	50
Carex rostrata		15.0	12.1						3.4	25
Carex simulata			9.7						1.2	12
Carex sitchensis	15.0	6.0	7.0	17.3	14.7	38.1	47.2	26.3	21.5	100
Deschampsia cespitosa				.2	+			11.3	1.4	38
Eleocharis pauciflora	85.0	19.7	22.3	67.7	25.3	41.3	26.5	38.8	41.2	100
Equisetum arvense		9.6		5.1	5.7				2.6	38
Juncus orthophyllus			.3					1.5	.2	25
Muhlenbergia filiformis		10.2	6.6	22.0	.3	31.9	6.6	20.6	12.3	87
Herbs:										
Dodecatheon alpinum		5.4	7.4	17.0	4.8	14.8	11.6	10.8	8.9	87
Drosera anglica			+		+				+	25

Eleocharis pauciflora/bryophyte community (*Meesia triquetra* phase)

	% Cover									
Plot no.	7	48	60	40	50	52	53	63	Mean Cover	Relative Constancy
Drosera rotundifolia	37.5								4.7	12
Epilobium alpinum var. *gracillimum*	3.0	1.4	.9	7.7	43.9	7.4	8.3	8.4	10.2	100
Hypericum anagalloides		4.2				12.9			2.1	25
Menyanthes trifoliata	3.0								.4	12
Mimulus primuloides		38.5	.9	7.2		14.1	.8	7.5	8.6	75
Oxypolis occidentalis							.4		+	12
Polygonum bistortoides		.6	1.4	.9	.3	.8	6.4	5.3	2.0	87
Ranunculus gormanii				+		6.0		.1	.8	38
Tofieldia glutinosa	3.0								.4	12
Utricularia intermedia	.5				.3				.1	25
Mosses:										
Aulacomnium palustre	.5		6.8	.2		+			.9	50
Bryum pallescens							.7		+	12
Drepanocladus exannulatus	15.0	3.8	32.6	1.6	36.7	14.5	41.0	32.6	22.2	100
Meesia triquetra	15.0	80.5	7.4	63.6	47.7	66.3	4.1	13.1	37.2	100
Philonotis fontana		15.7	14.2	8.2	7.4	5.1	21.0	40.0	14.7	87
Sphagnum squarrosum	.5								+	12
Sphagnum subsecundum	15.0		3.9	29.4	+			9.4	7.2	63

Total no. of microplots = 55

Average species richness/microplot = 9.78

Eleocharis pauciflora/bryophyte community (*Philonotis fontana* phase)

	% Cover							Mean Cover	Relative Constancy
Plot no.	11	69	38	59	58	65	41		
Species									
Shrubs:									
Vaccinium occidentale	.4		1.0		3.4			.7	43
Graminoids:									
Agrostis idahoensis					.3	.4		.1	29
Agrostis thurberiana	+		.6		.3	.4		.2	57
Carex jonesii					11.8			1.7	14
Carex muricata		6.8	4.5	1.9		.4		1.9	57
Carex rostrata	16.3							2.3	14
Carex simulata		17.6						2.5	14
Carex sitchensis	18.7	16.8	4.2	18.9	20.2	40.9	58.9	25.5	100
Deschampsia cespitosa		11.8	10.3	1.4	1.6	11.3	.9	5.3	86
Eleocharis pauciflora	22.9	38.0	58.5	48.4	59.8	47.2	37.5	44.6	100
Equisetum arvense			4.6		.6		1.5	1.0	43
Juncus ensifolius			+					+	14
Juncus orthophyllus				6.4				.9	14
Luzula campestris					.3			+	14
Muhlenbergia filiformis	9.1	20.5	22.7	11.4		20.5	3.9	12.6	86

Eleocharis pauciflora/bryophyte community (Philonotis fontana phase)

	% Cover							Mean Cover	Relative Constancy
Plot no.	11	69	38	59	58	65	41		
Herbs:									
Aster occidentalis					.3			+	14
Bidens cernua	.1							+	14
Dodecatheon alpinum	11.9	20.5	18.3	16.3	29.4	13.5	79.4	27.1	100
Drosera anglica	+							+	14
Epilobium alpinum var. gracillimum	.8	.6	.2	3.1		.4	8.4	1.9	86
Hypericum anagalloides	3.5		4.6					1.2	29
Mimulus primuloides		2.5	1.0	.8		1.9	7.6	2.0	71
Oxypolis occidentalis	+							+	14
Polygonum bistortoides	3.4	22.2	+	16.3	33.9		7.5	11.9	86
Ranunculus gormanii				.8	.6	.4	.1	.3	57
Spiranthes romanzoffiana	.4							+	14
Mosses and liverworts:									
Aulacomnium palustre	1.3	+	+	1.9	+			.5	71
Brachythecium frigidum	.4							+	14
Brachythecium sp.					.3			+	14
Bryum pallescens	1.4					1.1	4.5	1.0	43
Chiloscyphus polyanthos					.5			+	14
Drepanocladus aduncus	.6				8.0		.8	1.3	43
Drepanocladus exannulatus		8.5	11.0	11.5	44.3	6.8	5.3	12.5	86
Meesia triquetra	.4		6.9	.4		.8		1.2	57

Eleocharis pauciflora/bryophyte community (*Philonotis fontana* phase)

	% Cover								
Plot no.	11	69	38	59	58	65	41	Mean Cover	Relative Constancy
Species									
Philonotis fontana	63.3	87.6	8.6	88.4	50.6	82.5	32.5	59.1	100
Sphagnum subsecundum			1.5		+	.3	.8	.4	57

Total no. of microplots = 58
Average species richness/microplot = 9.24

Carex sitchensis community (*Hypericum anagalloides* phase)

	% Cover							
Plot no.	54	45	22	15	6	1	Mean Cover	Relative Constancy
Species								
Shrubs:								
Alnus incana				1.5			.3	17
Vaccinium occidentale		7.5					1.3	17
Graminoids:								
Agrostis idahoensis						.2	+	17
Agrostis thurberiana	3.8		1.0		2.0		1.1	50
Carex disperma				.3			+	17
Carex jonesii			10.0			1.1	1.9	33
Carex limosa	.8						.1	17
Carex sitchensis	99.4	80.0	70.0	85.0	77.5	71.3	80.5	100
Deschampsia atropurpurea				1.5		3.4	.3	33
Deschampsia cespitosa			10.0				1.7	17
Eleocharis pauciflora		15.0	5.0		1.0		3.5	50
Equisetum arvense			2.0	7.5			1.6	33
Juncus ensifolius					.2	+	+	17
Juncus orthophyllus		14.0					2.3	17
Muhlenbergia filiformis			.3		.2		+	33
Herbs:								
Aster occidentalis						1.1	.2	17

Carex sitchensis community (*Hypericum anagalloides* phase)

Plot no.	% Cover 54	45	22	15	6	1	Mean Cover	Relative Constancy
Species								
Herbs:								
Caltha biflora				1.5			.3	17
Dodecatheon alpinum		15.0	6.0		6.0		4.5	50
Epilobium alpinum var. *gracillimum*		.3	1.0		1.0		.4	50
Epilobium glandulosum				.3		1.1	.2	33
Epilobium palustre						1.6	.3	17
Galium trifidum						.1	+	17
Hypericum anagalloides		7.5	45.8		5.0	3.0	10.2	67
Mimulus primuloides		1.5					.3	17
Montia chamissoi						.2	+	17
Oxypolis occidentalis			5.0	7.5	10.0	6.7	4.9	67
Polygonum bistortoides		.3	.2		1.2		.28	50
Ranunculus gormannii		15.0		.3			2.6	33
Stellaria longifolia						.8	.1	17
Stellaria simcoei	3.8						.6	17
Viola adunca			.3				+	17
Viola sp.					6.0	2.5	1.4	33

*Impossible to determine if *V. macloskeyi* or *V. glabella*, both of which have been seen in this community, since flowers were gone at the time of sampling.

Carex sitchensis community (*Hypericum anagalloides* phase)

Plot no.	54	45	22	15	6	1	Mean Cover	Relative Constancy
	% Cover							
Mosses:								
Amblystegium serpens		1.5	7.0		.2	.9	1.6	67
Aulacomnium palustre			1.2				.2	17
Brachythecium sp.			.2	.3			+	33
Drepanocladus aduncus		.3			.3	1.4	.3	50
Drepanocladus exannulatus	67.0		6.0	18.8	1.2		15.5	67
Marchantia polymorpha					.2	+	+	17
Meesia triquetra			1.0		.2	1.3	.4	50
Philonotis fontana		7.5	.3		1.2	1.3	1.7	67
Sphagnum squarrosum					.2		+	17

Total no. of microplots = 184
Average species richness/microplot = 6.57

Carex sitchensis community (*Aster occidentalis* phase)

	% Cover								
Plot no.	4	26	57	3	28	30	33	Mean Cover	Relative Constancy
Species									
Trees:									
Pinus contorta		1.4						.2	14
Shrubs:									
Kalmia microphylla		+						+	14
Vaccinium occidentale			19.3		7.5		6.5	4.8	43
Graminoids:									
Agrostis thurberiana	2.0							.3	14
Carex jonesii		1.6	20.8					3.2	29
Carex rostrata	10.0							1.5	14
Carex sitchensis	65.8	54.8	73.8	96.9	48.0	80.0	95.4	73.5	100
Deschampsia atropurpurea				.7			6.3	1.0	29
Deschampsia cespitosa	10.0	38.9	18.5		34.0	3.0		15.0	71
Eleocharis pauciflora		.3				3.0		.4	29
Equisetum arvense		+	2.5					.4	29
Muhlenbergia filiformis	13.5	12.8		.1				3.8	43
Herbs:									
Aster occidentalis	33.3	30.1	8.0	.8	14.1	25.0	2.5	16.3	100

Carex sitchensis community (*Aster occidentalis* phase)

	% Cover								
Plot no.	4	26	57	3	28	30	33	Mean Cover	Relative Constancy
Caltha biflora							16.5	2.4	14
Dodecatheon alpinum		1.7	3.8					.7	29
Drosera anglica						3.0		.4	14
Epilobium glandulosum			.2	.7				+	29
Galium trifidum	.2	2.2		.7				.4	43
Hypericum anagalloides	12.5	1.4		.1				2.0	43
Mimulus guttatus				.1				+	14
Oxypolis occidentalis	1.0							.2	14
Polygonum bistortoides			3.0					.4	14
Ranunculus gormanii	.2		3.5					.5	29
Stellaria longifolia	6.0	.8		1.1				1.1	43
Viola adunca		16.9			37.1	3.0		8.1	43
Viola sp.	2.0							.3	14
Mosses and liverworts:									
Amblystegium serpens	.2	.3	.5					.2	43
Aulacomnium palustre	12.5		.5	9.6				3.3	43
Brachythecium sp.			+					+	14
Bryum pallescens	5.2							.7	14
Bryum sp.		.3			3.6			.6	29
Drepanocladus aduncus	.2		30.8					4.4	29
Marchantia polymorpha		1.7		+				.3	29
Meesia triquetra	.2	1.4						.3	29

Carex sitchensis community (*Aster occidentalis* phase)

Plot no.	% Cover 4	26	57	3	28	30	33	Mean Cover	Relative Constancy
Philonotis fontana			+					+	14
Polytrichum juniperinum		+						+	14

Total no. of microplots = 54
Average species richness/microplot = 4.48

Vaccinium occidentale/*Carex sitchensis* community (*Eleocharis pauciflora*/bryophyte phase)

	% Cover					
Plot no.	47	64	62	14	Mean Cover	Relative Constancy
Species						
Trees:						
conifer (dead)	9.4				2.4	25
Shrubs:						
Vaccinium occidentale	20.6	26.3	55.0	40.8	35.7	100
Graminoids:						
Agrostis thurberiana			.6	1.2	.5	50
Carex disperma				2.0	.5	25
Carex rostrata				6.0	1.5	25
Carex simulata			3.0		.8	25
Carex sitchensis	15.0	56.3	38.5	30.0	35.0	100
Deschampsia cespitosa		11.3	24.0		8.8	50
Eleocharis pauciflora	12.0	1.5	31.1	15.0	14.9	100
Equisetum arvense	20.6	1.0		3.0	6.2	75
Juncus orthophyllus	.8		6.6		1.9	50
Muhlenbergia filiformis	.8		18.5		4.8	50
Herbs:						
Aster occidentalis				1.0	.3	25

Vaccinium occidentale/*Carex sitchensis* community (*Eleocharis pauciflora*/bryophyte phase)

Plot no.	% Cover 47	 64	 62	 14	Mean Cover	Relative Constancy
Caltha biflora				33.4	8.4	25
Dodecatheon alpinum	3.3	7.5	9.6	5.0	6.4	100
Epilobium alpinum var. *gracillimum*	1.5	.8	1.4		.9	75
Habenaria dilatata				1.0	.3	25
Hypericum anagalloides	.8			.3	.3	50
Mimulus primuloides			.2		+	25
Pedicularis groenlandica				22.5	5.6	25
Polygonum bistortoides	.1		.7	6.2	1.8	75
Ranunculus gormanii				18.5	4.6	25
Mosses and liverworts:						
Amblystegium serpens		8.3	.6	5.0	3.5	75
Aulacomnium palustre	.8	.1	.7		.4	75
Bryum pallescens				.2	+	25
Chiloscyphus polyanthos	.8				.2	25
Drepanocladus aduncus	.8				.2	25
Drepanocladus exannulatus	4.0	21.9	40.0		16.5	75
Lophocolia heterophylla				.2	+	25
Meesia triquetra	32.0	.1	10.5		10.7	75
Philonotis fontana	1.5		12.2	2.0	3.9	75
Sphagnum subsecundum	6.0		.7	56.7	15.9	75

Total no. of microplots = 16
Average species richness/microplot = 10.75

Vaccinium occidentale/Aulacomnium palustre community

Plot No.	% Cover 24	20	51	17	19	5	9	42	Mean Cover	Relative Constancy
Species										
Trees:										
conifer (dead)								1.1	.1	13
Pinus contorta (seedling)				+					+	13
Tsuga mertensiana								6.1	.8	13
Shrubs:										
Kalmia microphylla	50.0	46.3	16.7	4.7	3.3				15.1	63
Lonicera caerulea						1.9			.2	13
Spiraea douglasii				5.4					.7	13
Vaccinium occidentale		38.3	36.3	67.1	88.3	60.0	62.5	67.8	52.5	88
Graminoids:										
Agrostis idahoensis		+	.7						.1	25
Agrostis thurberiana		1.0	1.0	.1	.9	.9	3.0		.9	75
Carex disperma				6.2	.4	.4		1.3	1.0	50
Carex limosa		.5		.4					.1	25
Carex muricata					1.9	1.9			.5	25
Carex rostrata						4.1			.5	13
Carex sitchensis	38.8	28.0	26.3	22.9	31.3	19.1		32.7	24.9	88
Deschampsia atropurpurea				.4					+	13

Vaccinium occidentale/Aulacomnium palustre community

	% Cover									
Plot No.	24	20	51	17	19	5	9	42	Mean Cover	Relative Constancy
Deschampsia cespitosa	9.0								1.1	13
Eleocharis pauciflora					3.4	16.9	15.0	3.0	4.8	50
Equisetum arvense		10.1	2.5	4.9				1.3	2.4	50
Juncus orthophyllus				5.1					.6	13
Luzula campestris				+					+	13
Muhlenbergia filiformis	18.8		2.5	+			.5		2.7	50
Herbs:										
Aster occidentalis	15.0								1.9	13
Caltha biflora				5.8					.7	13
Clintonia uniflora				.4					+	13
Drosera anglica			+						+	13
Drosera rotundifolia			1.1			2.8			.5	25
Dodecatheon alpinum	18.8	13.4	3.7	5.8		7.9	3.0		6.6	75
Epilobium alpinum var. *gracillimum*	1.5	.5	3.0	+	1.2	1.2			.9	75
Hypericum anagalloides	7.5	5.0	4.0	.5	.3	1.9			2.4	75
Mimulus primuloides			.6	.4					.1	25
Pedicularis groenlandica			2.6	7.9					1.3	25
Polygonum bistortoides			+	3.0					.4	25
Ranunculus gormanii				2.6					.3	13
Sphenosciadium capitellatum				5.4					.7	13
Tofieldia glutinosa			2.1	.9			15.0		2.2	38

Vaccinium occidentale/Aulacomnium palustre community

	% Cover									
Plot No.	24	20	51	17	19	5	9	42	Mean Cover	Relative Constancy
Viola adunca	26.3								3.3	13
Viola sp.						+			+	13
Mosses and liverworts:										
Amblystegium serpens	20.2		+	.5				1.3	2.8	50
Aulacomnium palustre		55.8	81.7	6.3	8.4	18.0	85.0	34.0	36.2	88
Brachythecium sp.				.4	.3				+	25
Bryum pallescens	.3			2.2		.4		1.1	.5	50
Drepanocladus exannulatus		2.7		.4		4.8		.2	1.0	50
Helodium blandowii			1.2					8.2	1.2	25
Lophocolea heterophylla		.5			.3				.1	13
Marchantia polymorpha					+	+			+	25
Meesia triquetra		16.8		5.1	+	2.3			3.0	50
Philonotis fontana	.3			12.9			3.0		2.0	38
Plagiothecium denticulatum								.2	+	13
Sphagnum squarrosum								7.0	.9	13
Sphagnum subsecundum		4.0	9.8	2.1	.3			.2	2.1	63

Total no. of microplots = 51
Average species richness/microplot = 8.41

Vaccinium occidentale/Carex sitchensis community

	% Cover											
Plot no.	39	25	66	31	2	37	46	29	34	32	Mean Cover	Relative Constancy
Species												
Trees:												
conifer (dead)	1.3		10.7		7.6		7.6				2.7	40
Picea engelmannii	.4				3.4		3.4				.7	30
Pinus contorta	9.8	5.0		.3							1.5	30
Shrubs:												
Kalmia microphylla		1.0									.1	10
Lonicera caerulea	1.1		.3	2.6							.4	30
Spiraea douglasii				.2							+	10
Vaccinium occidentale	64.9	54.2	63.0	85.0	73.8	92.0	73.8	97.5	37.5	75.7	71.8	100
Graminoids:												
Agrostis idahoensis							+				+	10
Agrostis thurberiana	.2		3.8	2.3	.4		.4		15.0		2.2	60
Carex disperma			19.4		11.2	3.9	11.2				4.6	40
Carex muricata			1.5								.2	10
Carex sitchensis	44.8		40.0	24.3	26.3	24.8	24.2	15.0	62.5	53.6	31.6	90
Deschampsia atropurpurea					1.5						.2	10
Deschampsia cespitosa	1.1	26.0	9.4	4.8		3.7	1.3				4.6	60
Eleocharis pauciflora	.2	1.0	.3	.8		.4	4.9				.8	60

Vaccinium occidentale/Carex sitchensis community

	% Cover											
Plot no.	39	25	66	31	2	37	46	29	34	32	Mean Cover	Relative Constancy
Equisetum arvense	1.1				.2		.2				.2	30
Juncus orthophyllus					1.3	1.4	1.3				.4	30
Muhlenbergia filiformis		13.7	1.3	.1							1.5	30
Herbs:												
Aconitum columbianum var. howellii									3.0		.3	10
Aster occidentalis		17.5	2.5	8.3	1.5	2.9	2.9				3.6	60
Caltha biflora				.9					85.0	2.1	8.8	30
Dodecatheon alpinum	.2	11.0				+	.3				1.2	40
Drosera rotundifolia		3.0									.3	10
Epilobium alpinum var. gracillimum					.7		.7				.1	20
Hypericum anagalloides			1.3			1.0					.2	20
Mimulus moschatus							+				+	10
Polygonum bistortoides	.2						+				+	20
Potentilla breweri				.8							+	10
Ranunculus gormanii			3.1	.8	.7		.7		3.0		.8	50
Senecio triangularis			.3				1.3				.2	20
Sphenosciadium capitellatum						2.5					.3	10
Tofieldia glutinosa					.1		.1				+	20
Vicia americana				.3							+	10
Viola adunca		6.0		2.3							.8	20
Viola sp.					+						+	10
Mosses and Liverworts:												
Amblystegium serpens	5.3		14.8	1.5	1.0	.5	1.0			+	2.4	60

Vaccinium occidentale/*Carex sitchensis* community

	% Cover										Mean	Relative
Plot no.	39	25	66	31	2	37	46	29	34	32	Cover	Constancy
Aulacomnium palustre	3.4	5.0		15.1		6.3	2.7				3.3	50
Brachythecium sp.			+			.2	.3				+	30
Chiloscyphus polyanthos										.4	+	10
Drepanocladus aduncus					.1		.1				+	20
Drepanocladus exannulatus			2.5				.7				.3	20
lichen				+							+	10
Lophocolia heterophylla	+										+	10
Marchantia polymorpha		6.0									.6	10
Philonotis fontana			3.9			1.0	.7				.6	30
Plagiothecium denticulatum							+				+	10
Sphagnum squarrosum				.6							+	10
Sphagnum subsecundum	+		1.3								.1	20

Total no. of microplots = 91
Average species richness/microplot = 4.83

Alnus incana/*Brachythecium* sp. community

Plot no.	% Cover 44	16	36	Mean Cover	Relative Constancy
Species					
Trees:					
Picea engelmannii		21.7	36.0	19.2	67
Pinus monticola			22.9	7.6	33
Shrubs:					
Alnus incana	97.5	33.7	25.4	52.2	100
Spiraea douglasii		41.4		13.8	33
Vaccinium occidentale		22.2	5.0	9.1	67
Vaccinium scoparium		.3		.1	33
Graminoids:					
Carex disperma		25.4	35.4	20.3	67
Carex sitchensis	33.5	12.8	29.6	25.3	100
Deschampsia atropurpurea		4.4		1.5	33
Equisetum arvense	6.0	5.3		3.8	67
Glyceria elegans			2.5	.8	33
Herbs:					
Aconitum columbianum var. *howellii*		9.2		3.1	33
Aster occidentalis	1.0	8.4	25.4	11.6	100

Alnus incana/*Brachythecium* sp. community

	% Cover			Mean	Relative
Plot no.	44	16	36	Cover	Constancy
Caltha biflora	14.5			4.8	33
Ligusticum grayii		.4		.1	33
Mitella pentandra	.4			.1	33
Pyrola asarifolia		.7		.2	33
Pyrola minor			2.6	.8	33
Rubus lasiococcus			13.8	4.6	33
Senecio triangularis		6.7		2.2	33
Streptopus roseus		2.4		.8	33
Mosses and liverworts:					
Amblystegium serpens	12.5	.4		4.3	33
Aulacomnium palustre		2.7		.9	33
Brachythecium sp.	1.0	.4	43.8	15.1	100
Bryum weigelii			2.5	.8	33
Chiloscyphus polyanthos			3.1	1.0	33
Mnium punctatum			6.3	2.1	33
Mnium rugicum			6.8	2.3	33
Philonotis fontana			3.1	1.0	33
Plagiothecium denticulatum		.1		+	33

Total no. of microplots = 18
Average species richness/microplot = 7.9

Salix barclayi community	% Cover
Plot no.	56
Species	
Shrubs:	
Salix barclayi	83.2
Graminoids:	
Carex disperma	.2
Carex sitchensis	12.9
Equisetum arvense	10.1
Luzula campestris	.2
Herbs:	
Aster occidentalis	1.0
Dodecatheon alpinum	1.0
Mimulus moschatus	1.0
Mitella pentandra	2.7
Senecio triangularis	1.3
Mosses and liverworts:	
Amblystegium serpens	3.1
Aulacomnium palustre	.2
Brachythecium sp.	9.3
Bryum weigelii	4.9
Chiloscyphus polyanthus	6.5
Drepanocladus aduncus	14.6
Mnium punctatum	11.0

Total no. of microplots = 15
Species richness = 5.93

Vaccinium scoparium/*Clintonia uniflora* community

	% Cover					
Plot no.	67	35	55	43	Mean Cover	Relative Constancy
Species						
Trees:						
conifer (dead)	2.5		40.8		10.8	50
Pinus contorta var. *murrayana*	87.5			7.5	23.8	50
Tsuga mertensiana	+			67.6	16.9	50
Shrubs:						
Spiraea densiflora		7.5			1.9	25
Vaccinium occidentale	42.1	97.5		3.8	35.9	75
Vaccinium scoparium		42.5	37.5	27.6	26.9	75
Graminoids:						
Carex disperma	53.8				13.5	25
Carex sitchensis	42.1	7.5	53.3	19.4	30.6	100
Eleocharis pauciflora				3.8	1.0	25
Equisetum arvense	2.5				.6	25
Mosses and liverworts						
Aulacomnium palustre	2.5		5.0	21.4	7.2	75
Brachythecium sp.			5.0		1.3	25
Bryum weigelii			1.0		.3	25
Chiloscyphus polyanthos			5.0		1.3	25

Vaccinium scoparium/*Clintonia uniflora* community

	% Cover				Mean Cover	Relative Constancy
Plot no.	67	35	55	43		
Species						
Dicranum pallidisetum			28.3	43.8	18.0	50
Polytrichum juniperinum				25.1	6.3	25

Appendix B. pH data, obtained by various methods, for different communities, at different times during the summer season.

		pH			
		Kelway soil tester	Soil pH testing kit	"Panpeha" colorimetric paper	Overall pH range
Community types	Sampling dates:	8/13	8/13	9/15	
Carex rostrata reedswamp		6.4	6.2	6.0 - 6.5	6.0 - 6.5
Eleocharis pauciflora - *Carex limosa* community				6.0	6.0 - 6.7
Eleocharis pauciflora community (*Philonotis fontana* phase)	#1	5.7	5.4 - 5.6	6.5	5.4 - 7.1
	#2			6.5	6.5 - 6.9
Eleocharis pauciflora community (*Meesia triquetra* phase)	#1	6.2	6.4	6.5	6.2 - 6.9
	#2			6.0	6.0 - 6.8
Carex sitchensis community (*Hypericum anagalloides* phase)	#1	6.2	6.0 - 6.2	6.0 - 6.5	6.0 - 6.75
	#2	6.3	6.0	6.0	6.0 - 6.8
Carex sitchensis community (*Aster occidentalis* phase)	#1	6.4	6.0 - 6.2	6.0	6.0 - 6.4
	#2	6.1 - 6.3	5.8	6.0	5.8 - 6.4
Vaccinium occidentale/*Aulacomnium palustre* thicket		5.5	5.6	6.0	5.5 - 6.0
Vaccinium occidentale/*Carex sitchensis* thicket	#1	5.8	5.6 - 5.8	6.0	5.8 - 6.6
	#2			6.0 - 6.5	6.0 - 6.6
Alnus incana/*Brachythecium* carr		5.95 - 6.0	5.8 - 6.0	6.0 - 6.5	5.8 - 6.6
Salix barclayi carr				6.0 - 6.5	6.0 - 6.5

APPENDIX C

DESCRIPTIONS AND SPECIES LISTS OF OTHER CASCADE MIRES

A brief description of five other mires, with legal description, and brief physiographic/hydrologic overview, followed by a species list for the area, overview of the communities present, and a brief characterization of each.

DESCHUTES COUNTY: Little Cultus Lake Bog Complex, Bog #1

Location: NE 1/4 Sec. 33, T. 20S., R. 7E.

Elevation: 4820 ft. (1470 m)

Date of visit: August 27, 1978

Physiography/Hydrology: a slightly sloping area fed by springs, with rivulets coursing through. Appears to be in a depression relative to the surrounding land.

Species list:

Trees
Abies sp.
Picea engelmannii
and seedlings
Pinus contorta

Shrubs
Betula glandulosa
var. *glandulosa*
Lonicera caerulea
Kalmia microphylla
Ribes lacustre
Salix geyeriana
Salix pseudocordata (?)
Vaccinium occidentale

Graminoids
Carex capitata
Carex cusickii
Carex jonesii
Carex limosa
Carex rostrata
Carex sitchensis
Deschampsia caespitosa
Eleocharis pauciflora
Equisetum arvense
Eriophorum gracile
Juncus ensifolius
Juncus orthophyllus
Muhlenbergia filiformis
Scheuzeria palustris

Herbs
Aster occidentalis
Caltha biflora
Castilleja miniata
Dodecatheon alpinum
Epilobium alpinum
var. *gracillimum*
Habenaria dilatata
Linnaea borealis
Menyanthes trifoliata
Mimulus guttatus
Mimulus primuloides
Oxypolis occidentalis (?)
Pedicularis groenlandica
Polemonium occidentale
Polygonum bistortoides
Potentilla palustris
Saxifraga oregana
Senecio triangularis
Sphenosciadium
capitellatum
Spiranthes romanzoffiana
Tofieldia glutinosa
Utricularia intermedia

COMMUNITIES:

A. *Eleocharis pauciflora*/*Carex limosa* -- no bryophytes, standing water
B. *Eleocharis pauciflora* -- bryophytes (*Meesia triquetra*).
C. *Eleocharis pauciflora* -- bryophytes (*Drepanocladus vernicosus*)
D. *Eleocharis pauciflora* -- bryophytes (*Philonotis fontana*)
E. forbs/*Tomenthypnum nitens*
F. *Carex sitchensis* (wet)
G. low *Vaccinium occidentale*/*Aulacomnium palustre* or *Sphagnum* sp.
H. *Vaccinium occidentale*/*Betula glandulosa*/*Pinus contorta*
I. *Betula glandulosa* carrs
J. *Salix geyeriana* carrs

A. *Eleocharis pauciflora*/*Carex limosa* -- no bryophytes, standing water

In low, wet areas, a typical flark community of *Eleocharis pauciflora*, *Menyanthes trifoliata*, *Carex limosa*, *Utricularia intermedia*, and *Carex sitchensis* is found. This community does not occupy large expanses.

Small, very wet patches have *Carex rostrata*, *Mimulus guttatus*, and *Saxifraga oregana*.

B. *Eleocharis pauciflora* -- bryophytes (*Meesia triquetra*)

A more or less continuous moss mat forms the ground layer of this community, composed predominantly of *Meesia triquetra*, with *Bryum pallescens*, *Drepanocladus exannulatus*, *Sphagnum subsecundum*, and small amounts of *Philonotis* mixed in. The herbaceous layer is composed of small forbs and graminoids, the basic composition being fairly comparable to similar *Eleocharis*/*Meesia* communities at Sphagnum Bog at Crater Lake. The presence of several species not found there, however, is significant -- *Scheuzeria palustris* (listed on the Oregon Provisional List of Rare and Endangered Plants), *Saxifraga oregana*, and *Potentilla palustris*, which at Sphagnum Bog is restricted to the deeper pools and adjacent areas of shallow standing water.

Other species present in this community: *Carex limosa*, *Carex capitata*, *Menyanthes trifoliata*, *Drosera anglica*, *Mimulus primuloides*, *Tofieldia glutinosa* (uncommon), *Pedicularis groenlandica*, *Epilobium alpinum* var. *gracillimum*, *Carex rostrata*, and *Juncus ensifolius*.

This community, although fairly broad, seems to be limited to the area at the upper end, above the small stream.

C. *Eleocharis pauciflora* -- bryophytes (*Drepanocladus vernicosus*)

On the other side of the stream, the composition of the moss mat changes to almost complete dominance by *Drepanocladus vernicosus*, although small amounts of *Meesia triquetra* are mixed in. The water is at the surface here, but not standing. Otherwise, the composition is much the same. *Tofieldia* grows much more densely here, and *Spiranthes romanzoffiana* and small *Vaccinium occidentale* individuals are found occasionally, as well as *Kalmia microphylla*, *Muhlenbergia filiformis*, and seedlings of *Picea engelmannii*.

This community type is quite extensive and continuous.

D. *Eleocharis pauciflora* -- bryophytes (*Philonotis fontana*).

On slight slopes near the edges of the mire, there are patches of communities rather similar to the *Eleocharis pauciflora*/*Philonotis fontana* type at Sphagnum Bog at Crater Lake, with abundant *Muhlenbergia filiformis*.

E. forbs/*Tomenthypnum nitens*

On another slight slope near the edge, the moss mat is completely dominated by *Tomenthypnum nitens*. *Dodecatheon jeffreyi*, a tall *Carex* sp. (perhaps *cusickii*), *Tofieldia glutinosa*, *Spiranthes romanzoffiana*, *Polygonum bistortoides*, *Polemonium occidentale*, *Saxifraga oregana*, and *Epilobium alpinum* are all prominent members of this community, which has no direct counterpart at Sphagnum Bog.

F. *Carex sitchensis* (wet)

In small rivulets of water running through the mire, *Carex sitchensis* dominates. *Fontinalis* and *Drepanocladus* are found floating in deeper parts of the streams, and *Menyanthes trifoliata*. This probably corresponds to the wet *Carex sitchensis* communities at Sphagnum Bog, which were also associated with streams.

G. low *Vaccinium occidentale*/*Aulacomnium palustre* or *Sphagnum* sp.

Hummocks of *Tomenthypnum nitens* and *Aulacomnium palustre*, or of *Sphagnum subsecundum*, have low shrubs, *Vaccinium occidentale*, *Kalmia microphylla*, or *Salix pseudocordata* growing on them with small numbers of *Pinus contorta* individuals. *Juncus orthophyllus* and *Eriophorum gracile* also occur in this community.

H. *Vaccinium occidentale*/*Betula glandulosa*/*Pinus contorta*

Large shrubby areas are dominated by *Betula glandulosa*, *Lonicera caerulea*, and *Vaccinium occidentale*, and exhibit some invasion by *Pinus contorta* and *Picea engelmannii*. The field layer includes *Saxifraga oregana*, *Carex cusickii*, *Habenaria dilatata*, *Polygonum bistortoides*, *Aster occidentalis*, *Deschampsia caespitosa*, *Sphenosciadium capitellatum*, *Spiranthes romanzoffianum*, and *Caltha biflora*. In general, this community is similar to the *Vaccinium occidentale*/*Aster occidentalis* community at Sphagnum Bog, with some of the same characteristic species. However, no *Betula* was present at Sphagnum Bog.

Prominent mosses are *Meesia triquetra*, *Aulacomnium palustre*, and *Tomenthypnum nitens*, with small amounts of *Drepanocladus exannulatus* and *Sphagnum subsecundum*. Near the edge, this community varies slightly to include *Salix pseudocordata*, and a different group of mosses: *Helodium blandowii*, *Mnium rugicum*, *Brachythecium* sp., and *Philonotis fontana*; and a slightly different group of forbs, including edge species such as *Senecio triangularis*, *Equisetum arvense*, *Linnaea borealis*, and *Castilleja miniata*.

As at Sphagnum Bog, it is this community that shows the prominent invasion by conifers.

I. *Betula glandulosa* carrs

At the far, lower end of this mire, is a dense *Betula glandulosa* carr with *Tomenthypnum nitens*, and little else. There is no direct counterpart to this at Sphagnum Bog, but there is at Gold Lake Bog.

J. *Salix geyeriana* carrs

Salix geyeriana forms large carrs at the far, low end, also.

LANE COUNTY: Gold Lake Bog

Location: S ½ Sec. 20, N ½ Sec. 29, T. 22S., R. 6E.

Elevation: 1463-1646 m

Date of visit: August 26, 1978

Physiography/Hydrology: A flat basin at the head of Gold Lake, between two forested mountain slopes, including three major streams and three small ponds. Underlain by olivine basalt and basaltic andesite that is covered by Mazama ash and pumice deposits (Franklin et al., 1972).

Species list:

Trees
- *Picea engelmannii*
- *Pinus contorta*
- *Tsuga mertensiana*

Shrubs
- *Betula glandulosa* var. *glandulosa*
- *Kalmia microphylla*
- *Lonicera caerulea*
- *Salix geyeriana* (unverified)
- *Spiraea douglasii*
- *Vaccinium occidentale*
- *Vaccinium ovalifolium*

Graminoids
- *Agrostis (thurberiana* or *idahoensis)*
- *Carex limosa*
- *Carex rostrata*
- *Carex simulata*
- *Carex sitchensis*
- *Eleocharis pauciflora*
- *Equisetum arvense*
- *Eriophorum* sp.
- *Juncus balticus*
- *Juncus orthophyllus*
- *Puccinellia pauciflora*

Herbs
- *Aconitum columbianum* var. *howellii*
- *Aster occidentalis*
- *Caltha biflora*
- *Dodecatheon jeffreyi*
- *Drosera anglica*
- *Drosera rotundifolia*
- *Epilobium alpinum* var. *gracillimum*
- *Galium trifidum*
- *Hypericum anagalloides*
- *Hypericum formosum*
- *Ligusticum grayii*
- *Menyanthes trifoliata*
- *Mimulus guttatus*
- *Mimulus primuloides*
- *Muhlenbergia filiformis*
- *Pedicularis groenlandica*
- *Polygonum bistortoides*
- *Potamogeton natans*
- *Pyrola asarifolia*
- *Ranunculus aquatilis*
- *Ranunculus gormanii*
- *Saxifraga oregana*
- *Senecio triangularis*
- *Sphenosciadium capitellatum*
- *Tofieldia glutinosa*
- *Utricularia intermedia*
- *Viola adunca*

COMMUNITIES:

A. *Carex rostrata*/*Menyanthes trifoliata* reedswamps
B. *Eleocharis pauciflora*--*Carex limosa* community
C. *Eleocharis pauciflora*/bryophyte community
D. Wet sedge--rush community
E. *Carex sitchensis* (?) fen
F. *Betula*--*Vaccinium*/bryophyte hummocks
G. *Vaccinium occidentale*--*Eleocharis*/bryophyte transitional community
H. *Vaccinium occidentale*/*Carex sitchensis* community with invading conifers
I. *Salix geyeriana* carr and *Betula glandulosa* carr
J. Forest edge mossy seep

A. *Carex rostrata*/*Menyanthes trifoliata* reedswamps

Two examples of Carex rostrata reedswamps were observed. The first occurs as a band of vegetation several feet out from the shore of Gold Lake, in standing water, dominated by very robust *Carex rostrata*, with patches of *Menyanthes trifoliata* and *Nuphar polysepalum*. There is no moss mat present. Occasionally, patches of *Potentilla palustris* are found in the shallower water nearer the shore.

Reedswamp vegetation also dominates the large, shallow pond in the area where water averages about two feet in depth. *Carex rostrata* and *Potamogeton natans* dominate in the standing water, and *Menyanthes trifoliata* and *Glyceria borealis* are found in shallower water near the edge, with small amounts of *Drepanocladus exannulatus*, *Utricularia intermedia*, and *Mimulus primuloides* bordering the pond. *Ranunculus aquatilis* and *Puccinellia pauciflora* grow in the broad, shallow flowing stream, Salt Creek, feeding into the pond.

B. *Eleocharis pauciflora*--*Carex limosa* community

In certain small depressions within community C, standing water 5-6 cm deep occurred. Here, mosses generally existed only along the edges: *Sphagnum subsecundum*, some submersed and some reaching up onto the logs, and *Drepanocladus vernicosus* at the edges. The dominant species was *Eleocharis pauciflora* with an abundance of floating *Utricularia intermedia*. Some *Drosera anglica* was also present where the substrate was elevated above the standing water.

C. *Eleocharis pauciflora* community (comparable to *Meesia triquetra* phase.

Large expanses at Gold Lake Bog are dominated by a light, golden-green carpet of *Drepanocladus vernicosus*, with 90-100%

cover, and smaller amounts of *Meesia triquetra* mixed in; and *Tomenthypnum nitens* dominated on an old log. *Bryum pallescens* also occurred in small mats, with small amounts of *Chiloscyphus polyanthus* or *Meesia triquetra* mixed in. Herbaceous species, dominated by *Eleocharis pauciflora*, with 25% cover, are rich and prominent in this community, but small islands of *Vaccinium occidentale* and *Betula glandulosa* are frequent, and *Kalmia microphylla* is scattered in the area. Other typical herbaceous species include *Ranunculus gormanii*, *Hypericum anagalloides*, *Tofieldia glutinosa*, *Drosera anglica* and *Drosera rotundifolia*, *Saxifraga oregana*, *Agrostis* sp., *Epilobium alpinum* var. *gracillimum*, *Mimulus primuloides*, *Eriophorum* sp., *Polygonum bistortoides*, *Carex rostrata*, *Utricularia intermedia*, and *Carex limosa*.

D. Wet sedge--rush community

Between the wet communities bordering the pond and the large area of conifer invasion, is a wet sedge--rush marsh, dominated by *Carex simulata* (species not verified) and *Juncus balticus*. Occasional patches of *Vaccinium* are seen, but there is no moss mat present.

E. *Carex sitchensis* fen

Northeast of the pond is a large, drier sedge fen, dominated by a dense growth of a robust sedge, probably *Carex sitchensis* or *Carex aquatilis*. Few other species are present. *Galium trifidum* occurs sporadically.

F. *Betula*--*Vaccinium*/bryophyte hummocks

Shrubby hummocks occur within the *Eleocharis*/bryophyte community, or form continuous, large patches. Generally, they appear to be higher than community C, and dominated by different mosses: *Sphagnum capillaceum*, *Aulacomnium palustre*, or *Tomenthypnum nitens*. Together, the bryophytes form a dense mat of 75-100% cover below the shrubs: *Vaccinium occidentale* and *Betula glandulosa*, or *Kalmia microphylla*, *Lonicera caerulea*, *Betula glandulosa* and small amounts of *Vaccinium* in other areas.

G. *Vaccinium occidentale*--*Eleocharis*/bryophyte transitional community

Bordering the edge of the pond are low, wet areas dominated by *Eleocharis pauciflora* and dwarf *Vaccinium occidentale*, with abundant *Mimulus primuloides*, *Carex* sp., *Muhlenbergia filiformis*, *Spiranthes romanzoffiana*, *Viola adunca*, and *Drepanocladus* in drier spots.

H. *Vaccinium occidentale*/*Carex sitchensis* community, with invading conifers

In some of the shrubby islands described in F, there has been invasion by *Pinus contorta*. In these islands, *Vaccinium occidentale* had a cover of 75-95%, *Carex sitchensis* 5%, *Lonicera caerulea* 10%, and there were scattered individuals of *Kalmia microphylla* and *Betula glandulosa*. Farther back from the lake edge were large shrubby areas with invasion by conifers presently approximately 150 ft in height, mostly *Pinus contorta*, but some *Picea engelmannii* also.

I. *Salix geyeriana* carr and *Betula glandulosa* carr

A large band of fairly large *Betula glandulosa* shrubs (1.5-2 m tall) occurs just back from the shore of Gold Lake. The willow carr is also near the lake's edge, but extends farther around the sides. It is dominated by a different willow species than at Sphagnum Bog in Crater Lake Park, *Salix geyeriana*, but that is of similar size, 1-2 m in height, and providing 30-50 % cover, with dense, decumbent branches. *Vaccinium occidentale*, 1 m tall, forms an almost continuous understory of 75% cover. Other characteristic species are *Betula glandulosa* (1-2 m tall, with 10-25 % cover), *Lonicera caerulea* (less than 1 m, with 10% cover), *Carex sitchensis* (1-5 % cover), *Spiraea douglasii* (1 % cover), *Pinus contorta* (1 % cover) and herbs *Aster occidentalis* and *Sphenosciadum capitellatum*, uncommon in this carr. There is no moss mat, but occasional patches of *Brachythecium frigidum* on the leaf litter or on the bases of the decumbent branches.

J. Forest edge mossy seep

Near the base of the hill above the northern edge of the bog area, the slope is gentle and a number of small springs seep down the slope. The area is dominated by large, but scattered *Abies concolor* and *Picea engelmannii*, with a few young *Tsuga mertensiana* in the understory, and scattered shrubs: *Vaccinium ovalifolium*, *Vaccinium occidentale*, *Betula glandulosa* and scattered *Kalmia microphylla*. The herbaceous layer is lush and diverse, including the following species: *Juncus orthophyllus*, *Tofieldia glutinosa*, *Carex sitchensis*, *Sphenosciadium capitellatum*, *Senecio triangularis*, *Ligusticum grayii*, *Hypericum formosum*, *Dodecatheon jeffreyi*, *Caltha biflora*, *Spiranthes romanzoffiana*, *Mimulus guttatus*, *Saxifraga oregana*, *Pyrola asarifolia*, *Equisetum arvense*, *Pedicularis groenlandica*, and *Aconitum columbianum* var. *howellii*.

KLAMATH COUNTY: Bybee Creek Bog

Location: 0.5 miles east of the western border of Crater Lake Park, at the headwaters of a fork of Bybee Creek.

Elevation: 5100-5200 ft (1554-1585 m)

Date of visit: September 28, 1978

Physiography/Hydrology: The mire lies in a relatively flat bench above a stream, with spring rivulets coursing through it. There are no marginal carr communities. On the whole, this area is less interesting than any of the others, as it contains only very small amounts of the open, moss-dominated communities, and mostly shrub-sedge types, with abundant stunted invading lodgepoles.

Species list:

Trees
- *Pinus contorta*

Shrubs
- *Salix* sp.
- *Spiraea douglasii*
- *Vaccinium occidentale*

Graminoids
- *Agrostis thurberiana*
- *Carex jonesii* (?)
- *Carex muricata*
- *Carex sitchensis*
- *Deschampsia atropurpurea*
- *Eleocharis pauciflora*
- *Equisetum arvense*
- *Juncus orthophyllus*

Herbs
- *Aster occidentalis*
- *Camassia quamash*
- *Castilleja miniata*
- *Dodecatheon alpinum*
- *Epilobium alpinum* var. *gracillimum*
- *Epilobium glandulosum*
- *Geum macrophyllum*
- *Hypericum anagalloides*
- *Hypericum formosum*
- *Madia* sp.
- *Mimulus guttatus*
- *Oxypolis occidentalis*
- *Pedicularis groenlandica*
- *Polemonium occidentale*
- *Polygonum bistortoides*
- *Ranunculus gormanii*
- *Senecio pseudaurea*
- *Senecio triangularis*
- *Solidago* sp.
- *Spiranthes romanzoffiana*
- *Tofieldia glutinosa*

COMMUNITIES:

A. *Eleocharis*/bryophyte communities
B. *Carex sitchensis* fen
C. *Vaccinium occidentale*/*Carex sitchensis* thicket
D. Low willow thicket

Bybee Creek Bog is basically a sedge-shrub fen, with two closely related communities dominating the major part of it: a *Carex sitchensis* fen, and *Vaccinium occidentale*/*Carex sitchensis* thickets, plus much smaller patches of low sedge, moss-carpeted types, and an occasional low willow thicket.

A. *Eleocharis*/bryophyte communities

The moss-dominated communities at Bybee Creek were poorly developed, consisting mostly of small patches as inclusions in other communities, or by the edges of streams or springs. Small patches dominated by *Philonotis fontana* had a mixture of herbs similar to those in the moss communities at Sphagnum Bog, such as *Eleocharis pauciflora*, *Tofieldia glutinosa*, *Carex sitchensis*, *Carex muricata*, *Pedicularis groenlandica*, *Ranunculus gormanii*, and *Polygonum bistortoides*. Three such areas were found, each about 3 X 4 m. *Philonotis* mats were also prominent at the edge of a spring and along them. Small, but dense patches of other mosses or moss associations were found, as *Meesia triquetra*, with *Drepanocladus aduncus* and *Aster occidentalis*; *Campylium polygamum*; *Drepanocladus aduncus*; and *Aulacomnium palustre* with *Carex jonesii*.

B. *Carex sitchensis* fen

In the *Carex sitchensis* community, 80% cover is provided by *Carex sitchensis*, with much smaller patches of *Vaccinium occidentale* included, covering about 10-15% of the area. Herbs typical of such a community are found, including *Juncus orthophyllus*, *Hypericum anagalloides*, *Ranunculus gormanii*, *Epilobium alpinum*, *Dodecatheon alpinum*, *Polygonum bistortoides*, *Senecio pseudaurea*, and *Equisetum arvense*. Small patches of mosses, particularly *Philonotis fontana* or *Drepanocladus aduncus* are scattered in the community.

This community varies in some parts to a more meadow-like association, with *Deschampsia atropurpurea* as a codominant. Other large, slender forbs typically found in such a meadow-like community included *Senecio triangularis*, *Aster occidentalis*, *Madia* sp., and *Solidago* sp.

C. *Vaccinium occidentale*/*Carex sitchensis* thickets

The patches of *Vaccinium occidentale* are quite dense, with small amounts of *Carex sitchensis* emerging through and above the shrubs.

Moss cover is low, consisting mainly of *Amblystegium serpens*. In some areas, the shrub patches become more extensive, forming a whole community.

D. Low willow thicket

A small thicket of a low *Salix* sp. was found in the eastern half, but not occurring as a marginal carr.

Succession: Throughout this mire, scattered, stunted *Pinus contorta* is found, averaging 20-50 ft in height, and providing approximately 5% cover. This whole area is comparable to the higher parts of Sphagnum Bog such as the east side of the upper third of the west arm, where *Vaccinium* and *Carex sitchensis* communities codominate, and *Pinus contorta* invasion is obvious.

KLAMATH COUNTY: Crescent Lake Junction Bog

Location: NW ¼ Sec. 6, T. 24S., R 7E.

Elevation: 4800 ft (1469 m)

Date of visit: August 27, 1978

Physiography/Hydrology: A poorly drained pumice flat, perhaps in a slight depression of the landscape. No inflowing streams evident. Rather dry.

Species list:

Trees
- *Pinus contorta*

Shrubs
- *Betula glandulosa*
- *Salix pseudocordata*
- *Vaccinium occidentale*

Graminoids
- *Agrostis idahoensis*
- *Deschampsia caespitosa*
- *Eleocharis pauciflora*
- *Equisetum arvense*
- *Juncus orthophyllus*
- *Muhlenbergia filiformis*
- *Phleum alpinum*

Herbs
- *Achillea millefolium*
- *Agoseris glauca* var. *dasycephala*
- *Aster occidentalis*
- *Dodecatheon jeffreyi*
- *Galium trifidum*
- *Hypericum anagalloides*
- *Mimulus guttatus*
- *Mimulus primuloides*
- *Pedicularis groenlandica*
- *Polygonum bistortoides*
- *Ranunculus gormanii*
- *Sphenosciadium capitellatum*
- *Spiranthes romanzoffiana*
- *Tofieldia glutinosa*

COMMUNITIES:

A. *Eleocharis pauciflora* (*Drepanocladus exannulatus* phase)
B. *Eleocharis pauciflora*-*Deschampsia caespitosa*/*Tomenthypnum nitens*
C. *Vaccinium occidentale*/*Aulacomnium palustre* mounds
D. *Betula glandulosa*-*Salix barclayi* carr

A. *Eleocharis pauciflora* (*Drepanocladus* phase)

This is limited to damper areas with channels running through them and often has Sphagnum or mounds of *Philonotis* mixed in.

B. *Eleocharis pauciflora*--*Deschampsia caespitosa*/*Tomenthypnum nitens*

This community, though having a more or less continuous moss layer of *Tomenthypnum*, is quite dry and meadow-like. *Juncus* is prominent here. Other characteristic harbaceous species include *Mimulus primuloides*, *Dodecatheon jeffreyi*, *Ranunculus gormanii*, and *Phleum* *alpinum*. Low *Salix pseudocordata* shrubs are scattered here. This community covers the most extensive areas in the mire.

C. *Vaccinium occidentale*/*Aulacomnium palustre* mounds

These are scattered across the area. *Polygonum bistortoides* and *Lonicera caerulea* are also found in this community type.

D. *Betula glandulosa*--*Salix barclayi* carr

This carr occupies marginal positions of the mire. Other characteristic species include *Pinus contorta*, *Vaccinium occidentale*, *Dodecatheon jeffreyi*, and sedges.

Succession: *Pinus contorta* has invaded quite obviously here. Overall, the area seems quite dry and likely to proceed towards a terrestrial climax.

DOUGLAS AND KLAMATH COUNTIES: Thousand Springs Bog

Location: SW ¼ Sec. 12, SE ¼ SE ¼ and N ½ SE ¼, Sec. 7, T. 31S., R. 4E.

Elevation: 4850-5000 ft (1479-1524 m)

Date of visit: September 16, 1978

Physiography/Hydrology: An area with numerous springs coursing across steep or flat banks of the headwaters of a large stream, which is a tributary of Union Creek. At the lower end of the surveyed area, there are numerous, short spring-fed streams that course through the forest and empty into the south side of the main stream. Small, boggy patches of shrubs with moss mats, willows, or sedge communities occur along some of these. Farther upstream, however, are large, sloping, open hillside mires that are relatively flat at the bottom, near the stream's edge.

Species list:

Trees
- *Picea engelmannii*
- *Pinus contorta*

Shrubs
- *Alnus incana*
- *Salix* sp.
- *Spiraea douglasii*
- *Vaccinium occidentale*

Graminoids
- *Agrositis thurberiana*
- *Carex lenticularis*
- *Carex muricata*
- *Carex sitchensis*
- *Carex* spp.
- *Equisetum arvense*
- *Juncus ensifolius*
- *Juncus orthophyllus*
- *Muhlenbergia filiformis*
- *Pleuropogon refractus*
- *Scirpus congdonii*
- *Scirpus microcarpus*

Herbs
- *Aconitum columbianum*
- *Aster modestus*
- *Boykinia major*
- *Camassia leichtlinii*
- *Dodecatheon alpinum*
- *Drosera rotundifolia*
- *Epilobium* sp.
- *Hypericum anagalloides*
- *Hypericum formosum*
- *Ligusticum grayii*
- *Linnaea borealis*
- *Lotus oblongifolius* var. *nevadensis*
- *Madia* sp.
- *Mimulus guttatus*
- *Mitella pentandra*
- *Oxypolis occidentalis*
- *Pedicularis groenlandica*
- *Polygonum bistortoides*
- *Potentilla* sp.
- *Ranunculus gormanii*
- *Saxifraga oregana*
- *Senecio triangularis*
- *Spiranthes romanzoffiana*
- *Tofieldia glutinosa*

COMMUNITIES:

A. Low sedge-herbs/bryophytes
    1. Philonotis phase
    2. Helodium-Aulacomnium phase
    3. Sphagnum capillaceum phase
    4. Tomenthypnum nitens phase

B. Sedge fens with no moss mat
C. Willow thickets
D. Alder edges
E. Small, boggy patches along spring-courses feeding the main stream that are within the forest
    1. Vaccinium occidentale/Helodium blandowii
    2. Vaccinium occidentale/Sphagnum capillaceum
    3. Sedge fens
    4. Spring associations

A. Low sedge-herbs/bryophytes

1. Philonotis phase

On slightly sloping, wet hillsides leading to the stream are large, herbaceous-low sedge communities with a continuous moss mat of Philonotis fontana. However, the vegetation is so dense that it is difficult to perceive the continuous nature of the mat. Ranunculus gormanii and Hypericum anagalloides are the most prominent herbs, each with a cover value of circa 70 %. Other species are less frequent, including: Scirpus congdonii, Pedicularis groenlandica, Equisetum arvense, Juncus orthophyllus, Juncus ensifolius, Vaccinium occidentale (very small), Muhlenbergia filiformis, Drosera rotundifolia, Hypericum formosum, Camassia sp., Senecio triangularis, Carex lenticularis, Oxypolis occidentalis, Carex muricata, and Saxifraga oregana.

Higher on the hill, the community is similar, but with large areas dominated by Lotus oblongifolius var. nevadensis. Seeps are abundant, with Philonotis dominating right at the seep.

2. Helodium-Aulacomnium phase

Another area close to the main stream is superficially similar to (1), but the moss mat is composed, instead, of Helodium blandowii and Aulacomnium palustre, with only small amounts of Philonotis. Dodecatheon alpinum and Carex sp. were also in this community.

3. Sphagnum capillaceum phase

A small patch near the stream's edge is dominated by a mat of

Sphagnum capillaceum with *Oxypolis occidentale*, *Linnaea borealis*, *Juncus orthophyllus*, *Vaccinium ovalifolium*, *Ranunculus gormanii*, *Pedicularis groenlandica*, *Potentilla* sp., *Vaccinium occidentale*, carices, and grasses.

4. *Tomenthypnum nitens* phase

Near the top of the hill, near the forest margin, is a small patch (5x5 m) with a very slight slope, dominated by *Tomenthypnum nitens*, with a little *Meesia triquetra* and *Agrostis thurberiana*. Otherwise, the community composition is rather similar to (1), the *Philonotis* phase, except that the herbaceous species are not so dense. Other common species include: *Carex muricata*, *Equisetum arvense*, *Saxifraga oregana*, *Ranunculus gormanii*, *Pedicularis groenlandica*, *Muhlenbergia filiformis*, *Juncus orthophyllus*, *Drosera rotundifolia*. There is no standing water, but the surface is saturated.

A similar patch is dominated by *Meesia triquetra* instead of *Tomenthypnum*. In this area, there are scattered trees around the edges. Three such areas were examined.

B. Sedge fens with no moss mat

In some areas, the community is similar to the above types, but the moss mat is not so continuous, and the sedge cover is denser.

C. Willow thickets

Higher up the creek, where the stream decreases to about half its later width, and several tributaries join together, there are large willow (*Salix* sp.) thickets. The surface is saturated with water. Mats of mosses are fairly common around these thickets, and are composed mostly of *Philonotis*, but also include some *Aulacomnium* and *Helodium*.

D. Alder edges

Very high on the hill, at the upper edge of the open mire, are scattered alders (*Alnus incana*).

E. Small, boggy patches along the spring-courses feeding the main stream that are within the forest

1. *Vaccinium occidentale*/*Helodium blandowii*

This is a small, wet patch along the forested edge of the stream, dominated by the shrubs *Vaccinium occidentale* and *Spiraea douglasii*, with a dense ground mat of mosses, predominantly *Helodium blandowii* and *Aulacomnium palustre*, plus

Mnium rugicum and *Sphagnum fuscum*. Herbs include: *Carex sitchensis*, *Senecio triangularis*, *Juncus orthophyllus*, *Lotus oblongifolius* var. *nevadensis*, *Mitella pentandra*, *Equisetum arvense*, *Linnaea borealis*, and *Oxypolis occidentalis*.

2. *Vaccinium occidentale/Sphagnum capillaceum*

In a similar spring-course area, the community is dominated by *Sphagnum capillaceum* and dwarf *Vaccinium occidentale*. This type is not as species-rich. There are small amounts of *Kalmia microphylla*, *Spiraea douglasii* and *Pinus contorta*, ranging from 2 ft to 20 ft, and a small *Picea engelmannii* individual. *Carex* sp., *Equisetum arvense*, *Lotus oblongifolius* var. *nevadensis* and *Linnaea borealis* were the only other observed species.

At the lower end was a band of *Sphagnum squarrosum*, with *Salix* sp. and *Ligusticum grayii*.

3. Sedge fens

Small patches of dense *Carex* sp. with scattered *Aconitum columbianum* var. *howellii*, *Oxypolis occidentalis*, *Equisetum arvense*, *Aster modestus*, and *Boykinia major*.

4. Spring associations

In small, slow, stagnant streams feeding into the main creek, floating mats of *Brachythecium frigidum* are found, with *Drepanocladus* sp., *Saxifraga oregana*, and *Mimulus guttatus*.

APPENDIX A

Species List

Non-vascular plants

Bryophytes

Musci

Amblystegium serpens (Hedw.) B.S.G.
Aulacomnium palustre (Hedw.) Schwaegr.
Brachythecium frigidum (C. Muell.) Jaeg. & Sauerb.
Brachythecium salebrosum (Web. & Mohr) B.S.G.
Brachythecium sp.
Bryum creberrimum Tayl.
Bryum pallescens Scheich *ex*. Schwaegr.
Bryum weigelii Spreng.
Dicranum pallidisetum (Bail. *ex*. Holz.) Irel.
Drepanocladus aduncus (Hedw.) Warnst.
Drepanocladus exannulatus (B.S.G.)Warnst.
Drepanocladus fluitans (Hedw.) Warnst.
Drepanocladus vernicosus (Lindb. *ex*. C. Hartm.) Warnst.
Fontinalis antipyretica Hedw.
Helodium blandowii (Web. & Mohr.) Warnst. var. *blandowii*
Hygrohypnum bestii (Ren. & Bryhn *ex*. Ren.) Holz *ex*. Broth.
Meesia triquetra (L.) Aongstr.
Mnium punctatum var. *elatum* Schimp
Mnium rugicum Laur.
Philonotis fontana (Hedw.) Brid
Plagiotheicum denticulatum (Hedw.) B.S.G.
Sphagnum squarrosum Crome
Sphagnum subsecundum Nees *ex*. Sturm

Hepaticae

Chiloscyphus polyanthus (L) Corda
Lophocolia heterophylla (Schrad.) Dumort.
Marchantia polymorpha L.

Vascular plants

Primitive vascular plants

Equisetaceae

Equisetum arvense L.	common horsetail

Ophioglossaceae

Botrychium multifidum (Gmel.) Trevis	leathery grapefern

Gymnosperms

Pinaceae

Abies lasiocarpa (Hook.) Nutt.	subalpine fir
Abies magnifica Murr. var. *shastensis* Lemmon	Shasta red fir
Picea engelmannii Parry	Engelmann spruce
Pinus contorta Dougl. var. *murrayana* Engelm.	lodgepole pine

Angiosperms

Salicaceae	
Salix pseudocordata Anderss.	false heart-leaved willow
Salix barclayi Anderss.	Barclay's willow
Betulaceae	
Alnus incana (L.) Moench	thin-leaf alder
Polygonaceae	
Polygonum bistortoides Pursh	American bistort
Portulacaceae	
Montia chamissoi (Ledeb.) Robins. and Fern.	water montia
Caryophyllaceae	
Stellaria longifolia Muhl.	long-leaved starwort
Stellaria simcoei (Howell) Hitchc.	Simcoe Mt. starwort
Nymphyceae	
Nuphar polysepalum Engelm.	Indian pond lily; wakas
Ranunculaceae	
Aconitum columbianum Nutt. var. *howellii* (Nels. and Macbr.)	monkshood
Caltha biflora D C.	twinflower
Ranunculus gormanii Greene	Gorman's buttercup
Cruciferae	
Cardamine pennsylvanica Muhl.	Pennsylvania bettercress
Droseracea	
Drosera anglica Huds.	great sundew
Drosera rotundifolia L.	sundew
Saxifragaceae	
Mitella pentandra Hook.	five-stamened mitrewort
Grossulariaceae	
Ribes lacustre (Pers.) Poir	swamp gooseberry
Rosaceae	
Potentilla drummundii Lehm.	Drummond's cinquefoil
Potentilla palustris (L.) Scop.	purple cinquefoil; marsh cinquefoil
Potentilla sp.	cinquefoil
Rubus lasiococcus Gray	dwarf bramble
Sorbus sitchensis Roemer var. *grayii* (Wenzig) Hitchc.	Sitka mountain ash
Spiraea densiflora Nutt.	subalpine spiraea
Spiraea douglasii Hook. var. *menziesii* (Hook) Presl.	Menzies' spiraea
Leguminosae	
Vicia americana Muhl. var. *truncata* (Nutt.) Brew.	American vetch
Hypericaceae	
Hypericum anagalloides C. and S.	bog St. John's-wort
Violaceae	
Viola adunca Sm.	early blue violet

Viola macloskeyi (Lloyd)	small white violet
Viola glabella Nutt.	stream violet

Onagraceae

Epilobium alpinum L. var. *gracillimum* (Trel.) Hitchc.	alpine willow-herb
Epilobium angustifolium L.	fireweed
Epilobium glandulosum Lehm. var. *glandulosum*	common willow-herb
Epilobium palustre L.	swamp willow-herb

Hippuridaceae

Hippurus vulgaris L.	common mare's tail

Umbelliferae

Ligusticum grayi Coult. & Rose	Gray's licoriceroot
Oxypolis occidentalis Coult. & Rose	western oxypolis
Sphenosciadium capitellatum Gray	swamp whiteheads

Ericaceae

Gaultheria humifusa (Grah.) Rydb.	alpine wintergreen
Kalmia microphylla (Hook.) Heller	small-leaved laurel
Pyrola asarifolia Michx.	alpine pyrola
Pyrola minor L.	lesser wintergreen
Vaccinium occidentale Gray	western bog blueberry
Vaccinium scoparium Leiberg	grouseberry; whortleberry

Primulaceae

Dodecatheon alpinum (Gray) Greene	alpine shooting star

Gentianaceae

Gentiana simplex Gray	oneflowered gentian

Menyanthaceae

Menyanthes trifoliata L.	buckbean

Labiatae

Stachys rigida Nutt. ex Benth.	rigid betony

Scrophulariaceae

Castilleja miniata Dougl.	scarlet paintbrush
Mimulus guttatus D C. var. *guttatus*	yellow monkeyflower
Mimulus moschatus Dougl. var. *moschatus*	musk-flower
Mimulus primuloides Benth.	primrose monkeyflower
Pedicularis groenlandica Retz.	elephant's head
Veronica americana Schwein	American brooklime
Veronica serpyllifolia var. *humifusa* (Dickson) Vahl.	thyme-leaved speedwell
Veronica wormskjoldii Roem. and Schult.	American alpine speedwell

Lentibulariaceae

Utricularia minor L.	lesser bladderwort
Utricularia intermedia Hayne	flat-leaved bladderwort
Utricularia vulgaris L.	common bladderwort

Rubiaceae

Galium trifidum L.	small bedstraw
Galium triflorum Michx.	sweet-scented bedstraw

Caprifoliaceae

Linnaea borealis L.	twinflower
Lonicera caerulea L.	sweet-berry honeysuckle
Lonicera involucrata (Rich.) Banks var. *involucrata*	bear-berry honeysuckle

Compositae

Arnica mollis Hook.	hairy arnica

Aster occidentalis (Nutt.) T. and G.	western mountain aster
Bidens cernua L.	nodding beggars-tick
Madia bolanderi (Gray) Gray	Bolander's tarweed
Senecio triangularis Hook.	arrowleaf groundsel

Potamogetonaceae

Potamogeton berchtoldii Fieb.	Berchtold's pondweed
Potamogeton gramineus L. var. *myriophyllus* Robbins	grass-leaved pondweed

Juncaceae

Juncus ensifolius Wikst.	dagger-leaf rush
Juncus orthophyllus Cov.	straight-leaved rush
Luzula campestris (L.) D C.	field woodrush

Cyperaceae

Carex cusickii Mack.	Cusick's sedge
Carex disperma Dewey	soft leaved sedge
Carex jonesii L.H. Bailey	Jones' sedge
Carex lenticularis Michx. var. *lenticularis*	Keelogg's sedge
Carex limosa L.	mud sedge
Carex rostrata Stokes	beaked sedge
Carex simulata Mack.	short-beaked sedge
Carex sitchensis Prescott	Sitka sedge
Eleocharis pauciflora (Lightf.) Link	few-flowered spike-rush
Eriophorum gracile Koch	slender cotton-grass
Scirpus congdonii Britt.	Congdon's bulrush

Gramineae

Agrostis idahoensis Nash	Idaho bentgrass
Agrostis thurberiana Hitchc.	Thurber bentgrass
Deschampsia atropurpurea (Wahl.) Scheele	mountain hairgrass
Deschampsia cespitosa (L.) Beauv. var. *cespitosa*	tufted hairgrass
Glyceria borealis (Nash) Batch.	northern mannagrass
Glyceria elata (Nash) Jones	tall mannagrass
Muhlenbergia filiformis (Thurb.) Rydb.	pullup muhly
Puccinellia pauciflora (Presl.) Munz var. *microtheca* (Buck.) Hitchc.	weak alkaligrass

Sparganiacea

Sparganium minium Fries.	small bur-reed

Liliaceae

Camassia leichtlinii (Baker) Wats. var. *suksdorfii*	great camas
Clintonia uniflora (Schult.) Kunth.	bead lily
Streptopus roseus Michx.	rosy twisted-stalk
Tofieldia glutinosa (Michx.) Pers.	tofieldia

Orchidaceae

Habenaria dilatata (Pursh) Hook.	white bog-orchid
Habenaria saccata Greene	slender bog-orchid
Spiranthes romanzoffiana Cham.	ladies-tresses