

**FLORISTICS AND SUCCESSIONAL PATTERNS OF
MICROBIOTIC CRUSTS IN PONDEROSA PINE
FORESTS OF SOUTHERN INLAND BRITISH COLUMBIA**

by

Patrick Williston

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Department of BOTANY

The University of British Columbia
Vancouver, Canada

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Abstract: Microbiotic crusts are an important component of the ecology and species diversity of terrestrial ecosystems in semiarid regions. This study documents 72 lichen species and 48 bryophyte species occurring in the ponderosa pine forests of southern inland British Columbia and contains a key to common species. Successional patterns are described for vascular plants, lichens, and bryophytes along a disturbance gradient reflecting past grazing activity by livestock. While species richness among vascular plants varied little with disturbance, microbiotic species richness was found to differ significantly. Maximum richness occurred in moderately disturbed sites. Indicator species for early versus late successional sites were discerned using Principal Components Analysis. Early successional sites were often dominated by xerophytic crustose and squamulose lichens, while late successional sites also supported foliose lichens, fruticose lichens, and bryophytes. It is hypothesized that this trend from smaller to larger species relates to increased moisture retention, and denotes a positive feedback mechanism. This study describes the floristics and successional patterns of microbiotic crusts; this is important for managing species diversity in one of British Columbia's most restricted ecosystems.

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Dedication

This thesis is dedicated to Carolyn Williston, Shona Ellis, Carol Ann Borden, Wilf Schofield, Trevor Goward, Andre Arsenault, and Gary Bradfield, who have taught me to admire and contemplate nature's richness with a sense of wonder. Nothing would please me more than to be able to do as they have done.

Chapter 1

INTRODUCTION

1.1 Microbiotic crusts

Microbiotic crusts are assemblages of lichens, bryophytes, algae, fungi, bacteria, and cyanobacteria that form directly on soils in arid and semiarid ecosystems. Microbiotic crusts are an important component of the species diversity and ecology of dryland communities; however, because they are inconspicuous and taxonomically challenging, they are also often overlooked in ecological studies and vegetation inventories. In most regions, the importance of microbiotic crusts is poorly understood and the basic floristics completely unknown. Indeed, only in the last 25 years have research efforts focussed upon how human caused disturbances, such as trampling by domestic livestock, affect microbiotic crust diversity and function.

While several terms such as cryptogamic, cryptobiotic, microphytic, biologic, and microfloral crusts have been used to describe this type of community, "microbiotic crust" is the most appropriate term because all the components are minute and biological. Some crust organisms do not produce gametes (i.e. cyanobacteria) and others are not plants (i.e. lichens, fungi, and bacteria), thus terms like cryptogamic (hidden seed) and microphytic (small plant) are not sufficiently inclusive. Despite this, the traditional term "cryptogamic crust" can be found in recent literature (Mommott et al. 1998). Other authors have chosen to use a variety of terms on different occasions (Belnap 1993, 1994, 1996, 1998; Eldridge 1993; Eldridge and Greene 1994; Eldridge and Tozer 1997; Eldridge et

al. 1997). West (1990), St. Clair and Johansen (1993), and more recently Perez (1997), have discussed the problems associated with naming this biological association.

Consensus is not imminent.

1.2 Distribution, diversity, and floristics

To understand the role of microbiotic crusts in ecosystems, it is important to establish where they occur, why they occur where they do, and how they contribute to the species diversity of regional floras.

Microbiotic crusts form the dominant vegetative ground cover in several diverse ecosystems. They occur in arid and semiarid deserts, grasslands, savannas, and forests from the equator to more temperate regions. The terms *arid* and *semiarid* have not been consistently applied (West 1983, Sidahmed 1990). This study follows Sidahmed (1990) who suggests that arid ecosystems receive a mean annual precipitation of 100-400mm yr⁻¹ while semiarid ecosystems receive 400-600mm yr⁻¹.

Studies on floristics and crust function in arid desert ecosystems have been conducted in Israel (Danin and Ganor 1991), Venezuela (Perez 1997), and the southeastern U.S. (Nash 1977). Crust research in arid and semiarid grasslands, savannas, and forests has focussed on the Great Basin region of the western U.S. (Fink 1909; Herre 1911; Loope and Gifford 1972; Kleiner and Harper 1977; Anderson et al. 1982; Johansen and Rushforth 1985; Rosentreter et al. 1988; Cole 1990; Beymer and Klopatek 1992; Belnap 1993, 1994; Harper and Pendleton 1993; Johansen 1993, Johansen et al. 1993; St. Clair and Johansen 1993; St. Clair et al. 1993; Memmott et al. 1998) and in south central Australia (Rogers and Lange 1971, 1972; Eldridge 1993, 1996, 1996b, 1998; Eldridge

and Greene 1994; Eldridge and Tozer 1996, 1997; Eldridge and Rosentreter 1999; Eldridge et al. 1997). Regions with extensive dryland crust communities that have received little scientific attention include the Mongolian steppe, the Middle East, the Mediterranean, Africa, Central America, South America, and Canada.

Microbiotic crusts also occur in polar and alpine ecosystems where moisture, temperature, and the length of the snow-free period limit the cover of vascular plants. The Canadian Arctic contains crust communities (Gold 1998), particularly over well-drained soils. Crust communities also occur in alpine ecosystems throughout the world, but have been the subject of few scientific studies (Perez 1997).

Microbiotic crusts occur on low and middle elevation rocky outcrops in the Coastal Douglas-fir zone of British Columbia's biogeoclimatic classification system (Meidinger and Pojar 1991). They also occur on alpine ridge tops and plateaus in both the coastal and inland mountain ranges. The most extensive microbiotic crusts in British Columbia are found in the semiarid inland lowlands and highland plateaus of the Cariboo region near Williams Lake; the rain shadow valleys of the Fraser River, the Thompson River, Okanagan Lake, and the southern Rocky Mountain Trench; and along the U.S. border from Princeton to Grand Forks. These areas correspond to Bunchgrass, Ponderosa Pine, and Interior Douglas-fir biogeoclimatic zones (Meidinger and Pojar 1991).

Microbiotic crust species richness is greatest on fine soils such as silts or fine sands (West 1990; Perez 1997). While bryophytes predominate on the humid coast, lichens are more abundant in cover and richness in the semiarid grasslands and forests. Here bryophytes are not commonly epiphytic and comprise a smaller fraction of the microbiotic crust than lichens in all but the wettest areas. Terrestrial lichens flourish in this

setting and demonstrate remarkable richness, particularly in the absence of disturbance. Ponderosa pine forests support a number of rare and poorly documented lichens and bryophytes (Goward 1996, Ryan 1996).

Crusts occur in ecosystems that are too physiologically challenging for most vascular plants. While moisture, or rather the absence of moisture, is key to the distribution of microbiotic crusts, other factors, such as nutrient-poor soils, short growing seasons, and very low or very high temperatures, are also characteristic of crust habitats. Many bryophytes and lichens have adapted to withstand desiccation. Bryophytes fold, roll, or curl their leaves or thalli to reduce water loss. Lichens have several adaptations that allow them to tolerate dry climates including small evaporative surfaces (i.e. crustose lichens), thickened cortexes, and the ability to produce pruina, or crystalline deposits that reflect light (Friedmann and Galun 1974). Furthermore, lichens have been shown to utilize dew and humidity as sources of moisture (Friedmann and Galun 1974; West 1990, Nash 1996).

Dryland soils are often nutrient poor. Several crust-dwelling lichens, such as *Collema* spp. and *Leptogium* spp., contain cyanobacteria photobionts, and are capable of fixing atmospheric nitrogen. Other lichens and bryophytes utilize air-borne dust particles as their source of necessary nutrients (Nash 1996).

British Columbia is home to roughly 2800 species of vascular plants, 1800 lichens, and 1005 bryophytes (Harding and McCullum eds. 1994; Goward pers. comm. 1999; Schofield pers. comm. 1999). While only a fraction of these organisms occur in the semiarid inland regions of the province, the numbers demonstrate how important lichens and bryophytes are in terms of species diversity. B.C. is the richest province in Canada

for lichens and bryophytes and contains roughly 75% of Canada's lichen and bryophyte floras (Goward pers. comm. 1999; Schofield pers. comm. 1999). This study reports 74 terrestrial lichens, 48 bryophytes, and 121 vascular plants from 19 sites in ponderosa pine forests and includes new collections for 27 potentially rare lichens and bryophytes. These values are higher than reports from other microbiotic crust studies, which implies that the study area contains a particularly rich crust community. Atwood (1998) lists 25 lichens and 17 bryophytes from the Okanagan Valley in British Columbia. Fink (1909) and Herre (1911) report 33 and 59 species of lichens respectively from the drylands of Nevada, though their studies include saxicolous and lignicolous species. Rogers and Lange (1972) report 42 taxa of soil dwelling lichens from 343 sites in southern Australia and Nash et al. (1977) report 61 lichens and 18 mosses from the Chihuahuan, the Sonoran, and the Mojave Deserts. A thorough study by Cooke (1955) reported 815 fungi, 145 lichens, and 79 bryophytes from the drylands of eastern Washington.

1.3 Microbiotic crust research

There has been considerably more research examining the ecology of microbiotic crusts than there has been in their floristics. This may reflect trends in science and science funding, or perhaps the difficult nature of the taxonomy of dryland bryophytes and lichens. Taxonomic research of dryland bryophytes and lichens has been hindered by the relative scarcity of appropriately trained taxonomists (Schofield pers. comm. 1998) and the dwindling support of field biology by the academic community.

Microbiotic crusts have been the focus of investigation in several localities world wide. In the Great Basin and Columbia Basin of the western U.S., efforts to describe crust

communities have been extensive (Fink 1909; Herre 1911; Loope and Gifford 1972; Kleiner and Harper 1977; Anderson et al. 1982; Johansen and Rushforth 1985; Rosentreter et al. 1988; Cole 1990; Beymer and Klopatek 1992; Belnap 1993, 1994; Harper and Pendleton 1993; Johansen 1993, Johansen et al. 1993; St. Clair and Johansen 1993; St. Clair et al. 1993; Memmott et al. 1998). This region is one of the few to have a treatment of the soil algal flora and the fungi (Cooke 1955; Johansen and Rushforth 1985; Johansen 1993). Research on microbiotic crusts in Australia was initiated by Rogers and Lange (1971, 1972) and has since been investigated by Eldridge and colleagues, covering both floristics and ecology (Eldridge 1993, 1996a, 1996b, 1998; Eldridge and Greene 1994; Eldridge and Tozer 1996, 1997; Eldridge et al. 1997; Eldridge and Rosentreter 1999). Perez (1997) conducted a rigorous study of the influences of microbiotic crusts on soil characteristics in the Andes of Venezuela and was the first to investigate crusts in a high elevation ecosystem. In the Negev desert of Israel, Danin and Ganor (1991) have shown that microbiotic crusts are important for entrapping wind-borne soils and organic debris. Looman (1964a, 1964b) studied microbiotic crusts on the Canadian prairie, where he described lichen associations and successional patterns and speculated about their phytogeographical relationships.

Despite the rich diversity of bryophytes and lichens of semiarid, inland British Columbia, this ecosystem has been the focus of relatively few studies. McIntosh (1986, 1997) conducted a thorough survey of the bryophytes of British Columbia's grasslands. His thesis included a key to 82 grassland bryophytes from 110 sites and reported several species new to the province. While his study did not specifically focus on ponderosa pine ecosystems, several of the species overlap from the grasslands to the neighbouring

forests. Schofield's (1988) general survey of the biogeoclimatic zones of British Columbia remains the most complete list for B.C.'s ponderosa pine forests.

Lichens have been intensively investigated in four regions of British Columbia: the Coastal Douglas-fir zone (Noble 1982), the Queen Charlotte Islands (Brodo 1995), and wet coastal and inland ecosystems (Goward et al. 1992, 1994, 1997). Dryland lichens and microbiotic crusts have been the focus of a single study in B.C. (Atwood 1998), and their floristics have yet to be described in detail. Basic floristic research is also required for the fungi, cyanobacteria, and algae of British Columbia's semiarid ecosystems.

The research presented here is the first to describe patterns of microbiotic crust succession in British Columbia's ponderosa pine forests. While not a thorough floristic treatment, this study adds 15 bryophytes to existing lists and is the first to report the terricolous lichens from this ecosystem.

1.4 Microbiotic crust ecology

Microbiotic crusts have been attributed the following six functions: 1) the stabilization of soils during water and wind erosion events, 2) the regulation of surface water, infiltration, and evaporation, 3) the formation of soil by the entrapment of eolian soil particles 4) the addition of nutrients such as nitrogen and organic carbon to the soil, 5) habitat for microorganisms, and 6) seedbed for vascular plants (Eldridge and Rosentreter 1999).

Several authors have reviewed the role of microbiotic crust functions in ecosystems. Among the most thorough are Harper and Marble (1998), West (1990), Edridge and Greene (1994), Perez (1997), Atwood (1998), and Belnap (1998). West (1990) criticized

earlier assertions of microbiotic crust functions that were intuitive and not based upon rigorous study. His comments inspired a re-examination of earlier assertions, many of which have been confirmed (Eldridge 1997; Perez 1997; Atwood 1998).

1.5 Stability and erosion

Soil stabilization is considered the most important functional role of microbiotic crusts (St. Clair and Johansen 1993) and has received considerable attention in the published literature (Harper and Marble 1988; West 1990; Eldridge 1993; Eldridge and Greene 1994; Perez 1997). Microbiotic crusts influence three types of erosion in dryland ecosystems: rain splash erosion, surface runoff erosion, and wind erosion.

Eldridge (1993) found a strong positive correlation between percent crust cover and the decrease in sediment loss related to splash erosion. As crust cover increased, the amount of clays, silts, and fine sands collected in the runoff decreased. Perez (1997) reported that it required nearly five times as many water drops to erode soil aggregates on crusted soils than on bare soil. Other studies have shown that splash erosion is slowest in moss dominated crusts, followed by crusts dominated by lichens, and then algal crusts (West 1990; Eldridge and Rosentreter 1999). Bare surfaces show the highest rates of splash erosion (Eldridge 1993; West 1990; Perez 1997).

If the rate of infiltration of a soil is slower than the rate of precipitation during a rain event, then surface runoff will occur, often carrying surface soil particles with it. Several studies have examined the role of microbiotic crusts in reducing the loss of sediments related to runoff erosion (Loope and Gifford 1972; Kleiner and Harper 1977). Kleiner and Harper (1977) found a lower proportion of silt and a higher proportion of sand in a

site with less crust than a neighbouring site with a higher cover of crust. It was not determined, however, whether the observation was a causal relationship or merely based upon differing geomorphic histories between the sites. Loope and Gifford (1972) found a greater proportion of silt to sand in sites with more cover of crust than sites where crusts had been removed. The relationship of greater crust cover with a higher proportion of silt-sized particles is consistent with observations made in splash erosion experiments (Eldridge 1993). However, while microbiotic crusts may influence the development of surface soils, soil texture has been identified as a factor influencing the development of microbiotic crusts (Anderson et al. 1982). Coarser textured soils support fewer species than fine textured soils, particularly on slopes where soil surfaces are less stable and have a reduced water holding capacity (West 1990; Perez 1997; Belnap 1998).

Wind erosion is an important geomorphic process in arid and semiarid ecosystems (West 1990, Eldridge and Greene 1994). West (1990) suggests that increases in wind-borne sediments observed in the past 150 years may relate to anthropogenic disturbance of microbiotic crusts. Wind tunnel experiments conducted in the field (Belnap and Gillette 1998) showed that microbiotic crusts provide protection against wind erosion, even at higher wind velocities than normally observed in nature. Furthermore, they found that crust disturbances from vehicles or simulated livestock trampling allowed wind erosion to occur at wind velocities well within the natural range. Simulated trampling decreased resistance to wind erosion by 20-83% on soils with microbiotic crusts, while vehicular disturbance decreased resistance 31-82% (Belnap and Gillette 1998). Electron microscopy has shown how filaments from microbiotic crusts bind soil particles to make soil aggregates more resistant to wind and water erosion (Belnap 1994; Eldridge and

Greene 1994). Complexity in the microtopography related to the presence of microbiotic crusts may enhance the surface boundary layer (Belnap 1998), reducing the rate of movement air or water at the soil surface.

1.6 Water regulation

Studies examining the relationships between microbiotic crusts and the movement of water at the soil surface have been numerous, and have occasionally produced conflicting results (West 1990; Eldridge 1993; Eldridge and Greene 1994; Eldridge et al. 1997; Perez 1997; Atwood 1998). Properties that have been examined include sorptivity, steady state infiltration, ponding, and runoff.

West (1990) notes that several studies have demonstrated that the presence of microbiotic crusts increases infiltration, while other studies have shown crusts to impede infiltration. In some instances, managers have actively removed crusts in an effort to improve hydrological relations in rangelands. Range managers employ strategies to maximize infiltration in arid and semiarid ecosystems because water is a limiting resource for primary production of forage for livestock (Eldridge et al. 1997). In the high equatorial Andes, Perez (1997) observed a 70% greater rate of infiltration on crusted soils than on soils without crusts. He also noted that soils beneath microbiotic crusts had a higher water storage capacity than neighbouring bare soils. In the semiarid interior of Australia, Eldridge (1993) found a positive correlation between percent crust cover and sorptivity and infiltration rates on sites in poor condition, and no correlation on sites in good condition. At a site where commercial grazing had not occurred in 20 years, Eldridge et al. (1997) found no relationship between time to ponding, time to runoff,

depth of wetting front, sorptivity, steady state infiltration, cumulative infiltration rate, and the cover of microbiotic crust. It was reasoned that microbiotic crusts had a positive influence on sorptivity and infiltration on rangelands in poor condition; however, once the soils had redeveloped their porosity and structure, the influence of microbiotic crusts on infiltration was insignificant (Eldridge et al. 1997).

Atwood's (1998) research in the grasslands of the Okanagan Valley of British Columbia determined that microbiotic crusts had a significant effect on water retention after rain events. She found that soils beneath crusts received less water during summer rain event, but that crust-covered soils retained twice as much moisture as uncrusted soils 5 days after the rain. She also found that mosses held more water and retained moisture longer than did lichens. Lichens allowed more water to enter the surface soil; however, lost this to evaporation more rapidly.

Contradictory conclusions regarding the influence of crusts on soil hydrology may be explained by variations in site characteristics and species compositions among research areas. One of the limitations of the term microbiotic crust, and its many synonyms, is that it does not differentiate between crusts of widely differing composition. This has led to comparisons of potentially unrelated communities (West 1990). Studies that have shown crusts to impede infiltration may have occurred in regions where microbiotic crusts are formed primarily by algae and cyanobacteria. Algal crusts absorb water and swell, creating a gelatinous, hydrophobic barrier, which holds and repels water at the soil surface where it evaporates rapidly. Microbiotic crusts comprised of a diverse assemblage of lichens, bryophytes, algae, cyanobacteria, and bacteria do not demonstrate the same hydrological relationships.

1.7 Soil nutrition

The fixation of atmospheric nitrogen by microbiotic crust organisms has been thoroughly examined (Sheilds 1957; Sheilds et al. 1957; West 1990; Harper and Pendleton 1993; Belnap 1994). Numerous studies have shown how cyanobacteria, occurring freely or as photobionts in cyano-lichens, are able to increase the availability of plant usable nitrogen (Harper and Pendleton 1993; Belnap 1994). Estimates of the amount of nitrogen fixed by microbiotic crusts range from 10-100 kg ha⁻¹ yr⁻¹ in the Great Basin region of the U.S. (Harper and Marble 1988; Harper and Pendleton 1993) and 2-41 kg ha⁻¹ yr⁻¹ in other arid regions (West 1990). This is in excess of the 10-12 kg ha⁻¹ yr⁻¹ required by dryland vascular plants (Harper and Marble 1988). However, West (1990) warns that most studies have been performed in a laboratory setting and do not correct for the high rates of denitrification that have been observed in arid ecosystems.

The availability of other plant essential nutrients is also positively influenced by the presence of microbiotic crusts. In the laboratory, *Vulpia octoflora*, a small annual grass, has been observed to contain higher levels of N, P, K, Fe, Ca, and Mg when grown on soils covered by microbiotic crusts than on uncrusted soils (Belnap 1994).

In many arid and semiarid ecosystems microbiotic crusts form the dominant vegetation type and can be the principal source of organic carbon in soils. Organic carbon contributions vary depending on species composition, microsite, and landscape conditions (West 1990; Belnap 1994; Eldridge and Greene 1994). Some algal crusts have been observed to have relatively fast growth rates, recovering from large disturbances in only four or five years (Johansen et al. 1993; Eldridge and Greene 1994). This implies a

correspondingly high rate of carbon accumulation. Other studies have documented very slow recovery rates ranging from 15-250 years in communities containing a diverse array of lichens and bryophytes (Belnap 1993; Eldridge and Greene 1994). Most research indicates that these slow developing ecosystems contain low amounts of carbon. Looman (1964a) suggests a growth rate of 1 mm yr^{-1} diameter in soil lichens in grasslands in Saskatchewan. Eldridge et al. (1997) report organic carbon levels in Australian semiarid soils containing commonly less than 1%.

1.8 Soil formation

Microbiotic crusts contribute to the formation of soils by entrapping aeolian soil particles. Research in Israel has shown how bryophytes are capable of trapping wind-borne dust, incorporating it into the soil surface horizons (Danin and Ganor 1991). It is possible that the surface complexity found in microbiotic crusts creates a boundary layer of slow moving air above the soil surface, causing the air to release dust particles which become trapped in the microtopography of the crust (Belnap 1998). Electron microscopy has been used to show how microbiotic hyphae bind soil aggregates, contributing to soil structure (Belnap 1993; Eldridge and Greene 1994). Lichen rhizines and bryophyte rhizoids, used in anchoring these organisms to the substratum, also contribute to the formation of soil aggregates. West (1990) suggests that a comparison of soil structure attributes between neighbouring crusted and uncrusted soils would improve our understanding of their relationships.

1.9 Microorganism habitat

Scientists dedicated to the study of microbiotic crusts are few in number. Those who study dryland insects and microorganisms are equally few. It is therefore understandable that studies examining the relationship among insects, microorganisms and microbiotic crusts are rare. West (1990) summarized previous studies, citing reports of isopods, snails, beetles, and other invertebrates that feed upon microbiotic crusts, or use them as habitat (1994). Eldridge and Greene (1994) speculate that with sufficient research, dryland microorganisms may prove to be important bioindicators of ecosystem health. Whitford (1996) examined keystone species of fungi, protozoa, nematodes, soil microarthropods, ants, and termites from the Chihuahuan Desert. The activity of these organisms was shown to be moisture dependent. Though microbiotic crusts are known to influence moisture, the interaction between crusts and microorganisms has not been investigated.

Studies from arid and semiarid regions of British Columbia have resulted in the description of many insect species new to Canada, several of which are considered extremely rare (Scudder 1991). How these species relate to the presence or absence of microbiotic crust is not yet known and is worthy of investigation.

1.10 Vascular plant germination

Review articles point to a general lack of sufficient data to generalize on whether microbiotic crusts aid in seedling establishment (West 1990; Eldridge and Greene 1994). The interaction between microbiotic crusts and vascular plants is poorly understood and likely highly complex. St. Clair et al. (1984) demonstrated in a laboratory setting that seedling establishment was higher in crust covered soils than in trampled soils. The

beneficial seedbed hypothesis suggests that crusts provide a stable, moist, nutrient rich niche that enhances germination. Belnap (1998) states that higher temperatures observed in crusted soils facilitate seedling germination of both forbs and grasses. Others have suggested that crusts prevent seeds from reaching the mineral soil and become vulnerable to drying out (West 1990). Recent studies indicate that crusts may be responsible for resisting the invasion of noxious weeds such as *Bromus tectorum* (Rosentreter 1999).

1.11 Influence of grazing

Scientific and anecdotal observations show that continual, high intensity grazing in arid and semiarid ecosystems is detrimental to native vascular plants and microbiotic crusts (Figure 1; Rogers and Lange 1971; Anderson et al. 1982; Beymer and Klopatek 1992; Eldridge 1998; Memmott 1998). Rogers and Lange (1971) noted a decrease in crust cover and changes in species distribution as sampling drew closer to a livestock water station. Memmott et al. (1998) found that, even on frozen ground, lichen cover is reduced by as much as 50% under moderate grazing regimes. Anderson et al. (1982) reported a 25% decrease in crust species richness and a 22% decrease in crust cover in a grazed site when compared to an ungrazed site. However, a reduction in crust cover is not always accompanied by a reduction in species richness. Beymer and Klopatek (1992) reported 80% less microbiotic crust cover on grazed sites, yet these sites contained 1-4 more species than ungrazed sites. Daubenmire (1968) suggested that moderate grazing regimes might lead to higher productivity, at least for higher plants. However, nitrogen fixation by crust organisms was reduced by 30-100% by disturbances caused by human footprints, bicycles, and vehicles (Belnap 1996).

Several authors have generalized about susceptibility of crust organisms though conclusions appear to be location dependent. Anderson et al. (1982) reported mosses to be the most reduced by grazing disturbance, whereas Memmott et al. (1998) suggested that mosses are more tolerant of trampling than are lichens. Differences in susceptibility may reflect morphological and physiological attributes of individual species, or may relate to the lifeform of the organism. A comprehensive effort to describe patterns of susceptibility was completed by Eldridge and Rosentreter (1999). They related susceptibility to lifeform complexity and reproductive strategy. Lichens are generally divided into the following lifeforms: gel lichens, crustose, squamulose, fruticose, and foliose (Goward et al. 1994; Eldridge and Rosentreter 1999; Goward 1999). Some researchers further divide the crustose into the dusts or leprose lichens, which are essentially comprised of soredia, and the crusts, which have a hardened upper cortex (Goward et al. 1994). Fruticose species may further be divided into the club lichens (*Cladonia* spp.), the shrub lichens (*Cladina* spp., *Cetraria* spp., etc.), and the hair lichens (*Usnea* spp., *Alectoria* spp., *Bryoria* spp., etc.) (Goward et al. 1994). Not all genera fit neatly into a single lifeform group. For instance the genus *Cladonia* may form a sorediate crust, a cluster of squamules, or a fruticose "club" with no basal squamules whatsoever. Bryophytes are commonly divided into acrocarpous species that have terminal sporangia, lateral innovations, and erect stems; and pleurocarpous species that have multiple lateral sporangia and creeping stems (Schofield 1985).



Figure 1. A photograph of an undisturbed site (left) and a disturbed site (right) divided by a fence. The site on the left has a high cover of the perennial bunchgrass, *Festuca campestris*, and a well developed microbiotic crust. The disturbed site is dominated by the weedy introduced species, *Bromus tectorum*, and has large patches of bare soil.

Eldridge and Rosentreter (1999) found that the simplest lifeforms, cyanobacteria and gel-lichens (*Collema* spp. and *Leptogium* spp.), were determined to have a low susceptibility to disturbance. Mosses, liverworts, and squamulose lichens were determined to have a high susceptibility if they relied upon asexual reproduction for propagation, and moderate if they reproduced sexually, or both sexually and asexually. Foliose and fruticose lichens were considered very highly susceptible, or if reproducing both sexually and asexually, then merely highly susceptible to disturbance. Eldridge and Rosentreter (1999) noted several species that recovered quickly after disturbance including the gel-lichen, *Collema*, and the bryophytes, *Bryum*, *Funaria*, and *Pterygoneurum*. Furthermore, they suggested that foliose and fruticose lichens were the slowest to recover.

The study of the ecology of morphological groups, or lifeforms, among lichens and bryophytes reflects a growing interest in the relationships between morphology and function. It also serves to facilitate the use of microbiotic crusts in the assessment of site condition by those not intimately familiar with the taxonomy of these organisms (Eldridge and Rosentreter 1999).

Ponderosa Pine Forests

1.12 Distribution and climate

At approximately 300,000 ha, or 0.3% of the total area of the province, the ponderosa pine forests equal the bunchgrass ecosystem as the smallest biogeoclimatic zones in B.C. (Campbell and Bawtree 1998). British Columbia's ponderosa pine forests are restricted to the lowlands and low slopes of the driest valleys in south-central and southeastern

regions of the province. This includes the benches and lower slopes of the Fraser River valley, the North and South Thompson River valleys, the Nicola River valley, the Similkameen, the Tulameen, and the Ashnola River valleys, the Okanagan Valley, and the southern Rocky Mountain Trench. Krajina (1959) classified this ecosystem the Ponderosa Pine-Bunchgrass zone, which later was separated into two distinct zones, the Bunchgrass (BG) and the Ponderosa Pine zones (Meidinger and Pojar 1991).

The mean annual rainfall of the Ponderosa Pine zone is 280-500mm (Meidinger and Pojar 1991). These forests are characterized by hot, dry summers and cool winters with little snowfall (Meidinger and Pojar 1991). The soils of B.C.'s ponderosa pine forests are classified as Eutric and Dystric Brunisols (Campbell and Bawtree 1998).

Ponderosa pine forests extend from southern British Columbia, throughout the western United States, and into California. To the east, these forests reach as far as North and South Dakota, Nebraska, Colorado, New Mexico, and Texas. *Pinus ponderosa* is the state tree of Montana (Kral 1993). According to Kral (1993), the current rate of harvest of ponderosa pine exceeds the rate of regrowth, which implies that the conservation issues in these forests are imminent, if not already present.

1.13 Vegetation

Ponderosa pine forests in a natural condition are rare in British Columbia (B.C. Ministry of Forests 1995a). Because most of these forests have been altered by the influence of humans, describing the characteristics of native ponderosa pine forests is speculative. The following represents an approximation of what a natural ponderosa pine forest is like. The canopy is comprised of large, well spaced *Pinus ponderosa* with

Pseudotsuga menziesii appearing in draws and wetter areas (Yazvenko and Rapport 1997). The understory is dominated by the perennial bunchgrasses *Festuca campestris* and *Agropyron spicatum*, and includes a diverse array of forbs and shrubs including *Gaillardia aristata*, *Arnica fulgens*, *Carex petesata*, *Antennaria* spp., *Erigeron* spp., *Allium cernuum*, *Calochortus macrocarpus*, *Castilleja thompsonii*, *Artemisia* spp., *Chrysothamnus nauseosus*, and *Amelanchier alnifolia*. Krajina's (1959) description of B.C.'s ponderosa pine forests includes a thorough list of understory vascular plants. The interstices of the bunchgrasses support a diverse assemblage of microbiotic crust species (Figure 1). Vascular plant litter comprises a small component of the ground cover, while parse patches of bare soil denote the presence of borrowing mammals and insects. Fire prevention and the introduction of grazing livestock have initiated vegetation changes in the ponderosa pine forests (B.C. Ministry of Forests 1995a; Yazvenko and Rapport 1997). In many areas, stands have become dense and the amount of needle litter has increased.

1.14 Influence of grazing

Rexford Daubenmire, one of the pioneers of rangeland ecology in North America, noted the following: "One gains the impression that each period of excessive grazing that reduces native perennial forage species and allows a corresponding increase of *Bromus* represents another irreversible step in range deterioration." (Daubenmire 1970, pp. 81-82). Historically, these forests were subject to natural, low-intensity fires that had a



Figure 2. Microbiotic crust occupying the interstices among the vascular plants (*Artemisia frigida* and *Agropyron spicatum*).

return interval of 4-50 years (B.C. Ministry of Forests 1995a); however, grazing has since replaced fire as the primary source of disturbance. Early successional plants such as *Plantago patagonica* and *Antennaria* spp., and noxious weeds such as *Bromus tectorum*, *Poa pratensis*, *Linaria genistifolia*, and *Centaurea* spp. are common in areas regularly utilized by livestock. Daubenmire (1970) noted that, once established, *Bromus tectorum* and *Poa pratensis* showed no sign of being replaced by native species, and instead formed monotypic swards with low species richness. Personal observations of rhizomatous *Poa pratensis* swards reveal an impoverished microbiotic community, a pattern worth investigating. Heavily grazed areas without rhizomatous *Poa* swards often contain extensive patches of bare soil. In these sites, microbiotic crusts are restricted to the protective cover of shrubs, such as *Artemisia tridentata*, which impede trampling.

Artemisia tridentata, *Antennaria* spp., *Opuntia fragilis*, *Plantago patagonica*, and *Stipa comata* are recognized as native vascular plants that increase with disturbance (McLean and Marchand 1968). Areas with fewer disturbances support mid-successional vegetation that includes a rich assemblage of grasses, forbs, and microbiotic crust species. Common grasses in these sites include *Poa secunda* and *Koeleria macrantha*, while forbs include *Gaillardia aristata*, *Castilleja thompsonii*, *Lomatium dissectum*, *Calochortus macrocarpus*, and *Zigadenus elegans*. Areas that have escaped historic grazing are also rich in forbs but are dominated by the native bunchgrasses *Agropyron spicatum* and *Festuca campestris*. These form a dense canopy under which moisture dependent lichens and mosses grow.

1.15 Classification and exclosures

By linking succession with rangeland condition, McLean and Marchand (1968) provided an early look at classifying grasslands in British Columbia. They developed four condition classes: poor, fair, good, and excellent, based upon the percent cover of “decreasers” and “increasers”. Decreasers were defined as those vascular plants that decrease in cover with excessive grazing, such as *Festuca campestris* and *Agropyron spicatum*. Increaseers were defined as species that increase with moderate grazing and generally increase with continued overuse, such as *Stipa comata* and *Artemisia tridentata*. While not used in their classification, they defined a third category, called “invaders”, as native and non-native species that, though not a part of the climax community, are able to establish themselves as the community deteriorates. Plants considered invaders include *Bromus tectorum*, *Vulpia octoflora*, and *Plantago patagonica*. Microbiotic crusts or crust species were not included in their analysis. Their classification is generalized in Table 1.

Table 1. A summary of McLean and Marchand's (1968) rangeland classification system.

	Increaseers	Decreasers
Poor	70%	0-20%
Fair	50-70%	20-40%
Good	30-50%	40-60%
Excellent	0-30%	60%

The McLean and Marchand approach was amended in the B.C. Forest Practices Code. The Code, which is the principal legislation governing rangeland management in the province, contains guidelines for landscape level objectives in terms of seral classes of a successional sequence. Seral class targets are <10% early seral and >85% late seral or Potential Natural Community (PNC). Of the latter 85%, >12% must be in PNC (B.C. Ministry of Forests 1995a). A Potential Natural Community is equivalent to a natural community in a climactic condition, but allows for the presence of non-native, invasive species that are not possible to eradicate. The Range Management Guidebook outlines the methodology for determining the seral class of a site (B.C. Ministry of Forests 1995b). Unlike McLean and Marchand, the assessment approach in the guidebook monitors lichens and bryophytes at the lifeform level. The percent cover of vascular plants, lichens, and bryophytes are compared between the assessed site and a predetermined PNC site with similar environmental characteristics. The similarity to the PNC is used to determine the seral class (Table 2). This method requires the establishment of PNC sites for each management area. The approach suffers from two obstacles: 1) sufficient inventories of PNCs have not been conducted and 2) PNCs in the bunchgrass and ponderosa pine ecosystems in B.C. are extremely rare (B.C. Ministry of Forests 1995a) and, in fact, may not occur in some localities.

Table 2. The Forest Practices Code seral classification system (B.C. Ministry of Forests 1995a).

Seral Class	Target	Similarity to the PNC
Early	(<10%)	0-25%
Mid	(+Early<15%)	25-50%
Late	(+PNC>85%)	50-75%
PNC	(>12%)	75-100%

The problem of determining the floristics and structure of natural grassland communities was anticipated in the early part of the century when range managers initiated an exclosure program. Exclosures are fenced areas that exclude cattle and other domestic livestock. Currently B.C. has an inventory of 361 exclosures which have been monitored and maintained by the provincial Range Reference Area program. Exclosures vary in age from 70 years to those only recently built. Some exclosures show dramatic differences with the surrounding, grazed vegetation, while others show virtually no change. Historical inconsistencies in exclosure monitoring and repair has contributed to their variable appearance. Several exclosures have been subjected to repeated grazing when the fencing has been damaged. Another problem is that the exclosures are located in sites with varying characteristics (i.e. slope, aspect, and elevation) which render them difficult to compare. For these reasons, exclosures were not utilized in this study.

Today, there is considerable interest in exclosures and their use in determining PNCs. Though many exclosures are only recently built, and few could be considered PNCs, B.C.'s exclosure system holds promise for the future as benchmarks for management

objectives. Unfortunately, recent budgetary constraint has led to the cancellation of the Range Reference Area Program (Gayton 1999).

Daubenmire (1968, p. 177) advises that "Efficient range management depends on (1) a knowledge of the potentialities of every habitat type in the grazing unit, (2) an understanding of the grazing autecologies of both desirable and undesirable species in each habitat type, and (3) an ability to predict what changes in each ecosystem, and in the mosaic as a whole, would follow in the current type and intensity of grazing." In British Columbia we are only beginning to comprehend the wisdom of these objectives. Range managers have initiated programs to fulfil them, but such programs have suffered from consistent under-funding.

In the past few years the ranching community has made some gains in the recognition of microbiotic crusts. The latest revision of "The Rangeland Handbook for B.C." (Campbell and Bawtree 1998) not only includes the term "cryptogam" in the glossary, but also contains a photograph of a microbiotic crust species (*Cladonia pyxidata*) with a short description of what microbiotic crusts are. This recognition is significant, though it does not explain the importance of the microbiotic crust community to rangeland health, or how range management affects it.

1.16 Succession and vegetation development

The theory of plant succession describes the directional change of a plant community after disturbance (Clements 1916; Daubenmire 1968; Connell and Slatyer 1977; Zhang 1998). When the disturbance is large enough to remove all traces of the previous vegetation, the ensuing recolonization process is called primary succession. When the

disturbance merely disrupts the existing community, leaving evidence of its former nature, then the process which follows is called secondary succession (Clements 1916; Daubenmire 1968).

Succession and disturbance are intimately linked. Early successional sites are those that have experienced a recent disturbance, while late successional sites have escaped large-scale disturbances for longer time periods. Some ecosystems are prevented from attaining late successional development by repeated, natural disturbances such as flooding or fire. The traditional view of succession suggests that each site has a single, potential expression of undisturbed (climactic) vegetation (Clements 1916). This theory has been challenged by those who argue that even long-lived vegetation associations are subject to change given sufficient time, thus there is no true climactic vegetation (Connell and Slatyer 1977). Furthermore, that a site might have multiple stable vegetation associations is now widely recognized by ecologists (Connell and Slatyer 1977). These associations vary based upon the nature of the disturbance and the composition of the colonizing species. Daubenmire (1970) described several possible stable vegetation associations in the grassland steppe of Washington. These included a native, perennial bunchgrass association, a monotypic turf-grass association of *Poa pratensis*, and an association dominated by the annual *Bromus tectorum*. The latter two vegetation types are comprised primarily of non-native grasses and were shown to establish after high intensity grazing disturbance. They were determined to be stable nonetheless.

Ecologists have amended and expanded the explanations of the mechanisms and processes of succession. The intermediate disturbance hypothesis and positive feedback

mechanisms are two successional theories that pertain to microbiotic crust development and warrant discussion here.

The intermediate disturbance hypothesis was developed to describe observations of ecosystems that demonstrated maximum richness after a moderate level of disturbance (Connell 1978; Collins et al. 1995). This hypothesis has two two separate, but related models. The first is that maximum richness is attained with disturbances of a moderate intensity (Connell 1978; Collins et al. 1995). It is reasoned that moderate disturbances create a heterogeneous microhabitat structure that provides the required characteristics for the greatest numbers of species. The second model suggests that maximum richness is reached after an intermediate time span since disturbance. At an intermediate time period, both invasive, early successional plants, as well as those species that require more time to become established, will occupy the same site.

Positive feedback mechanisms contribute to the stability and productivity of a community through internal interactions. This concept is also known as bootstrapping, so called because its circularity has been compared to picking oneself up by ones own bootstraps (Perry et al. 1989). Positive feedback mechanisms have been reported in forested ecosystems where the vascular plants and fungi have been shown to positively influence the diversity of one another (Perry et al. 1989). These same ecosystems were shown to be particularly susceptible to shifting or collapsing when sensitive components of their composition were disturbed (Perry et al. 1989). Rietkerk and van de Koppel (1997) found that in a grassland setting, water infiltration and nutrient retention was enhanced by higher densities of vascular plants. This positive feedback system was

shown to degrade into a stable, low-density community when sufficient grazing disturbance was applied.

Objectives of this study

The nature of this research project is both floristic and ecological. It adds to existing lists of the bryophytes, and is the first to report the common terrestrial lichens of B.C.'s ponderosa pine forests. This study also seeks to understand the dynamics of the crust community in a system that is directly affected by the grazing of domestic livestock. It examines patterns of cover, richness, and the Shannon Indices of vascular plants and microbiotic crust species in the context of disturbance and succession. Indicator species and lifeforms of lichens and bryophytes are evaluated for their use in determining successional progress. The objectives of the study are summarized as follows:

1. To document the liverworts, mosses, and lichens of microbiotic crusts in the ponderosa pine forests near Kamloops, B.C., and to produce an illustrated key to the common species occurring within the study area.
2. To examine successional patterns of vascular plants and microbiotic crust in areas subject to grazing.
3. To examine microbiotic crusts species, and lifeforms of lichens and bryophytes, as indicators of succession.

Chapter 2

METHODS

2.1 Study area

Climate

The climate of the Kamloops region is characterized by low annual precipitation (269.5 mm) that peaks in the summer and winter months (Figure 3). The mean annual temperature (8.6 °C) is greatly exceeded in the summer months, causing rapid evaporation. The ability to tolerate low moisture conditions is a primary determinant in the local vegetation. Precipitation increases dramatically northward up the North Thompson valley, and eastward, toward Shuswap Lake (Figure 6). This is marked by an associated change in the vegetation. Ponderosa pine (*Pinus ponderosa*) is replaced by Douglas-fir (*Pseudotsuga menziesii*), and later by hemlock (*Tsuga heterophylla*) and cedar (*Thuja plicata*).

Kamloops Weather 1951-1990 Environment Canada

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Mean Precipitation (mm)	26.1	13.8	9.6	14.8	21.8	28.6	27.9	30.2	27.6	14.4	22	32.6	269.5
Mean Temperature (Celsius)	-4.8	-0.6	4.5	9.4	14	18.3	20.8	20.3	14.9	8.5	1.7	-3.3	8.6

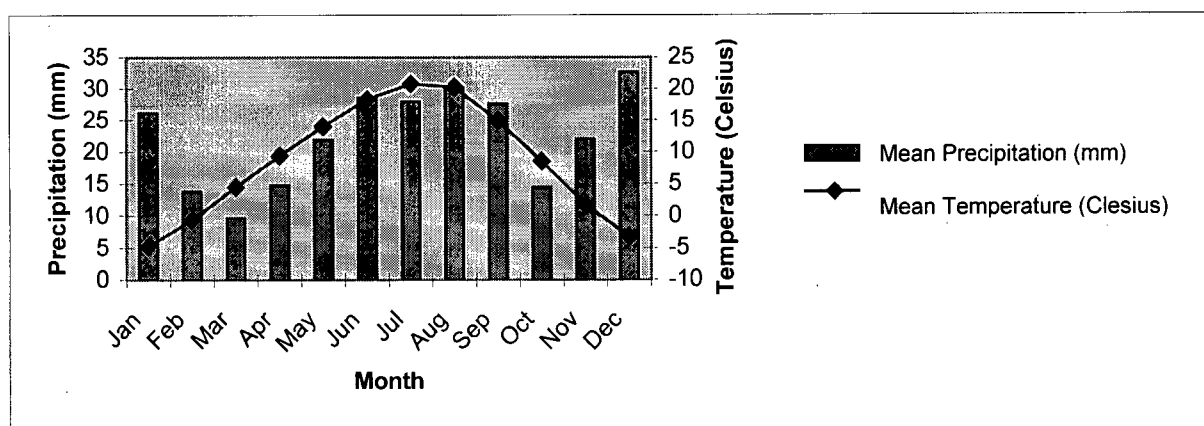


Figure 3. The climate of Kamloops. Mean monthly precipitation (mm) and temperature (Celsius) and yearly averages. (Environment Canada 1999)

Geomorphology

The post-glacial geomorphological history of the South Thompson valley has been thoroughly studied by Fulton (1965, 1967) whose work is summarized here. Ice from the Pleistocene glaciation carved a "U" shaped valley from the basalt parent material of the South Thompson valley. As the ice retreated, a blanket of glacial till was left on the valley floor. The retreating glacier fed a river that flowed east into the Okanagan Valley, depositing glacio-fluvial material over the till. Ice-dams, remnants of retreating glaciers, formed on both ends of the South Thompson Valley, at Kamloops to the east, and Chase to the west. Kamloops Lake and the North Thompson Valley were ice-filled at this time. These dams caused the valley to fill with water and the subsequent forming of Glacial Lake Thompson. Lake Thompson varied in size as the ice melted; however, its duration was sufficient to create a silt and sand lacustrine deposit over 150m deep in the central part of the valley.

When the ice dams finally melted, the river flowed west into the Fraser Valley, carving a river channel through the soft, silty, lacustrine substrate. The retreat of the ice was accompanied by strong winds that carried silt and fine sand, forming an eolian cap on the eroding lacustrine terraces. Finally, periodic flooding of the South Thompson River created flood plains (Figures 4 and 5). Over time, ponderosa pines, bunchgrasses, and microbotic crust species colonized the lacustrine terraces and upper till slopes. This study was conducted on these forested, lacustrine terraces (Figure 4).



Figure 4. Glacial lakebed terraces above the South Thompson River, 5km east of Kamloops, British Columbia. The study sites were located in ponderosa pine stands, on the top of the terrace, on the south (left) side of the river. The view is westward, toward Kamloops.

Cross section through South Thompson Valley

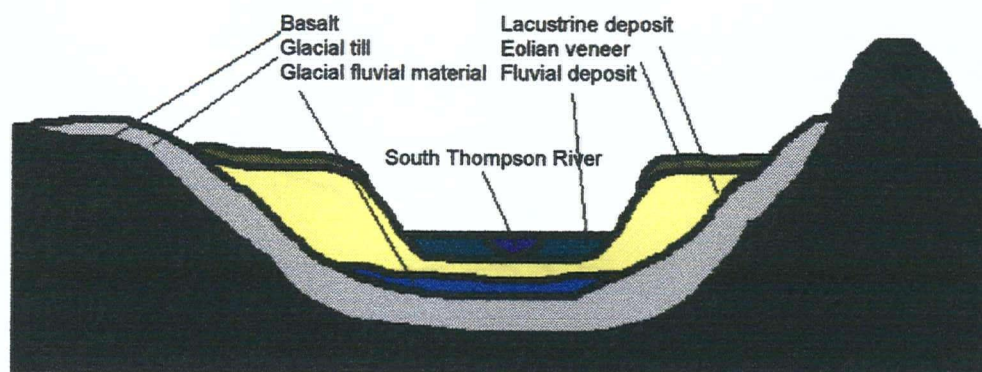


Figure 5. A cross section through the South Thompson Valley showing the geological composition of the study area.

A similar process of glacial lake formation and lakebed deposition occurred in the Nicola Valley, the Okanagan Valley, and the Rocky Mountain Trench. These localities also support ponderosa pine forests, though the relationship is incidental rather than causal. The distribution of ponderosa pine forests is primarily climatic, and not substrate dependent. The ecology of these terraced localities is very similar to the Kamloops research site. Conclusions from the present study also pertain to these other sites.

Site characteristics

Sites were oriented along an 18km long east-west transect on the south side of the South Thompson River (Figures 4 and 6). The elevation ranged between 500m and 600m and slopes remained between 2-15%, with a north aspect. Soils were Orthic Eutric Brunisols, characterized by a silty sand eolian veneer over silt and sand lacustrine terraces. Coarse fragments were rare or absent. Sites were restricted to a zonal position in the Ponderosa Pine zone as defined by the provincial biogeoclimatic classification system (Lloyd et al. 1990). In total there were 19 sites.

2.2 Field methods

Field sampling was conducted using a point-sampling frame (Figure 7). The frame, a one metre long aluminum bar with a vertical hole drilled every ten

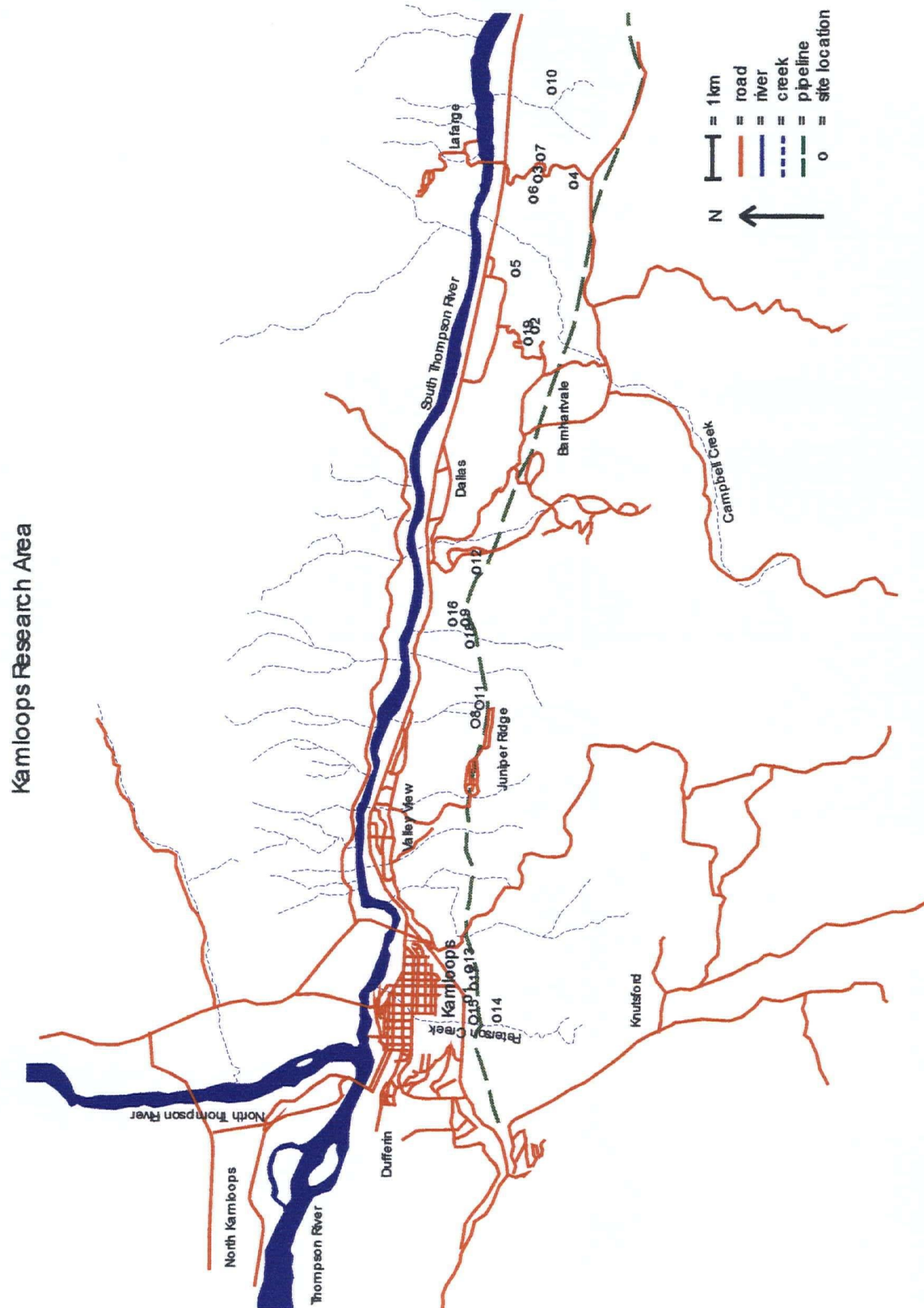


Figure 6. A map of the study area near Kamloops, British Columbia. Sites are labeled from most disturbed to least disturbed (1-19).

centimeters, was positioned using two tripods. A stainless steel rod with a fine point was directed through the holes in the frame and onto the vegetation, producing a series of precise sampling points. The sampling frame was positioned at random intervals along five 50m transects that were oriented at random distances along a 40m base line (Figure 8). Each transect was sampled with ten placements of the sampling frame to produce 100 points per transect. These points were used to determine the percent cover of microbiotic crust species, vascular plants, bare soil, rock, gravel, stone, litter, and standing dead vegetation. Location information and site characteristics including latitude, longitude, slope, aspect, biogeoclimatic zone, site series, soil texture, site history, and tree importance values were also recorded at each site.

2.3 Laboratory methods

Specimens were collected in paper bags and allowed to dry. Squamulose and crustose lichens borne on soil aggregates and susceptible to crumbling were curated by moistening the aggregate and removing excess soil with a razor, followed by soaking the aggregate in diluted white glue (4:1, water:glue). The glue infused aggregate was allowed to dry and was then fastened to an 8cm by 12cm card with undiluted glue. This methodology is discussed by Rosentreter et al. (1988).

Identifications of bryophytes were made using floras by Lawton (1971), Smith (1990), and McIntosh (1986). Lichens were identified using floras by Noble (1982), Goward et al. (1994), McCune and Goward (1995), McCune (1995), and Goward (1999).



Figure 7. A point sampling frame on a 50m transect. The frame contains ten point sampling slots and was positioned ten times on each of the five transects. This provided a sample of 500 points per site.

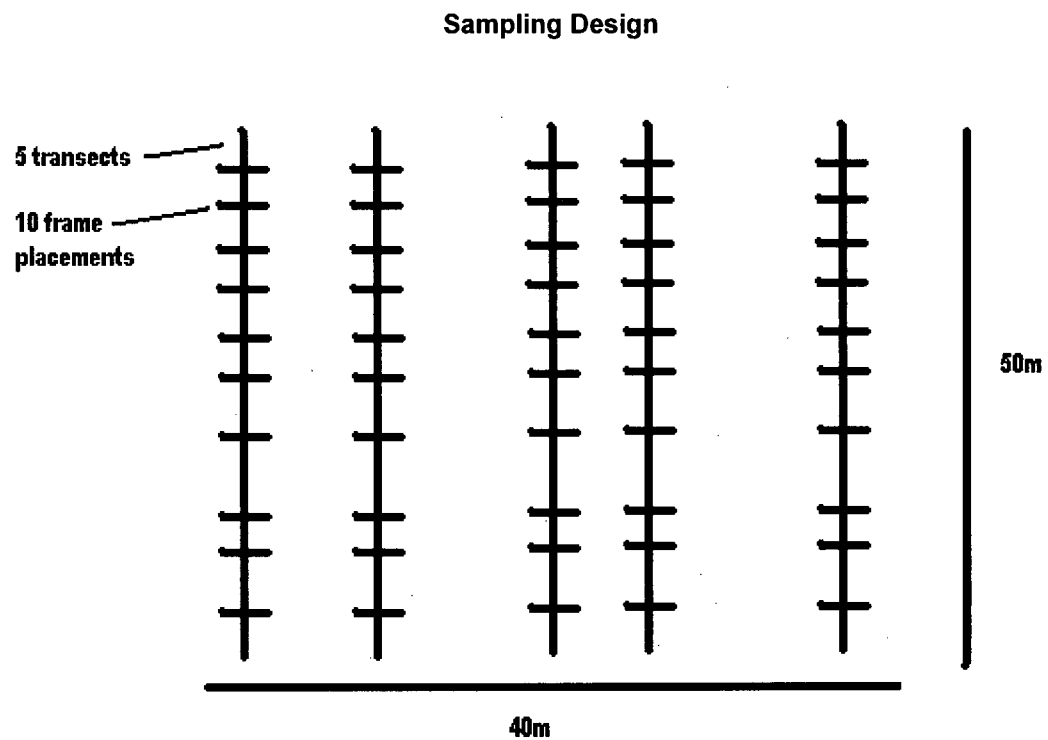


Figure 8. A diagram of the sampling design. Transects were arranged randomly along a 40m base line. In total, 19 sites were sampled.

Dr. W. Schofield, Dr. T.T. McIntosh, and T. Goward provided assistance with difficult taxa. Hitchcock and Cronquist (1973) and Douglas et al. (1989, 1990, 1991, and 1994) were used to identify vascular plants. Specimens were deposited in the University of British Columbia herbarium (UB.C.). Replicate specimens were submitted to the B.C. Ministry of Forests, Range Branch, in Victoria and in Kamloops, B.C. In total, over 1500 bryophyte and lichen specimens representing 120 species were collected and identified during the study. Nomenclature followed Douglas et al (1989, 1990, 1991, and 1994) for vascular plants, Esslinger and Egan (1995) for lichens, Anderson et al. (1990) for mosses, and Stotler and Crandall-Stotler (1977) for liverworts.

Some genera, particularly *Cladonia*, can be difficult to identify to species, particularly when reproductive structures are absent. When it was not possible to fully identify specimens, they were classified to genus. The species *Cladonia symphy carpia* posed a taxonomic problem, a result of its similarity to *C. cariosa* (Ach.) Sprengel. These two species were not differentiated during this study and were grouped under the name *C. symphy carpia*. *Cladonia pyxidata* and *C. pocillum* are also superficially similar, and required particular attention.

2.4 Analytical methods

Both multivariate and univariate approaches were used to elucidate the relationships among sites of varying disturbance and the succession of vascular plants and cryptogamic crust species. Principal Components Analysis (PCA) was used to examine site dependent patterns of microbiotic crust succession. All PCAs were performed using the statistical package SYSTAT version 8.0 (1998). PCA allows for comparisons of all species

variables by producing principal components that summarize the variance of all the variables in the matrix (Gauch 1982). As Gauch (1982, p. 143) states succinctly "Unquestionably, the most common function of PCA is simply descriptive- reduction of the dimensionality of a data set to manageable proportions while preserving as much of the original structure as possible." The matrix for the PCA included vascular plant and microbiotic crust species cover values for those species with a total cover value over all 19 sites greater than 10. Using the cover limit reduced the incidence of zero values in the matrix. The data matrices were comprised of 95 transects that were grouped by site. Sites were arranged from most disturbed to least disturbed (1-19) as ranked by the percent cover of the two large, native perennial bunchgrasses, *Festuca campestris* and *Agropyron spicatum*. These species were chosen as an index of disturbance because they are known to decrease in cover under intensive grazing systems, and are slow to recover once grazing is removed (Daubenmire 1968, 1970; McLean and Marchand 1968). Heavily grazed sites have little cover of these grasses, while undisturbed sites have the greatest cover. PCAs were used to examine patterns in vascular plants, microbiotic crust species, and all of the vegetation together.

Univariate analysis provided further insight into the nature of vascular plant and microbiotic crust succession. To better summarize the variability of the data, sites were placed into four disturbance groups. These were created by dividing the 19 sites into four groups, once again, based on the prevalence of the native perennial bunchgrasses *Festuca campestris* and *Agropyron spicatum*. Each group contained 5 sites with the exception of the first, which was arbitrarily chosen to have 4 sites. The data was analyzed by transect, each site having 5 transects, thus each group had $n=25$ except the first which had $n=20$.

The earliest successional sites, those with the most recent disturbance, belong to group 1 and the latest successional sites to group 4. Error bars were used to indicate the standard error. The cover of vascular plants and microbiotic crust species was plotted against the disturbance groups to determine cover patterns with succession. The cover of “increasers” and “decreasers” among vascular plants over the four disturbance groups was also plotted.

Richness, or the number of species per transect, was plotted using the same approach as for cover. The Shannon Diversity Index incorporates the number of species and their percent cover to form an index that is often used as a measure of biodiversity (Zar 1984). Shannon Indices were calculated using the formula:

$$S.I. = -\sum_{i=1}^k p_i \log p_i$$

where k is the number of species in each disturbance group and p_i is the proportion of the total cover occupied by species i . Shannon Indices were calculated by site and not by transect. Thus $n=5$ per group ($n=4$ for group 1).

Lifeforms were analyzed from cover values using the same approach as described for the vascular plants. Crustose and squamulose lifeforms were combined, as were foliose and fruticose lifeforms, and compared over the four disturbance groups. The crustose and squamulose lifeforms were combined because they were observed to occur together in drier, more open microsites, while foliose and fruticose were more common in shaded microsites.

Previous studies have divided the bryophytes into mosses and liverworts for analysis (Eldridge and Rosentreter 1999). This study takes a different approach and divides these species into acrocarpous and pleurocarpous lifeforms. Acrocarpous species are those with

sporophytes at the ends of determinate branches (Schofield 1985). Their main axes are vertically oriented. Pleurocarpous species have lateral sporophytes and have creeping, main axes. This division was chosen because it was postulated that the different lifeforms would respond differently to changes in ecological conditions related to grazing.

Chapter 3

RESULTS

3.1 Floristics

This study is the first to examine the floristics of microbiotic crusts of the ponderosa pine forests of the Kamloops area. While not an exhaustive floristic inventory, it includes most of the terrestrial bryophytes and lichens from the study area. An illustrated key to the common liverworts, mosses, and lichens of the ponderosa pine forests of British Columbia is provided in Appendix A. Species of lichens, bryophytes, and vascular plants recorded in the 19 sites are listed in Appendix B. Species found adjacent to, though not within, the 19 sites are shown on Table 3.

Table 3. Microbiotic crust species collected adjacent to the study sites within the study area.

Lichens

Bryonora castanea (Hepp) Poelt
Caloplaca cerina (Hedw.) Th. Fr.
Cladina arbuscula (Wallr.) Hale & Culb.
Cladina mitis (Sandst.) Hustich
Cladonia ecmocyna Leighton
Cladonia multiformis G. Merr.
Cladonia subulata (L.) F.H. Wigg.
Cladonia umbricola Tonsberg & Ahti
Cladonia uncialis (L.) F.H. Wigg.
Flavocetraria nivalis (L.) Karnefelt & Thell
Fulgensia desertorum (Tomin) Poelt
Lecanora muralis (Schreber) Rabenh.
Massalongia microphylliza (Nyl. ex Hasse) Henssen
Nephroma parile (Ach.) Ach.
Physconia enteroxantha (Nyl.) Poelt
Psora decipiens (Hedw.) Hoffm
Solorinella asteriscus Anzi.

Bryophytes

Aloina rigida (Hedw.) Limpr.
Buxbaumia aphylla Hedw.
Didymodon occidentalis (Mitt.) Zander
Didymodon rigidulus Hedw.
Hypnum revolutum (Mitt.) Lindb.
Leptobryum pyriforme (Hedw.) Wils.
Pseudoleskeella tectorum (Brid.) Broth.
Schistidium cuspidatum Blom
Mannia fragrans (Balbis) Frye et Clarke

McIntosh's (1986) thesis remains the most thorough and useful treatment of dryland bryophytes of British Columbia, and while the work focused on grassland communities, it includes many of the species from ponderosa pine forests. The present study contributes the following species to previous reports for B.C.'s ponderosa pine forests (Schofield 1988): *Barbula unguiculata*, *Buxbaumia aphylla*, *Dicranum polysetum*, *Ditrichum flexicaule*, *Encalypta rhaptocarpa*, *Encalypta vulgaris*, *Fissidens bryoides*, *Rhytidiopsis robusta*, *Sanionia uncinata*, *Schistidium cuspidatum*, *Timmia austriaca*, *Barbilophozia hatcheri*, *Lophozia excisa*, *Ptilidium ciliare*, and *Ptilidium pulcherrimum*.

Table 4 lists the potentially rare lichens and a single rare bryophyte observed during this study. Included is the number of collections for each species contained within the U.B.C. herbarium, B.C.'s largest collection. These values represent collections presently housed in the herbarium and do not account for loans or the collection maintained at the residence of Trevor Goward, U.B.C.'s curator of lichens. Included in Table 4 is the rarity status of listed species (Goward 1996, Ryan 1996).

Table 4. Potentially rare lichens and bryophytes of the study sites and adjacent areas. The number of collections in the U.B.C. herbarium do not include vouchers from the present study. S1 = critically imperilled within B.C. (Goward 1996, Ryan 1996). R = considered rare by Goward (1996).

Species	UB.C. Herbarium Collection	Rare Status
Lichens		
<i>Arthonia glebosa</i>	3	
<i>Bryonora castanea</i>	0	
<i>Buellia geophila</i>	1	
<i>Buellia papillata</i>	0	
<i>Caloplaca cerina</i>	4	
<i>Caloplaca jungermanniae</i>	4	
<i>Caloplaca tominii</i>	5	
<i>Candeleriella terrigena</i>	1	
<i>Catapyrenium lacinulatum</i>	6	
<i>Cladonia botrytes</i>	4	
<i>Cladonia rei</i>	0	
<i>Collema coccophorum</i>	1	R
<i>Collema crispum</i>	2	
<i>Collema tenax</i> var. <i>crustaceum</i>	0	
<i>Endocarpon pusillum</i>	2	
<i>Flugensia desertorum</i>	0	
<i>Massalongia microphylliza</i>	0	S1
<i>Phaeophyscia constipata</i>	11	
<i>Placyntheilla uliginosa</i>	0	
<i>Polychidium muscicola</i>	1	
<i>Psora cerebriformis</i>	8	R
<i>Psora globifera</i>	12	
<i>Psora montana</i>	0	R
<i>Psora nipponica</i>	6	
<i>Psora tuckermanii</i>	7	
<i>Solorinella asteriscus</i>	0	R
Mosses		
<i>Aloina bifrons</i>	13	S1

3.2 Principal Components Analysis

Figure 9 shows a PCA ordination of the vascular plant cover variables. Each number on the ordination represents a single transect. Four disturbance groups, label 1-4 (most disturbed to least disturbed), are indicated by 68.3% confidence ellipses. The factor loadings show how each vegetation variable relates to the principal components using

vectors. The vector length indicates the strength of the relationship to the component. The variance explained by principal component 1 and 2 are 15.1% and 14.4% respectively. Disturbed sites are distributed along the positive end of principal component 1 and undisturbed sites occur toward the negative end. Thus, the first PCA axis of the vascular plant data represents a disturbance gradient. The pattern of distribution of sites along component 2 (Figure 9) indicates variation among sites within disturbance groups. The factor loadings plot shows how early successional species, such as *Artemisia frigida* (ARTEFRI), *Antennaria parviflora* (ANTEPAR), and *Stipa comata* (STIPCOM) associate with the disturbed sites on component 1, while the late successional species *Agropyron spicatum* (AGROSPI) and *Festuca campestris* (FESTCAM) are negatively related, and thus are found in undisturbed sites. Species that tend to increase with disturbance such as *Antennaria umbelata* (ANTEUMB), *Artemisia tridentata* (ARTETRI), and *Achillea millifolium* (ACHIMIL) are positively related to component 2.

Figure 10 shows the PCA ordination of sites and the factor loadings plot for microbiotic crust species. The sites in the microbiotic crust PCA show a strong clustering toward the centre of the ordination, indicating much overlap in species composition regardless of disturbance. *Cladonia pyxidata* (CLADPYX), *Physconia muscigena* (PHYSMUS), and *Polytrichum piliferum* (POLYPIL) are species that proliferate in disturbed sites and positively relate to component 1. Species that inhabit moderately disturbed sites, such as *Diploschistes muscorum* (DIPLMUS), are positively related to component 2, while *Cladonia chlorophaea* (CLADCHL), a species that prefers undisturbed microsites, is

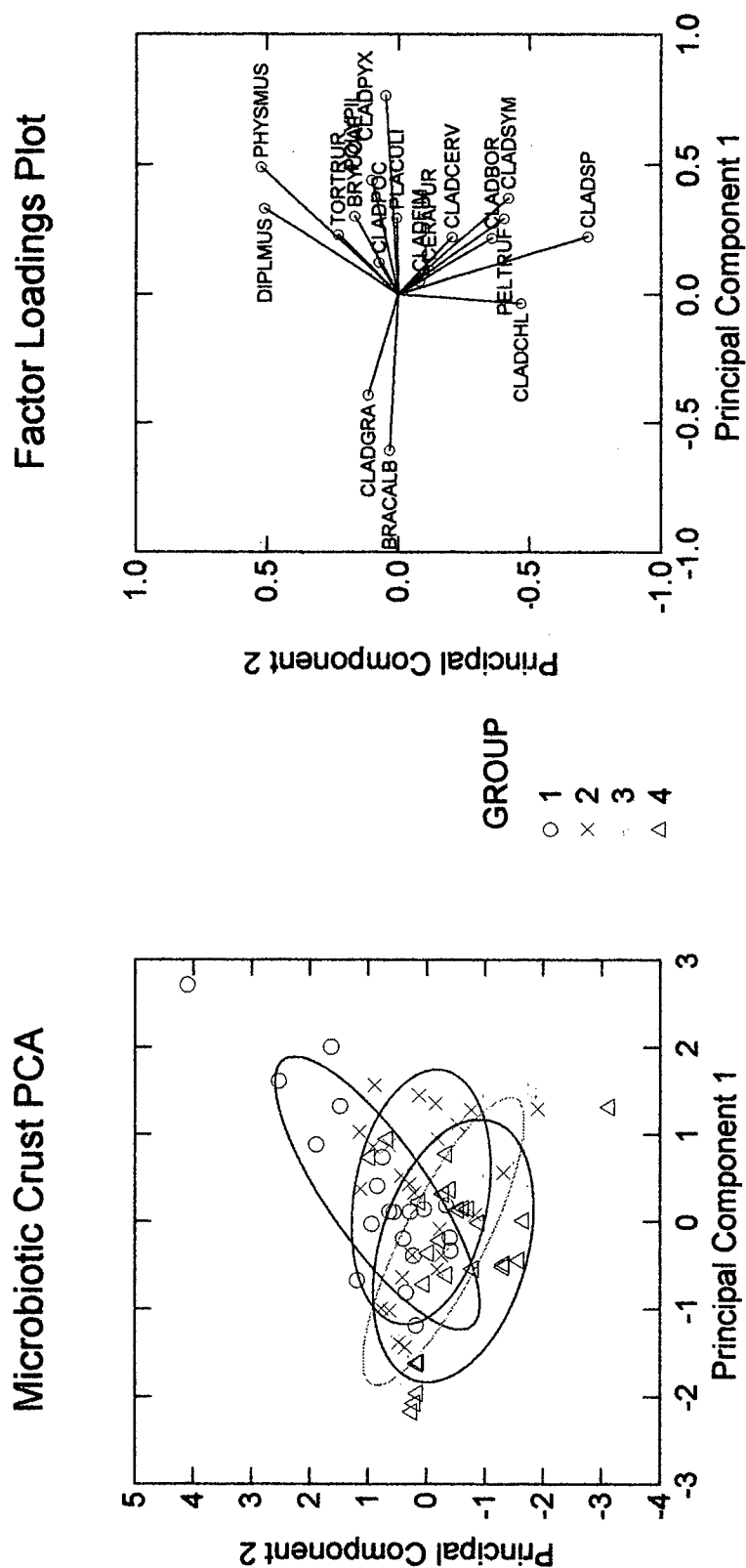


Figure 10. The PCA ordination and factor loadings plot of microbiotic crust species over four disturbance groups. The first two components account for 12.7% and 10.6% of the total variance respectively.

negatively related. *Brachyhectium albicans* (BRACALB) and *Cladonia gracilis* (CLADGRA), which are late successional species, are negatively related to the first component. Variances explained by the two components are 12.7% and 10.6% respectively.

Both vascular plant and microbiotic crust species were analyzed together to determine species affinities. This was plotted in Figure 11. The axes explain 10.6% and 9.0% of the total variance of the data matrix. The factor loadings plot shows a cluster of *Festuca campestris*, *Brachyhectium albicans*, and *Cladonia gracilis* in the least disturbed sites, while *Artemisia frigida*, *Stipa comata*, *Physconia muscigena*, *Diploschistes muscorum* (DIPLMUS), and *Cladonia pyxidata* occur in sites with the greatest disturbance. The distribution along component 2 suggests that the earliest and latest sites are low on the axis and the middle sites are high. Species that show a strong relationship to this axis include *Antennaria umbellata*, *Agropyron spicatum*, *Artemisia tridentata* (ARTETRI), and *Cladonia* spp. (CLADSP) squamules.

3.3 Cover, richness and Shannon Indices

Figure 12 shows the cover of increasers and decreasers among vascular plants. As expected, increasers respond positively to disturbance, while decreasers demonstrate the greatest cover in the latest group. The error bars indicate the standard error. Figure 13 shows the cover values of vascular plants and microbiotic crust species over the four disturbance groups. Both vascular plants and microbiotic crust species have the greatest cover in undisturbed sites (disturbance group 4); however, the differences within the vascular plants are small.

Vascular plant richness does not change over the four disturbance groups (Figure 14). It is possible that native perennials replace native and introduced early successional species in a way that the overall richness remains relatively even. Microbiotic crusts demonstrate the greatest richness in the second disturbance group, indicating that a moderate amount of disturbance increases the number of species present (Figure 15).

The Shannon Indices for both vascular plants and microbiotic crust species did not differ between disturbance groups (Figure 16 and 17).

3.4 Lifeform analysis

Crustose and squamulose lichens comprise 23% cover in disturbance group 1 and plateau between 34-39% in groups 2-4 (Figure 18). The cover of fruticose and foliose species is low (<10%) across all four disturbance groups (Figure 19); however, there is a modest increase from 5% to 8% in the disturbance group 4. Figures 20 and 21 show that the cover of acrocarpous and pleurocarpous bryophytes both increase when disturbance is removed. Acrocarpous species initially comprise 8% cover and attain up to 20% in undisturbed sites. The cover of pleurocarpous species is very low (2%) in recently disturbed areas, and most noticeably increases (from 7% to 17%) in disturbance group 4.

The Cover of Increasers and Decreasers

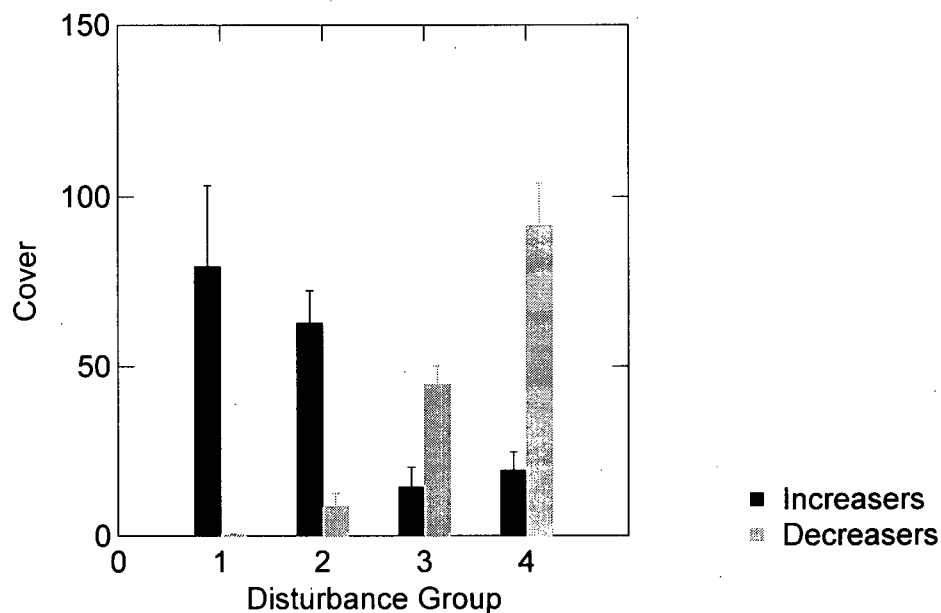


Figure 12. The cover of “increasers” and “decreasers” among vascular plants over four disturbance groups (+/- SE). Increasers include *Antennaria dimorpha*, *A. parviflora*, *Artemisia tridentata*, *Bromus japonicus*, *B. tectorum*, *Centaurea diffusa*, *C. maculosa*, *Medicago lupulina*, *Plantago patagonica*, *Poa pratensis*, *P. secunda*, and *Stipa comata*. Decreasers included *Agropyron spicatum*, *Amelanchier alnifolia*, *Arnica fulgens*, *Astragalus collinus*, *Carex petasata*, *Erigeron corymbosus*, *Festuca campestris*, *Gaillardia aristata*, *Heuchera cylindrica*, and *Lomatium dissectum*.

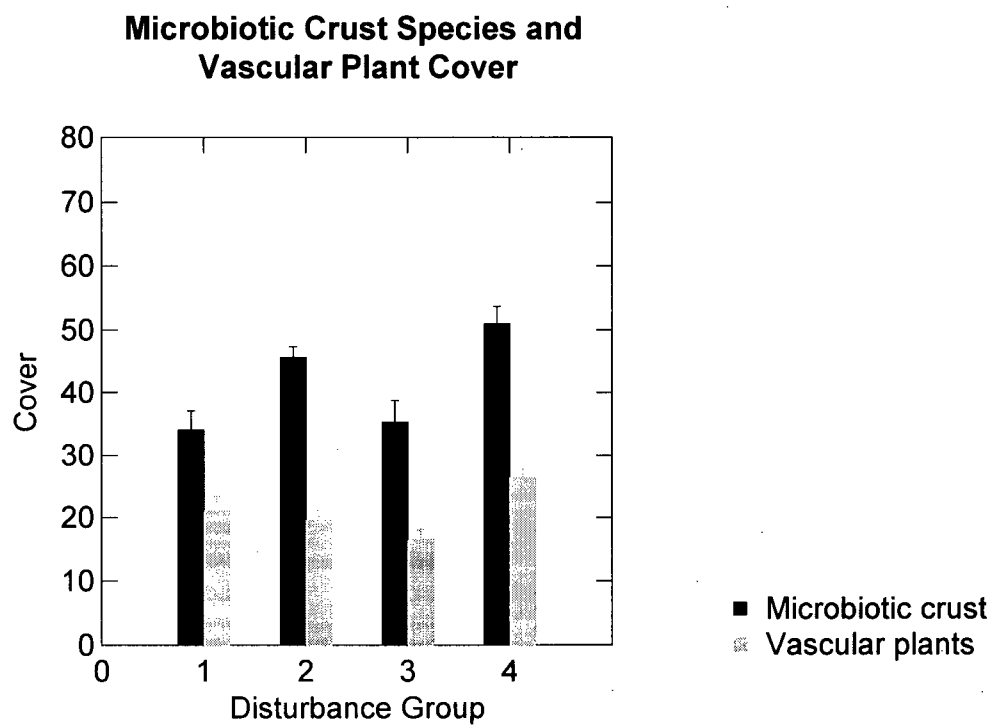


Figure 13. The cover of microbiotic crust species and vascular plants over four disturbance groups (+/- SE).

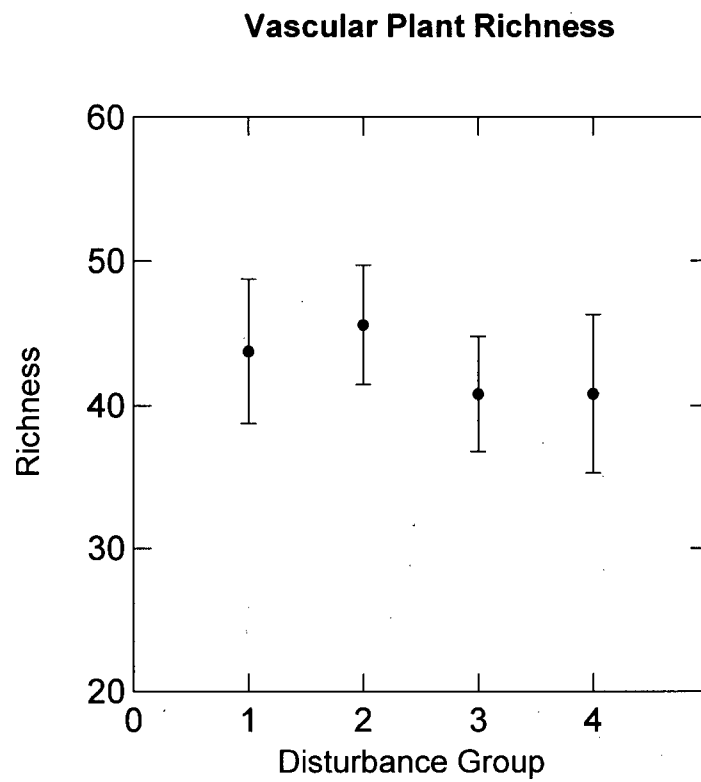


Figure 14. Vascular plant richness over four disturbance groups (+/- SE).

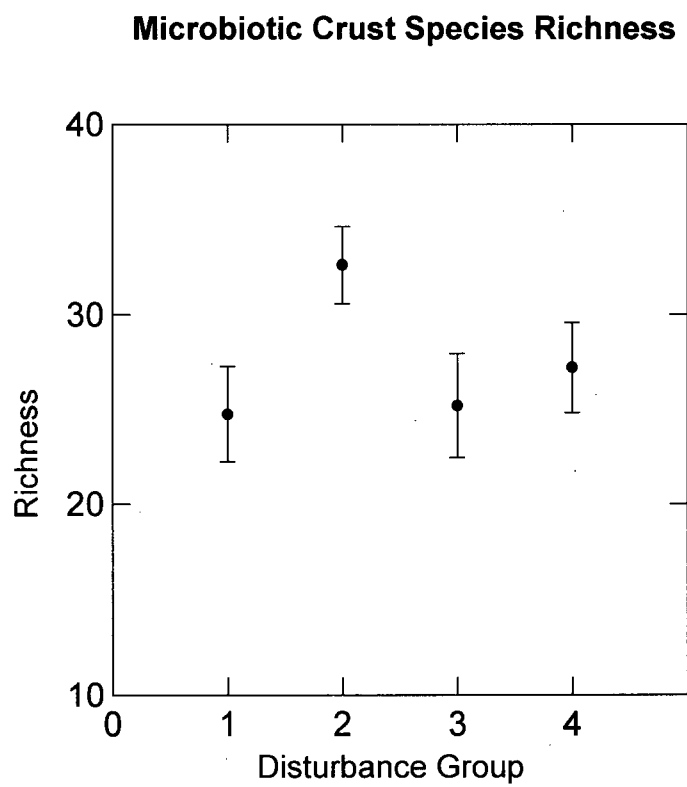


Figure 15. Microbiotic crust species richness over four disturbance groups (\pm SE).

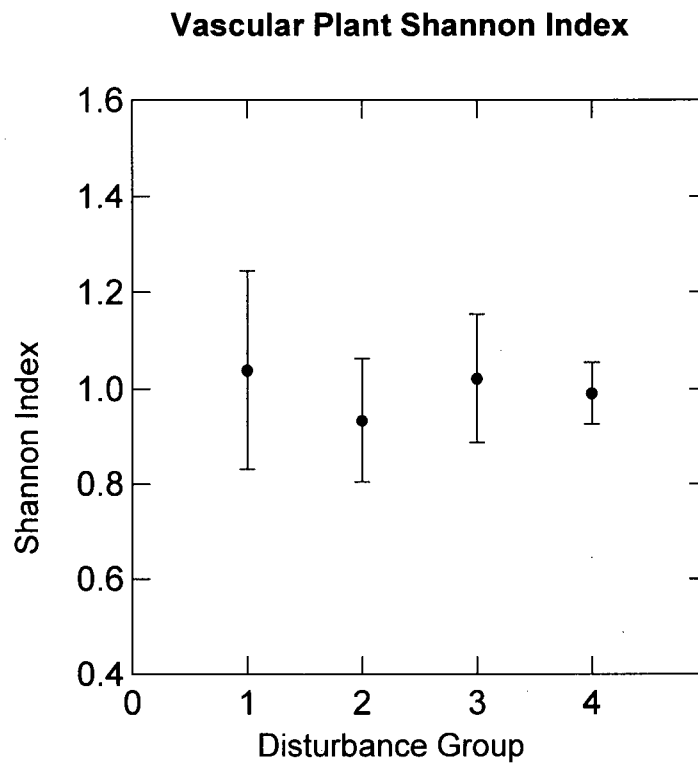


Figure 16. Vascular plant Shannon Index over four disturbance groups (+/- SE).

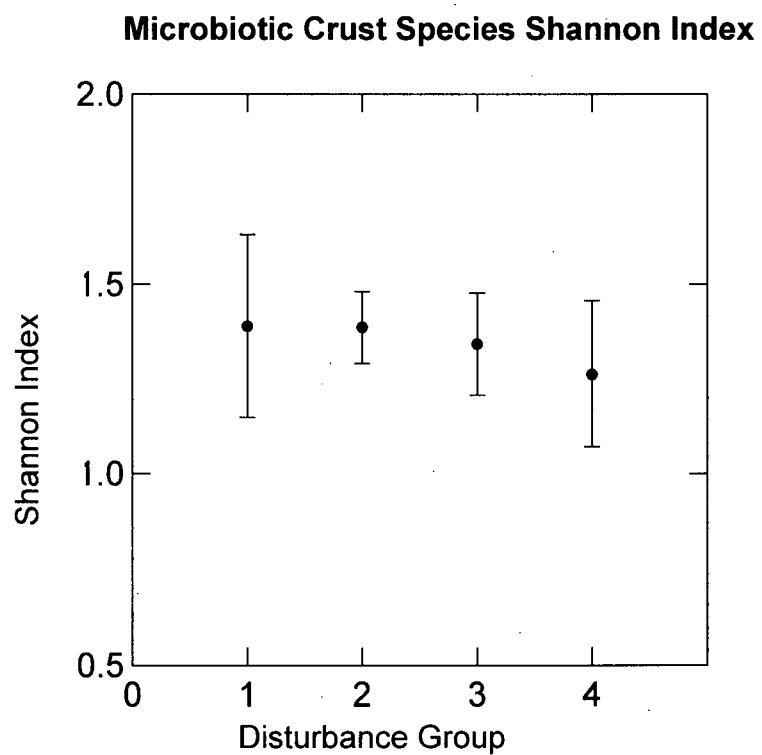


Figure 17. Microbiotic crust species Shannon Index over four disturbance groups (\pm SE).

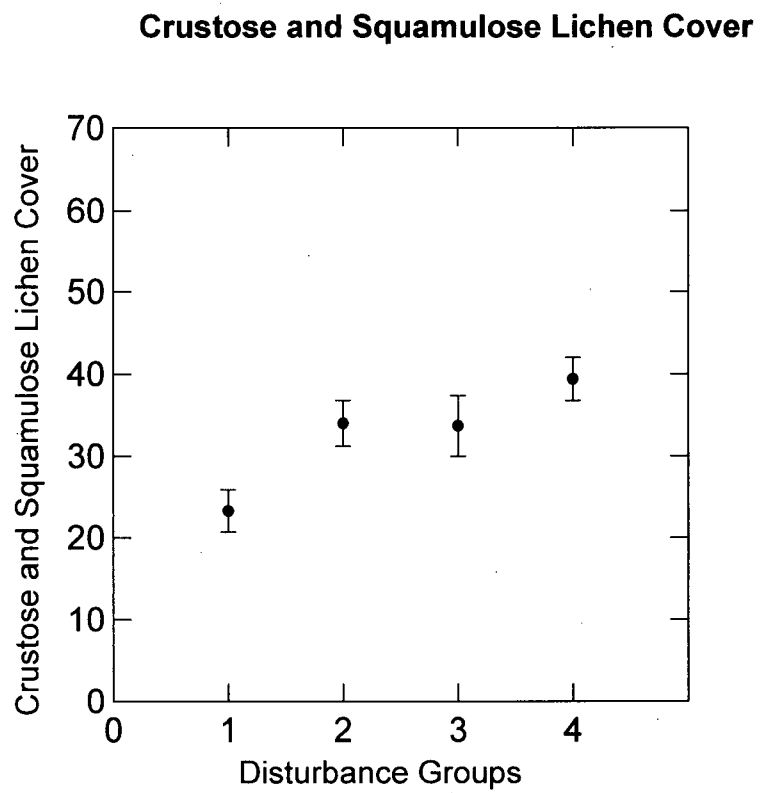


Figure 18. The cover of crustose and squamulose lichens over four disturbance groups (\pm SE).

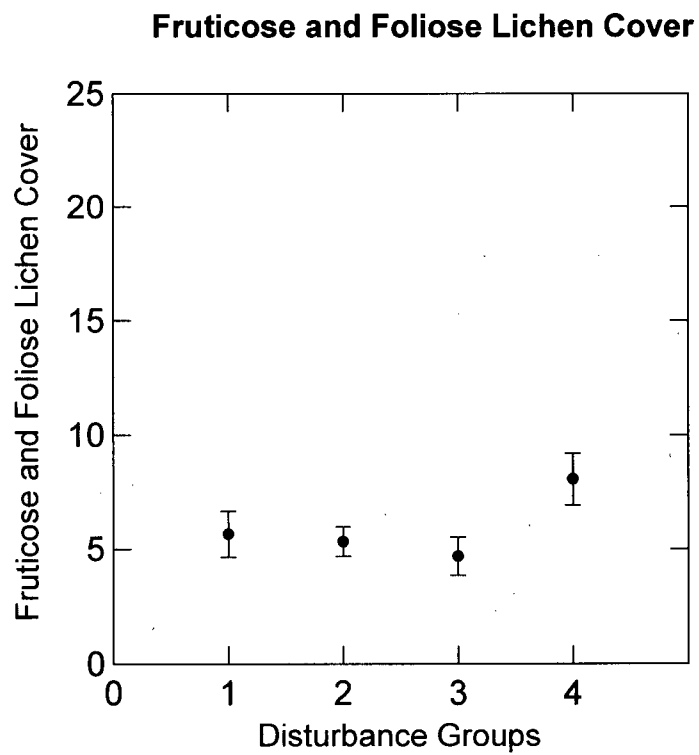


Figure 19. The cover of fruticose and foliose lichens over four disturbance groups (\pm SE).

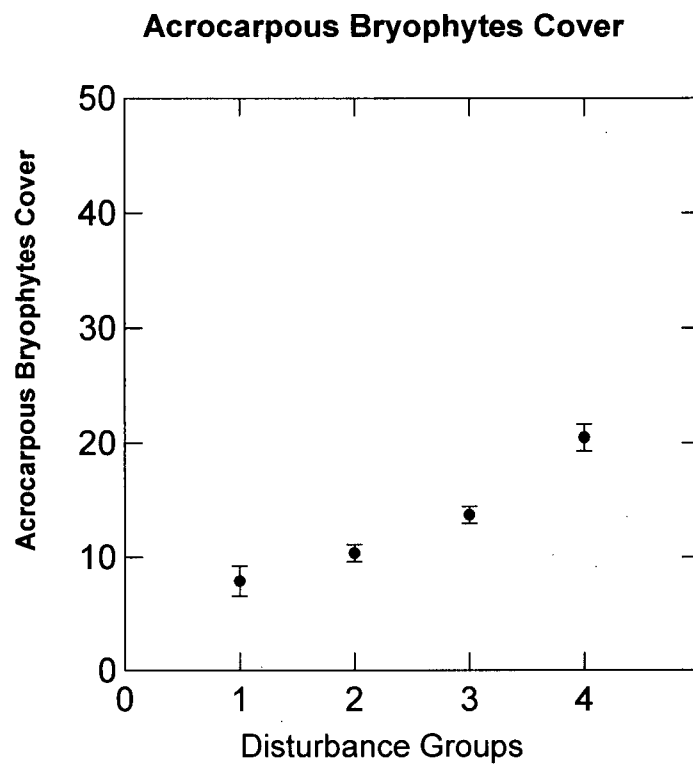


Figure 20. The cover of acrocarpous bryophytes over four disturbance groups (\pm SE).

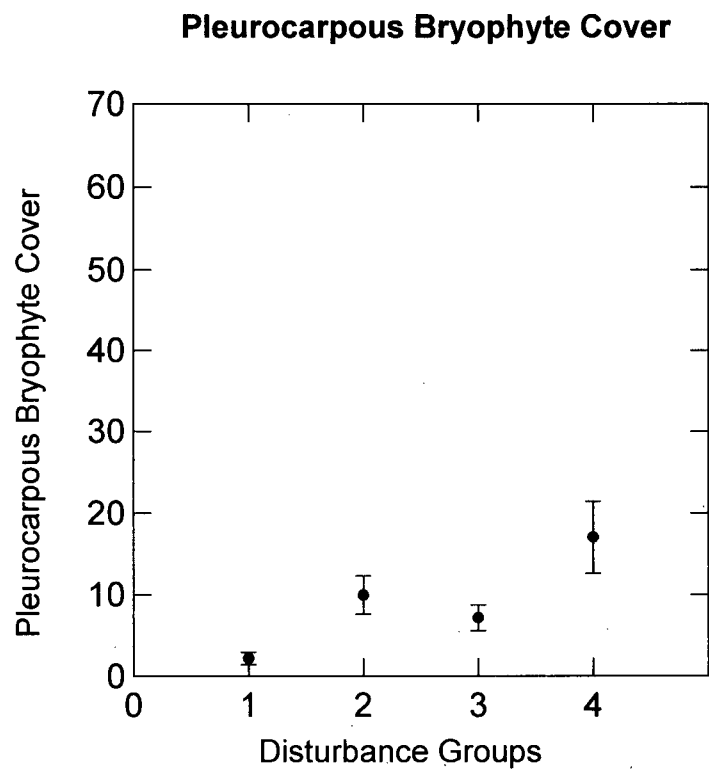


Figure 21. The cover of pleurocarpous bryophytes over four disturbance groups (\pm SE).

Chapter 4

DISCUSSION

4.1 Phytogeography

Much of British Columbia's dryland lichen and bryophyte flora occurs throughout the northern hemisphere (Lawton 1971; Thomson 1984, 1997; McIntosh 1986). This distribution pattern has been used to support the concept of widespread plant communities prior to continental drift. Looman (1964b) suggests that the North American flora resembles the European flora because they were once part of the same grassland ecosystem when both continents were joined as the Mesozoic continent, Laurasia. However, several of the species from the study area have also been reported from dryland ecosystems of the southern hemisphere, including the lichens *Acarospora schleicheri*, *Catapyrenium squamulosum*, *Collema coccophorum*, *Diploschistes muscorum*, *Endocarpon pusillum*, *Psora decipiens*, and the bryophytes *Aloina bifrons*, *Bryum argenteum*, *B. caespiticium*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, *Desmatodon convolutus*, and *Pterygoneurum ovatum* (Eldridge 1996a; Eldridge and Tozer 1996; Eldridge and Koen 1998). Lange (1971) argues that the North American and Australian continents, which were not joined in tectonic history, share many species in common, and thus demonstrate the dispersal capabilities of lichens and bryophytes.

The small size of bryophyte and fungus spores enables them to travel enormous distances. It is possible that the global distribution of microbiotic species may be less dependent upon the proximity of source populations than on the availability of suitable environmental conditions (Lange 1971; Friedmann and Galun 1974). However, Eldridge

and Rosentreter (1999) point to the lack of direct evidence for long distance establishment. They argue that there is a low probability of a lichenized fungal spore and its compatible photobiont encountering one another under the necessary environmental conditions. Instead, they suggest that species are more likely to colonize using asexual propagules that contain both the mycobiont and the phycobiont. While localized reintroductions are likely a result of larger diaspores such as soredia, isidia, or thallus fragmentation, this mechanism does not account for the common species of widely separated continents. Though lichen reproduction remains poorly understood, there is some evidence that fungal spores from one lichen are able to obtain algae from the soredia of another lichen. This suggests that compatible encounters over large distances may be more frequent than previously imagined, supporting the distance dispersal hypothesis.

Despite the relative proximity to the Columbia Basin and Great Basin, the Kamloops lichen and bryophyte floras are markedly different. Studies from the Great Basin report microbiotic communities that generally support fewer species than in the Kamloops area (St. Clair et al. 1993). B.C. is particularly rich in the genus *Cladonia* (Goward and Ahti 1997), which increases in species richness latitudinally from California to B.C. The increase in *Cladonia* richness reflects summer precipitation, a characteristic of more northerly latitudes (Goward and Ahti 1997).

4.2 Floristics

Ponderosa pine forests on silt terraces near Kamloops B.C. support an unusually rich assemblage of terricolous lichens and bryophytes. Previous to this study, this habitat had

not been recognized as containing unique biological attributes. Our understanding of the significance of this habitat is still rudimentary. Research comparing the floristics of silt terrace communities in the Pacific Northwest is needed. A review of microbiotic crust literature indicates that the number of species occurring in the study area exceeds that of many other semiarid localities (St. Clair et al. 1993; Eldridge 1996; Eldridge and Tozer 1996).

Three lichen genera represent 39% of the mycota. *Cladonia* is clearly the richest genus with 18 species, *Peltigera* has 6 species, and *Psora* has 4. Within the 19 study sites, 10 species were crustose, 12 squamulose, 19 fruticose, and 10 foliose. Among the bryophytes, no genus has greater than two species here, though the Pottiaceae, the Brachytheciaceae, and the Bryaceae are well represented, accounting for 41% of the species. These bryophyte families have been shown to dominate in semiarid ecosystems elsewhere, including the southern hemisphere (Eldridge and Tozer 1996). There were 8 pleurocarpous mosses within the study sites, 23 acrocarpous species, and 5 liverworts.

The lichen flora is unquestionably richer than indicated here, especially when epiphytic and lignicolous species are included. That a thorough inventory of the lichen flora of this ecosystem has yet to be conducted is telling of our neglect of these organisms, even during this era of concern for the conservation of diversity. Such an inventory was beyond the scope of the present study, but is strongly recommended for future research. Inventories are fundamental to the conservation of species diversity, a mandate of the legislation governing rangelands in British Columbia.

4.3 Rare species

Several species collected during this research have few records and are potentially rare (Table 7). More often, seldom-collected species are merely those that are inconspicuous or difficult to identify. Reference material for dryland lichens and bryophytes is sparse, reflecting the relative scarcity of adequately trained lichen and bryophyte taxonomists in B.C. Determining which species are truly rare requires extensive knowledge of the flora, the literature, and substantial field experience. Persons with such qualities are increasingly rare (Schofield pers. comm. 1998).

The prevalence of microbiotic crust communities, as a whole, has been dramatically reduced by grazing livestock. Several rare species occur in ecosystems that are used as pasturage (Goward 1996, Ryan 1996). It is possible that some species are threatened. While there are no reports of lichens or bryophytes becoming rare or endangered in British Columbia a result of disturbances caused by the grazing of livestock, this may reflect our lack of knowledge rather than our success in rangeland management. An absence of primary taxonomic research inhibits our ability to determine whether or not there are species facing localized extirpation.

Eldridge and Koen (1998) have shown that the genus *Xanthoparmelia* is useful as an indicator of rangeland health. This genus contains numerous unattached, vagrant species, also known as "tumble lichens". Rosentreter (1993) notes that vagrant lichens are a group of dryland species threatened by habitat disturbance related to grazing livestock. Goward et al. (1994) describe several vagrant species for B.C. and suggest at least one, *Xanthoparmelia camtschadalis* (Ach.), that is suspected to occur here though has yet to be collected. Investigating the status of this genus in British Columbia would provide an

opportunity to evaluate our success in managing for the protection of disturbance sensitive species.

4.4 Patterns of succession

Vascular plants and microbiotic crusts follow patterns of secondary succession when disturbed by trampling by grazing livestock. In this study, PCA and univariate analyses are used to describe these patterns in B.C.'s ponderosa pine forests.

PCA analyses show that the species composition of both vascular plants and microbiotic crust species change in response to disturbance. Among vascular plants, early successional species, those on the right side of the PCA factor loadings plot in Figure 9, include *Stipa comata*, *Poa pratensis*, *P. secunda*, *Artemisia frigida*, and *Antennaria parvifolia*. The dominant late successional vascular plants are the two native perennial bunchgrasses, *Festuca campestris* and *Agropyron spicatum*. It is not surprising that these plants are strongly related to principal component 1 because their cover was used to determine the disturbance ranking of the sites. It follows that they should relate to the principal component that best describes the differences between the sites.

Microbiotic species are examined in a second PCA (Figure 10), which demonstrates that within sites there is a much overlap in species composition, regardless of disturbance. That the disturbance groups do not separate as clearly in the microbiotic crust PCA as they do in the vascular plant PCA suggests that crusts species respond to disturbance at a different scale than vascular plants. The sampling method used here demonstrated a greater sensitivity to differences among vascular plants than among crust

species. Smaller sites, with more intensive sampling would improve the resolution of differentiation within the microbiotic crust community.

The most prominent early successional lichen is *Cladonia pyxidata*. Other early lichens include *Diploshistes muscorum* and *Physconia muscigena*. *Polytrichum piliferum* and *Bryum caespitium* are bryophytes that relate to disturbed sites. Species that relate negatively to the second component tend to proliferate in moderately disturbed sites and include *Tortula ruralis*, *Cladonia pocillum*, and *C. symphyarpa*. Late successional microbiotic crust species include the bryophyte *Brachythecium albicans*, and the lichen *Cladonia gracilis* (Figure 10).

When the vascular plants and microbiotic crust species are grouped together, the resulting PCA shows a stronger distribution over component 2 than in previous ordinations (Figure 11). Those sites that are positively related to component 2 are mid-successional sites, while early and late sites are negatively related. From the loadings plot (Figure 11) it is possible to describe species affinities and indicator species. *Antennaria parviflora* and *Artemisia frigida* are associated with *Diploshistes muscorum* and suggest recent disturbance. *Stipa comata* and *Poa secunda* are associated with *Physconia muscigena*, *Cladonia pyxidata*, *Placythium uliginosum*, and *Polytrichum piliferum* and are indicative of moderately disturbed sites. *Agropyron spicatum*, *Koeleria macrantha*, *Achillea millifolium*, and *Antennaria umbellata* are associated with *Peltigera rufescens*, *Cladonia* sp., *C. borealis*, *C. chlorophaea*, and *Ceratodon purpureus* and occupy later succession sites. The latest succession associates include *Festuca campestris*, *Brachythecium albicans*, and *Cladonia gracilis*.

Both West (1990) and Rogers and Lange (1971) assert that a lack of "weedy" microbiotic species, or species stimulated to form a greater cover with continued disturbance, render these organisms less useful for determining rangeland condition. While high intensity grazing severely disturbs the microbiotic crust community in dryland ecosystems, the present study, and others (Johansen et al. 1984; Eldridge and Tozer 1997; Eldridge and Koen 1998), have described several species that increase with moderate grazing. Eldridge and Tozer (1997) suggest that *Collema coccophorum*, *Peltula patellata*, and *Heppia lutos* (Ach.) Nyl. increase in sites subjected to repeated grazing. In B.C., microbiotic species associated with disturbance include *Cladonia pyxidata*, *Diploschistes muscorum*, *Physconia muscigena*, *Placythium uliginosum* and *Polytrichum piliferum*. Species that indicate late successional development are *Brachythecium albicans* and *Cladonia gracilis*.

While the total cover of vascular plants does not change with succession (Figure 13), the composition of this assemblage experiences substantial substitution (Figure 12). With time, species known as increasers (McLean and Marchand 1968), such as *Bromus tectorum*, *Stipa comata*, *Artemisia* spp., and *Poa* spp., are replaced by late successional species such as *Festuca campestris* and *Agropyron spicatum*. The cover of microbiotic crust species is lowest in the most disturbed sites and highest in the least disturbed sites (Figure 13). This is consistent with other studies that have examined the impact of grazing disturbance on microbiotic crusts (Rogers and Lange 1971; Anderson et al. 1982; Beymer and Klopatek 1992; Eldridge 1998; Memmott 1998).

It is clear that intensive trampling destroys microbiotic crusts; however, low levels of trampling may aid in the dispersal of some species, create microhabitats for others, leading

to an increase in microbiotic crust richness (Eldridge 1995, 1998). Microbiotic crusts demonstrate the highest richness in moderately disturbed sites (Group 2, Figure 15). This pattern supports the intermediate disturbance hypothesis, which predicts that maximum richness occurs in areas subject to moderate disturbances, or after an intermediate time period following disturbance. From the sampling methodology used in this study, it was not possible to determine which of these two processes was responsible for the observed pattern. The patchy nature of cattle grazing implicates the model of moderate disturbance; however, the development of late successional microbiotic species associations suggests that the intermediate time span hypothesis cannot be discounted. A combination of both models is most probable.

4.5 Diversity

The Shannon Indices for both the vascular plants (Figure 16) and the microbiotic crusts (Figure 17) do not appear to change significantly with succession. While diversity, as measured by the Shannon Index, remains relatively stable, the components of this diversity are seen to change. Thus, diversity, per se, is not sufficient to describe the dynamics of this community. Managing for maximum species diversity could lead to the exclusion of species that are restricted to sites that contain fewer species, for instance those species that occur in undisturbed habitats. Zhang (1998, p. 1379) states, "There is not one given direction of change in plant species diversity in relation to grazing or cessation of grazing. Stages of high and low diversity may follow each other during a succession, depending on resource partitioning and competitive patterns in vegetation. With the present widespread interest in biodiversity it is essential to realize that a high

species diversity, as such, is no guarantee for a healthy and productive vegetation, as the relatively high diversity of weedy annuals following heavy grazing in the present study indicates.”

4.6 Microbiotic lifeforms

Eldridge and Rosentreter (1999) proposed the use of morphological groups of lichens and bryophytes to facilitate monitoring of rangeland condition. They reason that the morphology of crusts species denotes their function and that the response of microbiotic crust species to perturbation is dependent upon both morphology and reproductive strategy. Because both the function and response to perturbation are linked to morphology, it is possible to use morphological groups, or lifeforms, to evaluate the condition of a dryland community (Eldridge and Rosentreter 1999).

Figure 18 shows that crustose and squamulose lichens increase in cover soon after disturbance, and then remain unchanged with time. Foliose lichen cover remains low until later in succession (Figure 19). Like the foliose lichens, pleurocarpous bryophytes demonstrate the greatest increase in cover in the latest succession sites (Figure 21). Acrocarpous bryophytes increase gradually over time and are also most abundant late in succession (Figure 20). Thus, a high cover of bryophytes and larger lichens correlates to an absence of disturbance. A relatively rapid, fire return interval, prior to European settlement, suggests that ponderosa pine forests thoroughly dominated by bryophytes, foliose lichens, and fruticose lichens were rare even in the past. They are most certainly rare today, though livestock grazing, not fire, is the principal cause of disturbance.

Problems and benefits of using morphological groups have been discussed by Eldridge and Rosentreter (1999). Sampling based upon morphology invariably overlooks rare species and is not useful for determining the richness or diversity of a site. The main advantage of this system is that it allows individuals who lack lichen and bryophyte taxonomy skills to obtain meaningful data with respect to rangeland condition. Eldridge and Rosentreter (1999) conclude that, if preceded by a thorough floristic inventory, a morphology-based system is an effective monitoring technique. While still in its preliminary stages, this approach is being considered for B.C.

4.7 Positive feedback

In general, disturbance tolerant species tend also to be dry tolerant and are often small. These include crustose and squamulose lichen lifeforms (Figure 18), and diminutive (often < 1mm tall) bryophytes. Late successional species tend to be larger, and among lichens, structurally more complex. This includes fruticose and foliose lichens, and large acrocarpous and pleurocarpous bryophytes (Figures 19, 20, and 21). In undisturbed sites, lichens will eventually be replaced by large pleurocarpous and acrocarpous mosses. Mosses have faster growth rates than lichens, and have been shown to be the most effective in retaining moisture among microbiotic crust organisms (West 1990; Atwood 1998).

The patterns of microbiotic crust succession suggest a positive feedback mechanism. As the microbiotic crust develops, it is able to regulate water so that moisture is retained longer than on bare soil (Atwood 1998). This enhances the germination of native perennial bunchgrasses, which in turn produce litter that also contribute to water retention

(St. Clair et al. 1984; Reitkerk and van der Koopel 1997). The microsite conditions beneath the bunchgrasses favor bryophytes and taller and broader lichens. These larger, broader species form a dense cover that slows evaporation. The system promotes the retention of water in an increasing cycle. Disruption of the system by grazing disturbance results in a loss of moisture and a change in the composition of the species in the community. This parallels observations by Reitkerk and van der Koppel (1997) who described how positive feedback loops within a semiarid vascular plant community were vulnerable to disruption, resulting in a loss of moisture and nutrients. Moisture also appears to positively influence the rate of succession. Sites with features that enable them to retain moisture longer, for example those with northerly aspects or fine textured soils, recover more quickly from disturbance than drier sites.

Chapter 5

CONCLUSIONS

Ponderosa pine forests on silt terraces near Kamloops B.C. support an unusually rich assemblage of terricolous lichens and bryophytes. Among them are numerous rare or seldomly collected species.

Patterns of succession after disturbance due to grazing livestock are described for vascular plants and microbiotic crust species. Together, they form successional assemblages that change in species composition over time. The pattern of richness in microbiotic species supports the intermediate disturbance hypothesis. The present study does not discern whether the observed pattern relates to moderate amounts of grazing or to an intermediate time period after disturbance. A combination of the two processes is probable; however, manipulation experiments would enhance our understanding of the precise nature of the relationships.

Biodiversity has been adopted as the primary objective for many management strategies. This study shows that managing for biodiversity, either in terms of richness or diversity indices, may not account for the unique structure and composition of late successional microbiotic crust communities.

Lifeforms of lichens and bryophytes are useful for describing the successional development of microbiotic crusts. The successional development of fruticose lichens, foliose lichens, and bryophytes support the hypothesis that microbiotic crust species contribute to a positive feedback mechanism that promotes the retention of moisture. This feedback mechanism can be disrupted by grazing livestock. Referring to vascular plants, Rietkerk and van de Koppel (1997, p. 74) assert that "plant-soil interactions serve as one

of the most influential positive feedback loops in semi-arid grazing systems.” This study shows how the same mechanism applies to the microbiotic crust community and may be of no less importance.

Microbiotic crusts are an important component of the floristics and ecology of B.C.’s ponderosa pine forests. Describing the floristics and patterns of succession of microbiotic crusts enhances our understanding of these communities and improves our ability to secure their continued existence. However, primary floristic inventories have still yet to be conducted, and current development trends are limiting opportunities for comparative research.

REFERENCES

- Anderson D.C., Harper, K.T., and R.C. Holmgren. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. *Journal of Range Management* 35: 180-185.
- Anderson, L.E., Crum, H.A., and W.R. Buck. 1990. List of North American mosses. *The Bryologist* 93: 448-499.
- Atwood, L. 1998. Ecology of the microbiotic crust of the antelope-brush (*Purshia tridentata*) shrub steppe of the south Okanagan, British Columbia. M. Sc. thesis, Univeristy of British Columbia, Vancouver, Canada. 130 p.
- B.C. Ministry of Forests. 1995a. *Bidiversity Guidebook (Forest Practices Code of British Columbia)*. B.C. Ministry of Forests, B.C. Ministry of Environment, Victoria, B.C. 99 p.
- B.C. Ministry of Forests. 1995b. *Range Management Guidebook (Forest Practices Code of British Columbia)*. B.C. Ministry of Forests, B.C. Ministry of Environment, Victoria, B.C. 34 p.
- Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assesment methods. *Great Basin Naturalist* 53: 89-95.
- Belnap J. 1994. Potential role of cryptobiotic soil crusts in semiarid rangelands. In: (S. B. Monsen and S. G. Kitchen eds.) *Proceedings: Ecology and Management of Annual Rangelands*. U.S.D.A. Intermountain Research Station. Pp. 179-185.
- Belnap, J. 1996. Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. *Biology and Fertility of Soils* 23: 362-367.
- Belnap, J. 1998. Structure and function of biological soil crusts. In: (Meurisse, R.T., Ypsilantis, W.G., and C. Seybold eds.) *Proceedings: Pacific Northwest Forest & Rangeland Soil Organism Symposium*. U.S.D.A., Forest Service, General Technical Report PNW-GTR-461. Pp. 161-178.
- Belnap, J. and D.A. Gillette. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments* 39: 133-142.
- Beymer, R.J. and J.M. Klopatek. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. *American Midland Naturalist* 127: 139-148.
- Brodo, I.M. 1995. Lichens and lichenicolous fungi of the Queen Charlotte Islands, British Columbia, Canada. 1. Introduction and new records for British Columbia, Canada, and North America. *Mycotaxon* 56: 135-173.

- Campbell, C.W. and A.H. Bawtree eds. 1998. *Rangeland Handbook for B.C.* British Columbia Cattlemen's Association, Kamloops, B.C. 203 p.
- Clements, F.E. 1916. *Plant succession: an analysis of the development of vegetation.* Carnegie Institute, Washington D.C. Publ. 242. 512 p.
- Cole, D.N. 1990. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. *Great Basin Naturalist* 50: 321-325.
- Collins, S.L., Glenn, S.M., and D.J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76: 486-492.
- Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* 111: 1119-1144.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Cooke, W.B. 1955. Fungi, lichens and mosses in relation to vascular plant communities in eastern Washington and adjacent Idaho. *Ecological Monographs* 25: 119-180.
- Danin, A., and E. Ganor. 1991. Trapping of airborne dust by mosses in the Negev Desert, Israel. *Earth Surface Processes and Landforms* 16: 153-162.
- Daubenmire, R. 1968. *Plant Communities: a Textbook of Plant Synecology.* Harper & Row, New York, USA. 300 p.
- Daubenmire, R. 1970. Steppe vegetation of Washington. Washington agricultural Experiment Station Technical Bulletin 62. 131 p.
- Douglas, G.W., Straley, G.B, and D. Meidinger. 1989. *The Vascular Plants of British Columbia. Part 1 – Gymnosperms and Dicotyledons (Aceraceae through Cucurbitaceae).* Special Report Series 1, B.C. Ministry of Forests, Research Branch, Victoria, B.C. 208 p.
- Douglas, G.W., Straley, G.B, and D. Meidinger. 1990. *The Vascular Plants of British Columbia. Part 2 – Dicotyledons (Diapensiaceae through Portulacaceae).* Special Report Series 2, B.C. Ministry of Forests, Research Branch, Victoria, B.C. 158 p.
- Douglas, G.W., Straley, G.B, and D. Meidinger. 1991. *The Vascular Plants of British Columbia. Part 3 – Dicotyledons (Primulaceae through Zygophyllaceae) and Pteridophytes.* Special Report Series 3, B.C. Ministry of Forests, Research Branch, Victoria, B.C. 177 p.

- Douglas, G.W., Straley, G.B., and D. Meidinger. 1994. *The Vascular Plants of British Columbia. Part 4 – Monocotyledons*. Special Report Series 4, B.C. Ministry of Forests, Research Branch, Victoria, B.C. 257 p.
- Eldridge, D.J. 1993. Cryptogams, vascular plants, and soil hydrological relations: some preliminary results from the semiarid woodlands of eastern Australia. *Great Basin Naturalist* 53: 48-58.
- Eldridge, D.J. 1996a. Distribution and floristics of terricolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. *Australian Journal of Botany* 44: 581-599.
- Eldridge, D.J. 1996b. Dispersal of microphytes by water erosion in an Australian semi-arid woodland. *The Lichenologist* 28: 97-100.
- Eldridge, D.J. 1998. Trampling of microphytic crusts on calcareous soils, and its impact on erosion under rain-impacted flow. *Catena* 33: 221-239.
- Eldridge, D.J. and T.B. Koen. 1998. Cover and floristics of microphytic soil crusts in relation to indices of landscape health. *Plant Ecology* 137: 101-114.
- Eldridge, D.J. and R.S.B. Greene. 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. *Australia Journal of Soil Research* 32: 389-415.
- Eldridge, D.J. and R. Rosentreter. 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments* 41: 11-25.
- Eldridge, D.J., and M.E. Tozer. 1996. Distribution and floristics of bryophytes in soil crusts in semiarid and arid eastern Australia. *Australian Journal of Botany* 44: 223-247.
- Eldridge, D.J. and M.E. Tozer. 1997. *A Practical Guide to Soil Lichens and Bryophytes of Australia's Dry Country*. Department of Soil and Water Conservation, Sydney. 80 p.
- Eldridge, N.E., Tozer, M.E., and S. Slangen. 1997. Soil hydrology is independent of microphytic crust cover: further evidence from a wooded semiarid Australian rangeland. *Arid Soil Research and Rehabilitation* 11: 113-126.
- Esslinger, T.L. and R.S. Egan. 1995. A sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada. *The Bryologist* 98: 467-549.
- Fink, B. 1909. The composition of desert lichen flora. *Mycologia* 1: 87-103.
- Fulton, R.J. 1965. Silt deposition in late-glacial lakes of southern British Columbia. *American Journal of Science* 263: 553-570.

Fulton, R.J. 1967. Deglaciation studies in Kamloops Region, an area of moderate relief, British Columbia. Geological Survey of Canada, Bulletin 154. 36 p.

Friedmann, E.I., and M. Galun. 1974. Chapt. IV. Desert algae, lichens, and fungi. In: (G.W. Brown ed.) *Desert Biology* Vol. II. Academic Press, London. Pp. 165-212.

Gaton, D. 1999. British Columbia: the Range Reference Area program cancelled. BEN (Botanical Electronic News) # 229. ben-l@victoria.tc.ca.

Gauch, H.G. Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, U.K. 298.

Gold, W.G. 1998. The Influence of cryptogamic crusts on the thermal environment and temperature relations of plants in a High Arctic polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research* 30: 108-120.

Goward, T. 1996. Lichens of British Columbia: rare species and priorities for inventory. Resource Branch, B.C. Ministry of Forests and Wildlife Branch, B.C. Ministry of Environment, Lands, and Parks. Victoria, B.C. Working Paper 08/1996. 34p.

Goward, T. 1999. *The Lichens of British Columbia: Part 2- Fruticose Species*. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Special Report Series 9. 319 p.

Goward, T., and T. Ahti. 1997. Notes on the distributional ecology of the Cladoniaceae (Lichenized Ascomycetes) in temperate and boreal western North America. *Journal of the Hattori Botanical Laboratory* No. 82: 143-155.

Goward, T., Bruess, O., Ryan, B., McCune, B., Sipman, H., AND C. Scheidegger. 1996. Notes on the lichens and allied fungi of British Columbia. III. *The Bryologist* 99: 439-449.

Goward, T., Diederich, P., and R. Rosentreter. 1994. Notes on the lichens and allied fungi of British Columbia. II. *The Bryologist* 97: 56-62.

Goward, T., McCune, B., and D. Meidinger, 1994. *The Lichens of British Columbia: Part 1- Foliose and Squamulose Species*. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Special Report Series 8. 181p.

Goward, T., and G. Thor. 1992. Notes on the lichens and allied fungi of British Columbia. I. *The Bryologist* 95: 33-37.

Guach, H. G., Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, England. 298p.

Harper, K.T., and J.R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. In: (P.T. Tueller ed.) *Vegetation science applications for rangeland analysis and management*. Kluwer Academic Publishers, Dordrecht. Pp. 135-169.

Harper, K.T., and R.L. Pendleton. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential mineral for higher plants? *Great Basin Naturalist* 53: 59-72.

Herre, A.W.C.T. 1911. The desert lichens of Reno, Nevada. *The Botanical Gazette* 51: 286-297.

Johansen, J.R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* 29: 140-147.

Johansen, J.R., Ashley, J., and W.R. Rayburn. 1993. Effects of range fire on soil algal crusts in semiarid shrub-steppe of the Lower Columbia Basin and their subsequent recovery. *Great Basin Naturalist* 53: 73-78.

Johansen, J.R. and S.R. Rushforth. 1985. Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah. *Great Basin Naturalist* 45: 14-21.

Johansen, J.R., St. Clair, L.L., Webb, B.L., and G.T. Nebeker. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. *The Bryologist* 87: 238-243.

Kleiner, E.F. and K.T. Harper. 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. *Journal of Range Management* 30: 202-205.

Krajina, V.J. 1959. Bioclimatic zones in British Columbia. The University of British Columbia Botanical Series No. 1. 47p.

Kral, R. 1993. 6. Pinus. In: (Flora of North America Editorial Committee eds.) *Flora of North America: vol 2 Pteridophytes and Gymnosperms*. Oxford University Press, NY, NY. Pp 373-398.

Lawton, E., 1971. *Moss flora of the Pacific Northwest*. Hattori Botanical Laboratory, Honmachi, Nichinan-shi, Miyazakiken, Japan. 362 p. 195 pl.

Lloyd, D., Angove, K., Hope, G., and C. Thompson. 1990. *A guide to site identification and interpretation for the Kamloops Forest Region*. B.C. Ministry of Forests, Victoria, Canada. 399 p.

Looman, J. 1964a. Ecology of lichen and bryophyte communities in Saskatchewan. *Ecology* 45: 481-491.

Looman, J. 1964b. The distribution of some lichen communities in the prairie provinces and adjacent parts of the Great Plains. *The Bryologist* 67: 209-225.

Loope, W.L. and G.F. Gifford. 1972. Influence of a soil microfloral crust on select properties of soils under pinyon-juniper in southeastern Utah. *Journal of Soil and Water Conservation* 27: 164-167.

Maikawa, E., and K.A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce-lichen woodland in the Abitau Lake Region, N.W.T. *Canadian Journal of Botany* 54: 2679-2687.

McCleary, J.A. 1968. Chapt. V. The Biology of Desert Plants. In: (G.W. Brown ed.) *Desert Biology* Vol. I. Academic Press, London. Pp. 141-194.

McCune, B., 1997. Key to the lichen genera of the Pacific Northwest. Unpublished report. Oregon State University, Corvallis, Oregon. 70 p.

McCune, B., and T. Goward. 1995. *Macrolichens of the Northern Rocky Mountains*. Mad River Press, Eureka, California. 208 p.

McCune, B., and R. Rosentreter. 1995. Field key to soil lichens of central and eastern Oregon. Unpublished report. Oregon State University, Corvallis, Oregon. 9 p.

McIntosh, T.T. 1986. The bryophytes of the semi-arid steppe of south-central British Columbia. Ph.D. thesis, University of British Columbia, Vancouver, Canada. 345 p.

McIntosh, T.T. 1997. The biogeography of the bryophytes of the semi-arid steppe of south-central British Columbia, Canada. *Journal of the Hattori Botanical Laboratory* No. 82: 157-169.

McLean, A., and L. Marchand. 1968. Grassland ranges in the southern interior of British Columbia. Canada Department of Agriculture, publication 1319. 28 p.

Meidinger, D., and J. Pojar (eds.). 1991. *Ecosystems of British Columbia*. Research Branch, The British Columbia Ministry of Forests, Victoria, B.C. 330 p.

Memmott, K.L., Anderson, V.J., and S.B. Monsen. 1998. Seasonal grazing impact on cryptogamic crusts in a cold desert ecosystem. *Journal of Range Management* 51: 547-550.

Nash III, T.H. 1996. Chapter 8. Nutrients, elemental accumulation and mineral cycling. In: (T.H. Nash III ed.) *Lichen Biology*. Cambridge University Press, Cambridge, U.K. 303 p.

Nash, T.H., White, S.L., and J.E. Marsh. 1977. Lichen and moss distribution and biomass in hot desert ecosystems. *Bryologist* 80: 470-479.

Noble, W.J. 1982. The lichens of the Coastal Douglas-fir subzone of British Columbia. Ph. D. thesis, University of British Columbia, Vancouver, Canada. 942 p.

Perez, F.L. 1997. Microbiotic crusts in the high equatorial Andes, and their influence on paramo soils. *Catena* 31: 173-198.

Perry, D.A., Amaranthus, M.P., Borchers, J.G., Borchers, S.L., and R.E. Brainerd. 1989. Bootstrapping in ecosystems. *BioScience* 39: 230-237.

Rietkerk, M. and J. van de Koppel. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79: 69-76.

Rogers, R.W. and R.T. Lange. 1971. Lichen populations on arid crusts around sheep watering places in South Australia. *Oikos* 22: 93-100.

Rogers, R.W. and R.T. Lange. 1972. Soil surface lichens in arid and subarid south-eastern Australia. I. Introduction and floristics. *Australian Journal of Botany* 20: 197-213.

Rosentreter, R. 1986. Compositional patterns within a rabbitbrush (*Chrysothamnus*) community of the Idaho Snake River Plain. In: (MacArthur, D.E., and B.L. Welsh eds.) *Proceedings: Symposium on the Biology of Artemisia and Chrysothamnus*. July 9-13, 1984; Provo, Utah. U.S.D.A Forest Service GTR INT-200. Pp. 273-277.

Rosentreter, R., Debolt, A., and C. Bratt. 1988. Curation of soil lichens. *Evansiana* 5:23-25.

Rosentreter, R. 1993. Vagrant lichens in North America. *The Bryologist* 96: 333-338.

Rosentreter, R. 1999. Restoration of community structure and composition in cheatgrass dominated rangelands. In: (Rose, R. and D.L. Haase eds.) *Symposium Proceedings: Native Plants Propagation and Planting*. December 9-10, 1998; Oregon State University, Corvallis, Oregon. Pp. 92-99.

Ryan, M. 1996. Bryophytes of British Columbia: rare species and priorities for inventory. Resource Branch, B.C. Ministry of Forests and Wildlife Branch, B.C. Ministry of Environment, Lands, and Parks. Victoria, B.C. Working Paper 12/1996. 100 p.

Schofield, W.B. 1985. *Introduction to Bryology*. Macmillan Publishing Company, New York, NY. 431 p.

Schofield, W.B. 1988. Bryogeography and the bryophytic characterization of biogeoclimatic zones of British Columbia, Canada. *Canadian Journal of Botany* 66: 2673-2686.

Scudder, G.G.E. 1991. Threatened and endangered invertebrates of the south Okanagan. In: (Susanne Rautio ed.) *Community Action for Endangered Species*. The Federation of British Columbia Naturalists/Northwest Wildlife Preservation Society, Vancouver. Pp. 47-58.

Sheilds, L.M. 1957. Algal and lichen floras in relation to nitrogen content of certain volcanic and arid range soils. *Ecology* 38: 661-663.

Sheilds, L.M., Mitchell, C., and F. Drouet. 1957. Alga- and lichen-stabilized surface crusts as soil nitrogen sources. *American Journal of Botany* 44: 489-498.

Sidahmed, A.E. 1995. Towards sustainable development of reangelands/livestock in dryland areas of the Near East of North Africa. In: (Omar, S.A.S., Razzaque, M.A., and F. Alsdarawi eds.) *Proceedings of the Second International Conference on Range Management in the Arabian Gulf*. Kuwait Institute for Scientific Research. Pp. 53-69.

Simonson, R.W. 1959. Outline of a generalized theory of soil genesis. *Soil Science Society of America Proceedings* 23: 152-156.

Smith, A.J.E., 1990. *The Liverworts of Britain & Ireland*. Cambridge University Press, Cambridge. 362 p.

St. Clair, L.L. and J.R. Johansen. 1993. Introduction to the symposium on soil crust communities. *Great Basin Naturalist* 53: 1-4.

St.Clair, L.L., Johansen, J.R., and S.R. Rushforth. 1993. Lichens of soil crust communities in the intermountain area of the western United States. *Great Basin Naturalist* 53: 5-12.

St. Clair, L.L., Webb, B.L., Johansen, J.R., and G.T. Nebeker. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. *Reclamation and Revegetation Research* 3: 129-136.

Stotler, R. and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. *The Bryologist* 80: 405-428.

SYSTAT Version 8.0. © SPSS, 1998.

Thomson, J.W. 1984. *American Arctic Lichens: Vol. 1. The Macrolichens*. Columbia University Press, New York, New York. 504 p.

Thomson, J.W. 1997. *American Arctic Lichens: Vol. 2. The Microlichens*. The University of Wisconsin Press, Madison, Wisconsin. 675 p.

West, N.E. 1983. Chapter 1: Approach. In: (N.E. West ed.) *Ecosystems of the World Part 5: Temperate deserts and Semi-deserts*. Elsevier Scientific Publishing Company, Amsterdam, Netherlands. Pp 1-2.

West, N.E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. *Advances in Ecological Research* Vol. 20: 179-223.

Whitford, W.G. 1996. The importance of the biodiversity of soil biota in arid ecosystems. *Biodiversity and Conservation* 5: 185-195.

Yazvenko, S.B. and D.J. Rapport. 1997. The history of ponderosa pine pathology: implications for management. *Journal of Forestry* 95: 16-20.

Zar, J.H. 1984. *Biostatistical Analysis*. Prentice-Hall Inc., Englewood Cliffs, New Jersey. 718 p.

Zhang, W. 1998. Changes in species diversity and canopy cover in steppe vegetation in Inner Mongolia under protection from grazing. *Biodiversity and Conservation* 7: 1365-1381.

APPENDICES

APPENDIX A: a key to the common liverworts, mosses, and lichens of the ponderosa pine forests of British Columbia

Introduction

This key is the first illustrated field guide which focuses specifically on the common terricolous liverworts, mosses, and lichens of B.C.'s ponderosa pine ecosystems, also known as the Ponderosa Pine (PP) Biogeoclimatic Zone. Because of the intergradation of the grasslands and ponderosa pine forests, several grassland species have also been treated here. This key is not a complete treatment of the cryptogams of this ecosystem; however, it represents most of the common species, and a few that are less common, and will be a useful resource to ecologists, botanists, range managers, students, teachers, and naturalists who have an interest in B.C.'s ponderosa pine forests.

Using the keys

The following keys are based, wherever possible, on characteristics observable in the field using a hand lens; however, because many dryland liverworts, mosses, and lichens are rather diminutive, most specimens will require collecting for identification where a dissecting and compound microscope are available. Having access to accurately identified herbarium specimens is also a valuable aid to identifying many of these species. Some species require sectioning for identification and some lichens, particularly in the genus *Cladonia*, are most reliably identified using chemical reaction tests and an ultra-violet lamp. This key only superficially treats the genus *Cladonia*, and does not base dichotomies on the use of chemical tests. For a more complete treatment of the lichens of

B.C. use Goward et al. (1994) "The Lichens of British Columbia: Part 1- Foliose and Squamulose Species" and Goward (1999) "The Lichens of British Columbia: Part 2- Fruticose Species". A good resource for identifying crustose and squamulose lichens is McCune's (1995) "Field key to soil lichens of central and eastern Oregon" and the most complete treatment of the dry-land liverworts and mosses of B.C. is McIntosh's 1986 Ph.D. thesis "Bryophytes of the semi-arid steppe of south-central British Columbia".

Methods of collecting

The following is a summary of the method of preparing herbarium specimens for crust-forming lichens and bryophytes described by Rosentreter et al. (1988). Soil aggregates containing the desired specimens are trimmed to flat in the field using a knife. To prevent the aggregate from breaking to pieces, it is often useful to use a small mist bottle to wet the lower surface before trimming. Individual specimens are collected in separate paper bags (#10 sized) and labeled with an accession number that corresponds with the number written in a field book.

While in the field, the specimen bags are loosely stored in a plastic shopping bag so as to avoid crushing the specimens. Site information including collector, date, location (general description plus latitude and longitude), associated plants, elevation, slope, and aspect is recorded in a field book. This information will be transferred onto the herbarium labels upon identification of the specimens. After returning from the field, the specimens in the paper bags are air-dried. Reinforcing glue is made by diluting brown, water-based, carpenter's glue with water (1:4). The aggregate is first moistened with a mist bottle, then carefully dipped in the reinforcing glue and left to dry on a table covered with plastic.

The reinforced aggregate is then glued onto thin cardboard, or heavy card stock (approx. 6 X 10 cm) with cut styrofoam pieces glued on the margins to protect the specimen from compacting when placed in the herbarium. Specimens are stored in herbarium packets using cotton bond herbarium paper for both the packets and labels. It is useful to write the accession number on the card and on the outside of the herbarium packet. All chemical tests, measurements taken, and drawings made should be noted in each herbarium packet. Arrows are used to indicate identified specimens on soil aggregates that contain more than one species.

A list of the species treated

Liverworts

Barbilophozia hatcheri (Evans) Loeske
Cephaloziella divaricata (Sm.) Schiffn.
Lophozia excisa (Dicks.) Dum.
Mannia fragrans (Balbis) Frye et Clark
Ptilidium ciliare (L.) Hampe
Ptilidium pulcherrimum (G. Web.) Hampe

Mosses

Aloina bifrons (De Not.) Delgadillo
Aloina brevirostris (Hook & Grev.) Kindb.
Aloina rigida (Hedw.) Limpr.
Barbula convoluta Hedw.
Barbula unguiculata Hedw.
Brachythecium albicans (Hedw.) Shimp. in B.S.G.
Brachythecium collinum (Schleich. ex C. Mull.) Shimp. in B.S.G.
Bryum argenteum Hedw.
*Bryum caespiticiu*m Hedw.
Buxbaumia aphylla Hedw.
Ceratodon purpureus (Hedw.) Brid.
Desmatodon convolutus (Brid.) Grout
Dicranum polysetum Sw.
Dicranum scoparium Hedw.
Didymodon occidentalis (Mitt.) Zander
Didymodon rigidulus Hedw.
Didymodon vinealis (Brid.) Zander
Ditrichum flexicaule (Swaegr.) Hampe
Encalypta rhaptocarpa Schwaegr.
Encalypta vulgaris Hedw.

Fissidens bryoides Hedw.
Funaria hygrometrica Hedw.
Homalothecium aeneum (Mitt.) Lawt.
Hylocomium splendens (Hedw.) B.S.G.
Hypnum revolutum (Mitt.) Lindb.
Hypnum vaucheri Lesq.
Mnium spinulosum B.S.G.
Phascum cuspidatum Hedw.
Pohlia nutans (Hedw.) Lindb.
Polytrichum juniperinum Hedw.
Polytrichum piliferum Hedw.
Pseudoleskeella tectorum (Brid.) Broth.
Pterygoneurum subsessile (Brid.) Jur.
Pterygoneurum ovatum (Hedw.) Dix.
Rhytidiadelphus triquetrus (Hedw.) Warnst.
Rhytidiopsis robusta (Hedw.) Broth.
Sanionia uncinata Loeske
Tortula ruralis (Hedw.) Gaertn. et al.
Weissia hedwigii Crum

Lichens

Acarospora schleircheri (Ach.) A Massal.
Amandinea punctata (Hoffm.) Coppins & Scheid
Arthonia glebosa Tuck.
Bryonora castanea (Hepp) Poelt
Buellia geophilla (Florke ex Sommerf.) Lynge
Buellia papillata (Sommerf.) Tuck.
Caloplaca cerina (Hedw.) Th. Fr.
Caloplaca jungermanniae (Vahl) Th. Fr.
Caloplaca tominii Savicz
Candelariella terrigena Rasanen
Catapyrenium squamulosum (Ach.) Bruess
Cetraria ericetorum Opiz
Cladina arbuscula (Wallr.) Hale & Culb.
Cladina mitis (Sandst.) Hustich
Cladina rangiferina (L.) Nyl.
Cladonia borealis S. Stenroos
Cladonia botrytes (K. Hagen) Willd.
Cladonia carneola (Fr.) Fr.
Cladonia cenotea (Ach.) Schraerer
Cladonia cervicornis (Ach.) Flot.
Cladonia chlorophaea (Florke ex Sommerf.) Spreng.
Cladonia cornuta (L.) Hoffm.
Cladonia deformis (L.) Hoffm.
Cladonia ecmocyna Leighton
Cladonia fimbriata (L.) Fr.
Cladonia gracilis (L.) Willd.
Cladonia multiformis G. Merr.
Cladonia phyllophora Hoffm.
Cladonia pocillum (Ach.) Grognot
Cladonia pyxidata (L.) Hoffm.
Cladonia rei Schraerer
Cladonia subulata (L.) F. H. Wigg.
Cladonia sulphurina (Michaux) Fr.

Cladonia symphycarpa (Florke) Fr.
Cladonia uncialis ((L.) F.H. Wigg.
Coelocaulon aculeatum (Schreb.) Link
Collema coccophorum Tuck.
Collema crispum (Hudson) F.H. Wigg.
Collema tenax var. *crustaceum* (Kremp.) Degel.
Collema sp.
Diploschistes muscorum (Scoop) R. Scant
Endocarpon pusillum Hedw.
Flavocetraria nivalis (L.) Karnefelt & Thell
Fulgensia desertorum (Tomin) Poelt
Massalongia microphylliza (Nyl. ex Hasse) Henssen
Nephroma parile (Ach.) Ach.
Ochrolechia upsaliensis (L.) A. Massal.
Peltigera canina (L.) Willd.
Peltigera didactyla (With.) Laundon
Peltigera didactyla var. *extenuata* (Nyl.) Goffinet & Hastings
Peltigera lepidophora (Vainio) Bitter
Peltigera malacea (Ach.) Funck
Peltigera ponojensis Gyel.
Peltigera rufescens (Weis) Humb.
Phaeophyscia constipata (Norrlin & Nyl.) Moberg.
Physconia enteroxantha (Nyl.) Poelt
Physconia muscigena (Ach.) Poelt
Placynthiella uliginosa (Schrader) Coppins & P. James
Polychidium muscicola (Sw.) Gray
Psora cerebriformis W. A. Weber
Psora decipiens (Hedw.) Hoffm.
Psora globifera (Ach.) A. Massal.
Psora montana Timdal
Psora nipponica (Zahlbr.) Goth. Schneider
Psora tuckermanii R. Anderson ex Timdal
Solorinella asteriscus Anzi
Stereocaulon sp.
Xanthoria wyomingica (Gyel.) Hale

Characters that Differentiate Cryptogams

<u>Lichens</u>	<u>Mosses</u>	<u>Liverworts</u>
-comprised of an association of a fungus with an alga and/or a cyanobacterium	-comprised mainly of green photosynthetic tissue	-comprised mainly of green photosynthetic tissue
-occasionally green	-leaves in >3 rows	-leaves usually in rows of 2 or 3, or thallus strap-like
-not organized into leaves	-leaves often with a midrib	-leaf cells isodiametric
-capsule absent	-leaf cells usually elongate	-capsule on fleshy, ephemeral, colourless seta
-sexual reproduction by spore producing apothecia	-capsule born on long, persistent, wiry seta	-capsule opens along 4 longitudinal slits
	-capsule opens with a terminal pore	

Liverworts

1a Thallose, >15mm long, with purple scales on underside and female receptacles arising from clear scales at the lobe tips. Easiest to find in the early spring when the soil is moist. Rare. (Note: *Riccia* spp. and *Athalamia hyalina* are other thallose liverworts from the region but they do not have a female receptacle at the lobe tips, arising from clear scales.)

1b Comprised of a stem with leaves. Not thallose.	<i>Mannia fragrans</i>
2a Leaves broad (2-4mm) with 3 or 4 discrete lobes.	2
2b Leaves small (<2mm) with 2 lobes.	<i>Barbilophozia hatcheri</i>
3a Leave lacking cilia.	3
4a Minute black threads (<0.5mm wide) common in the PP zone, forming crusts on and between soil aggregates.	4
4b Green, larger (> 0.5mm wide), rare in the PP zone, occurring as a short green turf.	<i>Cephaloziella divaricata</i>
3b Leaves with marginal cilia.	<i>Lophozia excisa</i>
5a Leaf bases ~0.5mm wide, ~0.8mm long. Leaf bases narrower than the length of the cilia. Green.	5
5b Leaf bases ~0.8mm wide, ~1.0-1.3mm long. Leaf bases wider than the length of the cilia. Green to copper/red coloured.	<i>Ptilidium pucherrimum</i>
	<i>Ptilidium ciliare</i>

Mosses

1a Main axis vertical (acrocarpous).	2
2a Leaves awned or with long hair points.	KEY A
2b Leaves without awns or long hair points.	3
3a Plants <5mm tall, "bud-shaped", with < 10 leaves.	KEY B
3b Plants >5mm tall, not "bud-shaped", with > 10 leaves.	4
4a Small (<10mm). Leaves usually <2mm long, forming a dense cushion, short turf, or occurring as individuals.	KEY C
4b Large (>10mm). Leaves usually >5mm long, forming a thick mat or occurring as individuals.	KEY D
1b Main axis horizontal (pleurocarpous).	KEY E

KEY A

Mosses with awns or long hair points

- 1a Leaves with barbed awns. Plants usually >10mm tall. 2
 2a Leaf margins recurved, leaves broadly triangulate and yellow-green. Leaves contorted when dry, expanding rapidly when wetted. Common in the grasslands. *Tortula ruralis*
 2b Leaf margins incurved, wrapping around the midrib. Leaves green-brown, straight, vertical when dry, with a short, stout awn. *Polytrichum juniperinum*
- 1b Leaves awns without barbs (smooth), or simply a long hair point. Plants often <10mm tall. 3
 3a Leaf margins strongly incurved. 4
 4a Plants <2mm tall with thick, rounded ("thumb-like") leaf apices. *Aloina bifrons*
 4b Plants >2mm tall, lacking thick, rounded leaf apices. 5
 5a Leaves darkly coloured, straight or weakly curved when dry, and lacking a shiny midrib. Calyptra hairy, capsule four sided. *Polytrichum piliferum*
 5b Leaves bright green, strongly contorted when dry, and with a shiny midrib. Calyptra long and hairless, capsule long and cylindrical when present. *Encalypta rhaptocarpa*
- 3b Leaf margins plane or recurved. 6
 6a Leaves yellow-green, gradually tapering to a long hair point. Capsule immersed among the leaves. Leaves lacking flaps (lamellae) over the midrib. *Phascum cuspidatum*
 6b Leaves brown, spatulate with obtuse leaf apices from which long awns emerge. Capsule immersed or emergent. Leaves containing lamellae over the midrib. 7
 7a Capsule immersed in the leaves. *Pterygoneurum subsessile*
 7b Capsule held 4-7mm above the leaves by a short seta. *Pterygoneurum ovatum*

KEY B

Minute (<5mm), "bud-shaped" mosses with fewer than 10 leaves

- 1a Leaves dark brown to green-brown, with thick, rounded apices. Leaves not strongly contorted when dry. 2
 2a Leaves dark brown with a large midrib (5 cells wide). Cell walls papillose. Leaf margins not folded to make leaves appear thick. *Desmatodon convolutus*
 2b Leaves green-brown with folded margins that make the blade appear thick. Cell walls without papillae. Leaves resemble small thumbs. 3
 3a Leaves short and stout, the clear leaf base longer than the dark leaf blades. Leaf length to width ~2:1. *Aloina brevirostris*
 3b Clear leaf base shorter than the dark leaf blade. Leaf length to width ratio ~3:1. *Aloina rigida*
- 1b Leaves bright yellow-green, apices rounded, though not thickened. Leaves strongly contorted when dry. 4
 4a Leaves blunt and broad. Obvious papillae on the cell walls. Leaves not appearing interwoven when dry. *Barbula convoluta*
 4b Leaves acute, weakly papillate. Leaves appear tubular and interwoven when dry. *Weissia brachycarpa*

KEY C

Small (<10mm) mosses with leaves <2mm, not "bud-shaped"

- 1a Leaves lacking. Only capsule apparent. Rare in the PP zone. *Buxbaumia aphylla*
- 1b Leaves present. 2
- 2a Leaves silver-white, forming a short turf on soil. *Bryum argenteum*
- 2b Leaves green or green-brown. Substratum soil or litter. 3
- 3a Leaves dark green. Leaf cell length to width ratio ~1:1 (isodiametric). Leaf cells with papillae or else deeply channeled above the midrib. 4
- 4a leaves without serration on the margins. Leaves channeled above the midrib. 5
- 5a Leaf channel ending well before the leaf apex. *Didymodon rigidulus*
- 5b Leaf channel extending to the leaf apex. 6
- 6a Usually on rock. Dry leaves straight with broken tips. *Didymodon occidentalis*
- 6b Occurring on soil. Dry leaves twisted, without broken tips. *Didymodon vinealis*
- 4b Leaves with serrated margins at the apices, or leaves not channeled above the midrib. 7
- 7a Leaves often serrated at the apices. Leaves often long acuminate with leaf bases sheathing the stem. *Ditrichum flexicaule*
- 7b Leaves rarely serrated. Leaves acuminate, leaf bases not sheathing the stem. Capsule, if present, curved, dark, and beak shaped. Very common. *Ceratodon purpureus*
- 3b Leaves bright green. Leaf cell length to width ratio >2:1. Leaves lacking papillae and deep channel. 8
- 8a Leaf margins without serrations. 9
- 9a Leaves long acuminate, tapering to one cell wide. Capsule, when present, bright green and urn shaped, broadest near the middle. Very common. *Bryum caespitium*
- 9b Leaves abruptly tapering. Capsule short, curved, broadest near the opening. *Funaria hygrometrica*
- 8b Leaf margins serrated at the apices. 10
- 10a Leaves long acuminate, though more than one cell wide. Leaf bases sheathing the stem. Leaves involute. Lower stem not reddish. *Ditrichum flexicaule*
- 10b Leaves acute but not long acuminate. Leaf bases not sheathing the stem. Leaves not involute. Lower stem often reddish. *Pohlia nutans*

KEY D

Large (>10mm), conspicuous mosses with leaves >5mm

- 1a Leaves linear, acuminate, tapering to a gradual point. 2
- 2a Leaves open and undulating with toothed margins. Often more than one sporophyte originating from a single shoot apex. *Dicranum polysetum*
- 2b Leaves strongly keeled or involute, often sickle-shaped. 3
- 3a Leaves and stems robust, not hair-like, shiny gold-green. Midrib toothed at the apex. *Dicranum scoparium*
- 3b Leaves and stems weak, hair-like. Midrib not toothed at the apex. Leaf bases clasping the stem. *Ditrichum flexicaule*
- 1b Leaves spatulate or broadly triangulate. Not tapering to a gradual point. 4
- 4a Leaves broad, spatulate, dark green and plane when moist. Strongly contorted when dry. Leaf margins with double-sided teeth. Occurs infrequently in shaded areas. *Mnium spinulosum*
- 4b Leaves broad, triangulate, bright green, and keeled. Imbricate when dry. Leaf margins not toothed. Rare, occurs in open habitats. *Encalypta vulgaris*

KEY E

Creeping mosses (pleurocarpous)

- 1a Leaves longitudinally pleated. 2
 2a Leaves tightly curled in one direction. Branches <2mm wide. 3
 3a Central midrib present. Leaves yellow-green. *Sanionia uncinata*
 3b Central midrib absent. Leaves copper-green. 4
 4a Leaf margins recurved. Branches not julaceous. *Hypnum revolutum*
 4b Leaf margins plane. Branches julaceous. *Hypnum vaucheri*
 2b Leaves not tightly curled in one direction. Branches >2mm wide. 5
 5a Branch apices divergent. Leaf orientation random. Leaf tips acuminate. *Rhytidiadelphus triquetrus*
 5b Branches apices curved into a paw shape in a uniform direction. Leaf tips blunt. *Rhytidiopsis robusta*
 1b Leaves not longitudinal pleated. 6
 6a Branches julaceous or thread-like. Leaves imbricate. 7
 7a Branches thin and thread-like (~1mm). Leaf cells large and diamond shaped. Leaf cell length to width ratio ~2:1. *Pseudoleskeella tectorum*
 7b Branches thick (>1mm). Leaf cells long and rhombic, the length to width ratio ~4:1. 8
 8a Leaves with a long single midrib. *Brachythecium collinum*
 8b Leaves with a short, double midrib, or midrib absent. *Hypnum vaucheri*
 6b Branches not julaceous or thread-like. Leaves spreading. 9
 9a Leaves with a short, double midrib. Leaf apices blunt and toothed. Branching arranged in a series of "steps". *Hylocomium splendens*
 9b Leaves with a single midrib. Leaf apices acuminate. Branching not arranging in "steps". Very common in the PP zone. *Brachythecium albicans*

Lichens

- 1a Main axis vertical, radially symmetrical with cups or three dimensional branching. Generally not differentiated into upper and lower surfaces. 2
 2a Thallus always branched. Basal scales and cup shaped podetia absent. Note: *Cladonia* spp. key here. **Shrub fruticose lichens: KEY F**
 2b Thallus occasionally branched. Basal scales present, podetia cup shaped or not, usually with a single main axis. Note: *Cladonia* spp key here. **Club fruticose lichens: KEY G**
 1b Main axis horizontal. Thallus without three dimensional branching. Thallus flattened with a differentiated upper and lower surface. 3
 3a Thallus broad and leaf-like. Lower surface often loosely attached to the substratum by root-like rhizines. **Foliose lichens: KEY H**
 3b Thallus scale-like or crust forming. Lower surface firmly attached to the substratum, though margins may be raised. Rhizines absent. 4
 4a Small scales, often overlapping. Margins occasionally raised. **Squamulose lichens: KEY I**
 4b Crust-forming. Margins never raised. Some appearing merely as small orange or yellow apothecia. **Crustose lichens: KEY J**

KEY F

Shrub fruticose lichens

- 1a Thallus dark brown. 2
 2a Branches round or oval in cross section. 3
 3a Thallus branches minute (<1mm long), black, shiny, once branched. Appearing as tiny black antlers. Apothecia occasional, appearing as minute reddish cups. *Polychidium muscicola*
 3b Thallus dark brown, shiny, much branched with numerous minute, spiny projections. Main stems ~1mm wide. Entire thallus 10-40mm tall. Locally common. *Coelocaulon aculeatum*
 2b Branches flattened in cross section. Numerous short projections on the margins. *Cetraria ericetorum* subsp. *reticulata*
 1b Thallus pale. 4
 4a Thallus yellowish or greenish. 5
 5a Branches flattened. *Flavocetraria nivalis*
 5b Branches round or oval in cross section. 6
 6a Branches hollow, stout (1-2.5mm wide), straight, and abruptly pointed. *Cladonia uncialis*
 6b Branches slender (>1.2mm wide), often curved, and tapering to a point. 7
 7a Principle division of main axis near apex. *Cladina mitis*
 7b Principle division of main axis near base. *Cladina arbuscula*
 4b Thallus whitish. 8
 8a Main axis appearing cottony with subspherical branching lobules. *Stereocaulon* sp.
 8b Main axis hard corticate. Branches discrete, not divided into lobules. *Cladonia rangiferina*

KEY G

Club fruticose lichens (*Cladonia* spp.)

- 1a Occurring on an organic substratum (forest floor, litter, or wood). KEY G1
 1b Occurring on mineral soil. KEY G2

KEY G1

Club fruticose lichens (*Cladonia* spp.) on organic substrata

- 1a Podetia yellow or yellowish green. 2
 2a Podetia without cups and basal scales absent. Podetia much branched. Branches stout (1-2.5mm wide), hollow, and pointed. Occurring on litter. *Cladonia uncialis*
 2b Podetia cup shaped. Basal squamules present. Podetia unbranched. Occurring on wood. 3
 3a Podetia usually <15mm tall. Basal squamules 1-3mm wide. *Cladonia carneola*
 3b Podetia usually >15mm tall. Basal squamules 5-10mm wide. 4
 4a Podetia often torn. Inner thallus UV+ brilliant ice blue. *Cladonia sulphurina*
 4b Podetia rarely torn. Inner thallus UV- or UV+ dull white. *Cladonia deformis*
 1b Podetia not yellow. 5
 5a Podetia not cup shaped. 6
 6a Apothecia peach coloured and common, on the tips of branching corticate podetia. *Cladonia botrytes*
 6b Apothecia brown, or red, or lacking, but not peach coloured. Podetia branched or unbranched. 7

- 7a Podetia not branched, however, occasionally bearing short (2-5mm) projections at the apices. **8**
- 8a Podetia with continuous soredia. Some podetia with short (2-5mm) projections at the apices. Rare. ***Cladonia rei***
- 8b Podetia corticate at the base with patches of soredia. Becoming increasingly sorediate toward the apex. Not branched at the apex. Common. ***Cladonia cornuta***
- 7b Podetia conspicuously branched. Branches not merely short projections. **9**
- 9a Squamules often ascending the podetia. Podetia tips felty, not hard corticate. Terminal branches >1mm wide. ***Cladonia phyllophora***
- 9b Few, if any squamules on the podetia. Podetia tips hard corticate. Podetia finely branched with terminal branches <1mm wide. ***Cladonia multiformis***
- 5b Podetia cupped. **10**
- 10a Podetia bearing soredia. **11**
- 11a Tips opening into deep cups that appear as open holes into the thallus. ***Cladonia cenotea* (no photograph)**
- 11b Tips not opening into deep holes. **12**
- 12a Podetia cup margins lacking extensions. ***Cladonia fimbriata***
- 12b Podetia cups often with extensions originating from the cup margins. ***Cladonia subulata***
- 10b Podetia lacking soredia. **13**
- 13a Podetia covered with squamules. Podetia light coloured, not darkening toward the base. Apothecia not common. ***Cladonia ecmocyna***
- 13b Podetia occasionally with squamules. Podetia light to tan coloured, darkening toward the base. Apothecia common, chocolate brown. ***Cladonia gracilis***

KEY G2

Club fruticose lichens (*Cladonia* spp.) occurring on soil

- 1a Thallus yellow. **2**
- 2a Podetia cups and basal scales absent. Podetia much branched. Branches stout (1-2.5mm wide), hollow, and pointed. Apothecia absent. Uncommon. ***Cladonia uncialis***
- 2b Podetia with small cups (<15mm tall). Basal scales present. Apothecia, when present, bright red. ***Cladonia borealis***
- 1b Thallus not yellow. **3**
- 3a Podetia not cup shaped. **4**
- 4a Podetia not branched. Appearing as slender spikes with a patchy corticate surface. ***Cladonia cornuta***
- 4b Podetia branched. Not appearing as slender spikes. **5**
- 5a Podetia bearing numerous squamules. Podetia apices not bearing black apothecia. Basal squamules without conspicuous white, upturned margins. ***Cladonia phyllophora***
- 5b Podetia lacking squamules. Podetia apices conspicuously covered with black apothecia. Basal squamules with upturned margins and white lower surfaces. ***Cladonia symphylicarpa***
- 3b Podetia cup shaped. **6**
- 6a Squamules ascending the podetia, particularly on cup margins. Tiers of podetia cups arising from the centres of lower cups. ***Cladonia cervicornis***
- 6b Squamules not ascending the podetia. Tiers of podetia cups not arising from the centres of lower cups. **7**
- 7a Podetia bearing soredia. **8**
- 8a Cup margins giving rise to more cups. ***Cladonia subulata***
- 8b Cup margins not giving rise to more cups. **9**

- 9a Podetia long and slender (10-40mm tall) with an abruptly widening cup. Soredia two or more layers thick. *Cladonia fimbriata*
- 9b Podetia short (5-20mm tall), flaring gradually from the basal squamules. Soredia one layer thick. *Cladonia chlorophaea*
- 7b Podetia corticate, not bearing soredia, though ovoid scales present within cups. 10
- 10a Basal squamules usually raised at the margins. Squamules grey or tan coloured, not symmetrically arranged around the podetia. *Cladonia pyxidata*
- 10b Basal squamules closely appressed to the substratum, symmetrically arranged around the podetia in rosette. Squamules often olive-brown. *Cladonia pocillum*

KEY H

Foliose lichens

- 1a Thallus surface yellow. Narrow lobes (1-2mm wide) and long (10-30mm), much branched, and lacking marginal cilia and pruina. Undersurface black-brown. *Xanthoparmelia wyomingica*
- 1b Thallus surface not yellow. If narrow, then bearing marginal cilia or strongly pruinose. 2
- 2a Thallus lobes <1mm wide and <15mm long. Thallus woven and ascending, loosely attached to the substratum. Thallus white, or grey-brown, becoming brown at the lobe tips. Long, thin cilia originating on lobe margins. *Phaeophyscia constipata*
- 2b Thallus >1mm wide and often >15mm long. Thallus not woven, and usually firmly attached to the substratum. Lacking marginal cilia. 3
- 3a Upper surface with soredia, either in discrete patches or on lobe margins. 4
- 4a Soredia occurring in small round or oval patches on the thallus. Soredia absent on lobe margins. 5
- 5a Thallus <20mm wide. Occurring on soil. Occasionally with apothecia. Rhizenes matted together. *Peltigera didactyla* var. *extenuata*
- 5b Thallus larger >20mm wide. Occurring over moss. Never with apothecia. Rhizenes discrete. *Peltigera didactyla* var. *didactyla*
- 4b Soredia occurring on the thallus margins and occasionally on the central thallus. 6
- 6a Lobes <5mm wide. Lobe tips often pruinose. Occurring in dry grasslands over soil or mosses. *Physconia enteroxantha*
- 6b Lobes 5-20mm wide. Pruina absent. Occasional on mossy soil in shaded sites. *Nephroma parile*
- 3b Soredia lacking. 7
- 7a Thallus lobes narrow, <5mm wide. Lobe tips strongly pruinose. Over moss. *Physconia muscigena*
- 7b Thallus lobes >5mm wide. Lobe tips at most weakly pruinose. Mainly growing over soil though occasionally over mosses. 8
- 8a Thallus bearing minute, brown, ovoid scales (1-2mm wide) on the upper surface. Thallus usually <20mm wide. Occurring over soil. *Peltigera lepidophora*
- 8b Thallus lacking scales on the surface. Usually >20mm wide. On soil or litter. 9
- 9a Veins on lower surface indistinct. Thallus thick and grey-green. Upper surface smooth, but with numerous fissures. Margins inrolled. Sparse short hairs on lobe tips. Common in the PP zone. *Peltigera malacea*
- 9b Veins on lower surface distinct. Thallus light or dark grey, not obviously thick or bearing fissures. Margins up or down turned. Surface somewhat felty. 10
- 10a Lobes >15mm wide. Lobe tips down turned. Rhizines with squarrose hairs, matting together. *Peltigera canina*
- 10b Lobes <15mm wide. Lobe tips up turned. Rhizenes without squarrose hairs. 11

- 11a Veins becoming dark brown toward the center of the lower surface. Veins appearing felty, not conspicuously overlapping. Rhizenes matted. Common. *Peltigera rufescens*
 11b Veins remaining pale toward the center of the lower surface. Veins ropey, appearing overlapping. Rhizines mainly distinct. Occasional. *Peltigera ponojensis*

KEY I

Squamulose lichens

- 1a Thallus black or dark black/brown. With or without <1mm wide ovoid scales on upper surface of the thallus. 2
 2a Thallus 90-130um thick with distinct, vertical hyphal strands apparent in cross section. Minute (<1mm) ovoid scales on upper surface. *Collema* sp.
 2b Thallus 200-250um thick, without perpendicular strands. With or without scales. 3
 3a Thallus black-brown, 6-8mm wide with minute (<1mm), black, ovoid scales on the upper surface. *Collema crispum*
 3b Thallus usually <5mm wide. With or without scales. 4
 4a Thallus often arranged in a rosette. Spores two celled. *Collema coccophorum*
 4b Thallus irregularly lobed. Spores four celled. *Collema tenax* var. *crustaceum*
 1b Thallus white, beige, tan, or brown. Lacking scales on upper surface. 5
 5a Thallus absent. Apothecia dark red-brown occurring over litter. Rare. *Bryonora castanea*
 5b Thallus present. Apothecia not dark red-brown. If red, then growing directly over soil. 6
 6a Overlapping brown squamules without apothecia. Forming a small but continuous mat. Lobe margins appressed to the substratum. *Massalongia microphylliza*
 6b If squamules overlap, then apothecia present. Not forming a continuously overlapping mat. Lobe margins appressed or raised. 7
 7a Thallus with immersed perithecia that appear as small bumps (<0.5mm diameter) or minute dots (~0.1mm diameter) on the surface. Thallus lacking convex apothecia. 8
 8a Upper surface with perithecia appearing as raised bumps (<0.5mm diameter) with black centers. Thallus white or brown. *Endocarpon pusillum*
 8b Thallus lacking raised bumps. Thallus tan, brown, or grey. 9
 9a Thallus tan to brown. Perithecia appearing as minute dots (~0.1mm diameter) rather than raised bumps. *Catapyrenium squamulosum*
 9b Thallus grey to brown, often white on undersurface. Lobe margins often ascending. *Cladonia* spp. squamules. Look for associated podetia and use KEY G.
 7b Thallus lacking perithecia. Often with conspicuous black or brown, convex apothecia. 10
 10a Apothecia restricted to the thallus margins. 11
 11a Thallus bright red with black apothecia. Occurring on soil in the grasslands. *Psora decipiens*
 11b Thallus white with pruina or tan coloured. 12
 12a Thallus white pruinose with numerous surface fissures. Occuring on rock or soil. *Psora cerebriformis*
 12b Thallus tan, lacking surface fissures. Occuring on soil. *Arthonia glebosa*
 10b Apothecia central on the thallus, or at least not restricted to the margins. 13
 13a On thin layer of soil over rock. 14
 14a Apothecia black. Thallus darkly coloured green-brown. Margins strongly ascending. *Psora nipponica*
 14b Apothecia brown. Thallus pink to tan with margins occasionally ascending. *Psora tuckermanii*
 13b On thick soil substratum, not over rock. 15

15a Thallus scales ~1mm with black apothecia approximately as broad as the scales. Thallus often strongly pruinose, not shiny. *Psora montana*

15b Thallus scales usually >1mm. Apothecia black or brown, not as broad as the scales. Thallus either weakly pruinose, or distinctly shiny. 16

16a Apothecia black. Upper surface distinctly shiny brown. *Psora globifera*

16b Apothecia brown. Upper surface brown to cream coloured, weakly pruinose, not distinctly shiny. *Psora tuckermanii*

KEY J

Crustose lichens

1a Thallus yellow, with sunken black apothecia. *Acarospora schleircheri*

1b Thallus bright orange, beige, brown, white or black. With or without black apothecia. 2

2a Apothecia orange or yellow orange. On soil. 3

3a Thallus white, tinged with orange or yellow. Uncommon. *Fulgensia desertorum*

3b Thallus orange or absent. 4

4a Rim of apothecia grey. Uncommon. *Caloplaca cerina*

4b Rim of apothecia the same, or slightly lighter than the center. 5

5a Apothecia 1-2mm wide, dark orange. No associated thallus apparent

Caloplaca jungermanniae

5b Apothecia <1mm wide, bright yellow-orange. Associated thallus yellow-orange or absent. 6

6a Individual apothecia discrete and isolated. *Candelariella terrigena*

6b Apothecia clumped together. Occasionally with a minutely lobed thallus densely covered in soredia. *Caloplaca tominii*

2b Apothecia not yellow-orange. On soil or rock. 7

7a Thallus white. 8

8a Thallus lobate-crustose, white with orange or yellow tinges near the margins.

Fulgensia desertorum

8b Thallus crustose, white with white or black apothecia. 9

9a Apothecia white or pink. Rarely on soil, usually over moss or litter. Common on less disturbed sites. *Ochrolechia upsaliensis*

9b Apothecia black. 10

10a Apothecia concave, inbedded into the thallus. Thallus usually >20mm wide and segmented into distinct polygons. Common on heavily grazed sites. *Diploschistes muscorum*

10b Apothecia convex. Thallus usually <20mm wide and not segmented into distinct polygons. Uncommon. 11

11a Apothecia pruinose, appearing as a light white dusting. Spores four celled. Over soil.

Buellia geophila

11b Apothecia not pruinose. Apothecia dark black and highly contrastive. Spores two celled. Over soil or litter. *Buellia papillata*

7b Thallus grey, grey-brown, dark brown or apparently lacking. 12

12a Thallus minute (1-2mm wide). Sunken, black apothecia bordered by white, triangular blocks of thallus. Occurring on silt cliffs. Very rare, known from three sites in North America, including Kamloops. *Solorinella asteriscus*

12b Thallus >2mm wide, brown or grey. Usually occurring on litter. Lacking white triangular fragments. Common. 13

13a Thallus light grey or grey-brown with black apothecia. Occurring on litter. *Amandinea punctata*

13b Thallus dark brown and granular. Very common on soil and litter. *Placynthiella uliginosa*

Glossary

Acrocarpous- branches terminate with a reproductive organ. Main axis is vertical.

Acuminate- a long tapering narrow point.

Apothecia- the disc-shaped, or hemispherical spore producing sexual reproductive structure of the fungal partner in a lichen.

Awn- a sharp, thin extension of the midrib beyond the apex a moss leaf.

Capsule- the spore producing structure in a moss. Often urn-shaped or cylindrical.

Corticate- having a hard, compact outer layer in a lichen.

Crustose- a form of lichen that has a hard upper surface, but that integrates with the substratum on the lower surface.

Cryptogamic crust- an association of liverworts, mosses, lichens, fungi, algae, and cyanobacteria living as a thin stratum over soil.

Foliose- a form of lichen that resembles a leaf, with a differentiated upper and lower surface.

Fruticose- a form of lichen that grows along a vertical axis, is loosely radially symmetrical, and is often branched.

Imbricate- closely overlapping.

Incurved- leaf margins that are weakly rolled toward the top (ventral) side of the leaf.

Involute- leaf margins that strongly roll toward the ventral side of the leaf.

Julaceous- leaves overlapping so as to form a cylindrical structure, round in cross section.

Lamellae- flaps of tissue along the midrib.

Lobate- having distinct lobes.

Lobule- small lobes.

Papillae- small bumps in the outer cell wall of a moss.

Papillate- having papillae.

Pleurocarpous- reproductive structures are borne laterally. Main axis is horizontal.

Podetia- hollow, upright stalks that bear the apothecia in the genus *Cladonia*.

Pruina- a white frosting of minute crystals.

Recepticle- the structure that bears the female archegonia and the sporangia in thallose liverworts.

Recurved- leaf margins that are weakly rolled toward the bottom (dorsal) side of the leaf.

Revolute- leaf margins that strongly roll toward the dorsal side of the leaf.

Rhizine- a root-like anchoring structure made up of fungal hyphae, common in the foliose lichens.

Seta- the thin stalk that bears the sporangium (capsule) in the mosses and liverworts.

Soredia- powdery asexual propagules in lichens. Comprised of a few cells of algae or cyanobacteria surrounded by a minute ball of fungal hyphae.

Spathulate- spoon shaped.

Sporangium- the spore producing structure in a moss or liverwort.

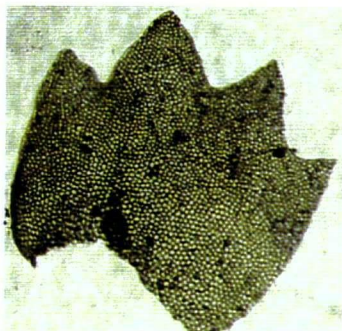
Squamulose- a form of lichen that resembles small scales closely appressed to the soil. Occasionally with ascending or overlapping margins.

Squamule- a scale.

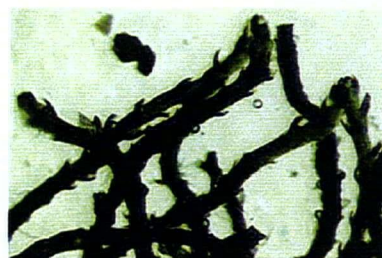
Thallose- flattened, strap-like. Having a thallus.

Thallus- the vegetative body of a lichen, moss, or liverwort.

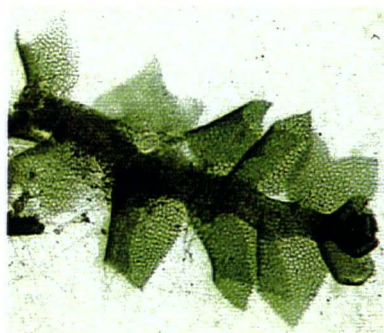
Liverworts



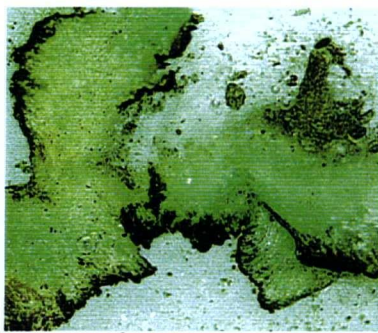
Barbilophozia hatcheri



Cephaloziella divaricata



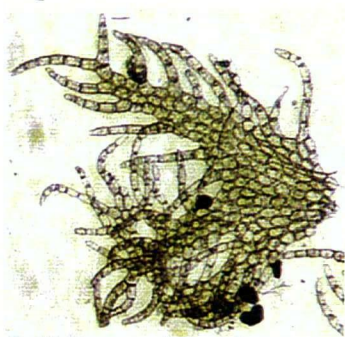
Lophozia excisa



Mannia fragrans



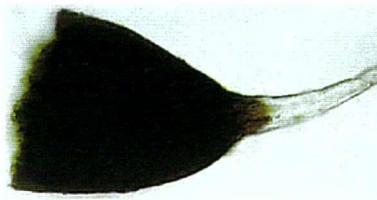
Ptilidium ciliare



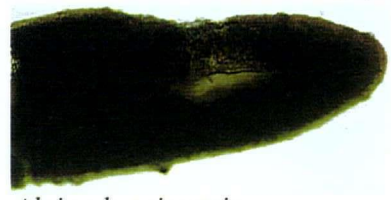
Ptilidium pulcherrimum

Mosses

101



Aloina bifrons



Aloina brevirostris



Aloina rigida



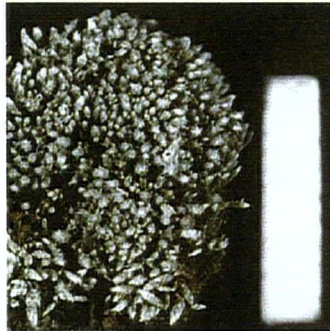
Barbula convoluta



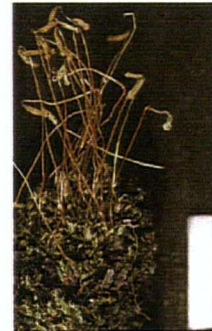
Brachythecium albicans



Brachythecium collinum



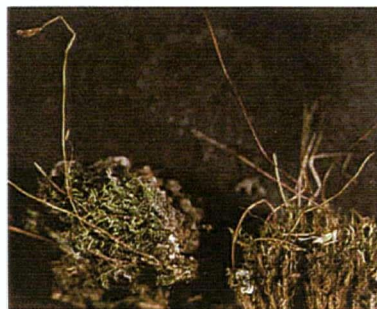
Bryum argenteum



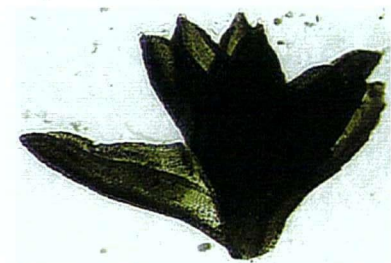
Bryum caespitium



Buxbaumia aphylla



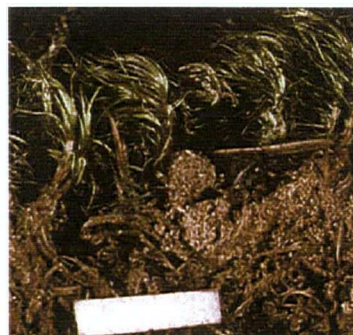
Ceratodon purpureus



Desmatodon convolutus



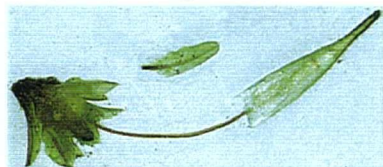
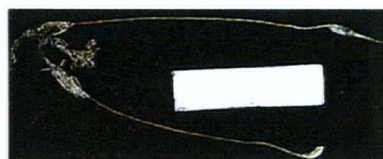
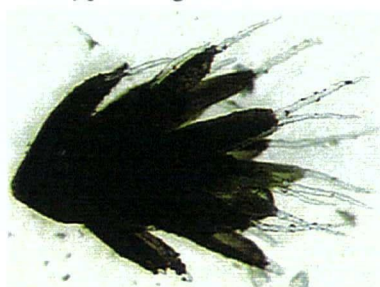
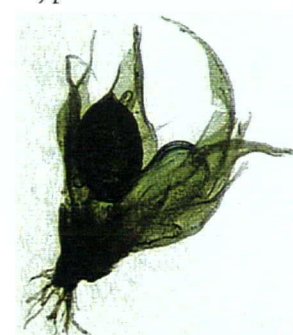
Dicranum polysetum



Dicranum scoparium



Didymodon occidentalis

*Didymodon rigidulus**Didymodon vinealis**Ditrichum flexicaule**Encalypta rhaptocarpa**Encalypta vulgaris**Fissidens bryoides**Funaria hygrometrica**Grimmia alpestris**Grimmia pulvinata**Homalothecium aeneum**Hylocomium splendens**Hypnum revolutum**Hypnum vaucheri**Mnium spinulosum**Phascum cuspidatum*



Pohlia nutans



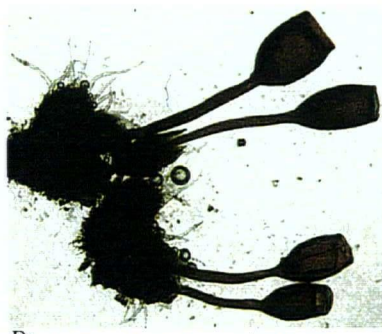
Polytrichum juniperinum



Polytrichum piliferum



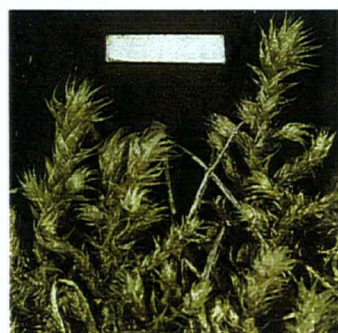
Pseudoleskeella tectorum



Pterygoneurum ovatum



Pterygoneurum subsessile



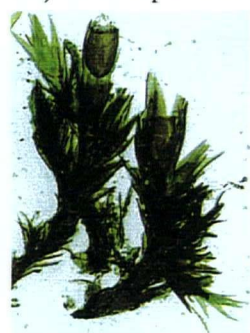
Rhytidiadelphus triquetrus



Rhytidiopsis robusta



Sanionia uncinatus



Schistidium cuspidatum

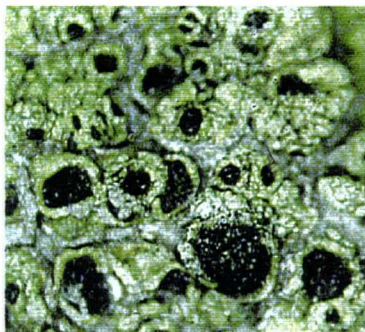


Tortula ruralis



Weissia hedwigii

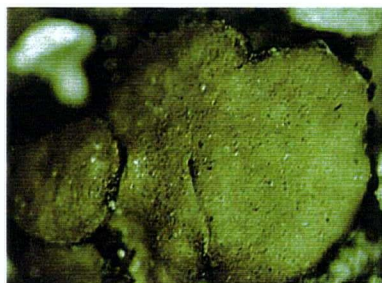
Lichens



Acarospora schleicheri



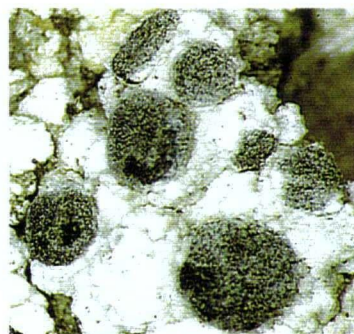
Amandinea punctata



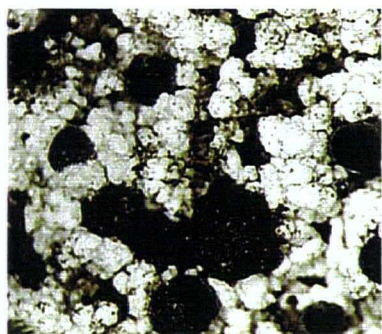
Arthonia glebosa



Bryonora castanea



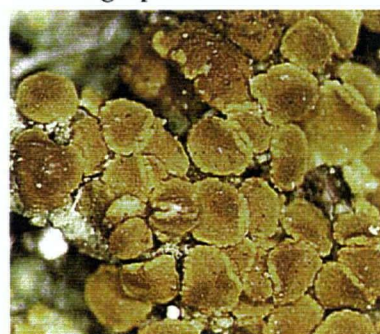
Buellia geophilla



Buellia papillata



Caloplaca cerina



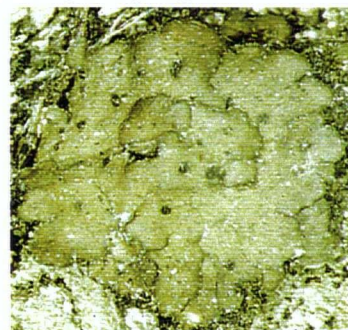
Caloplaca jungermanniae



Caloplaca tominii



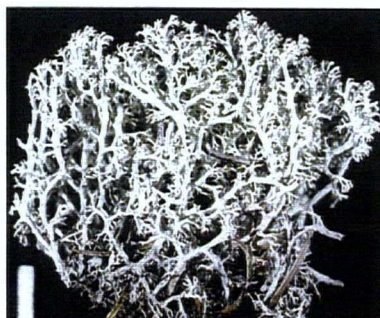
Candelariella terrigena



Catapyrenium squamulosum



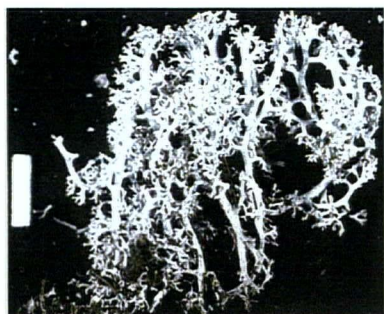
Cetraria ericetorum



Cladina arbuscula



Cladina mitis



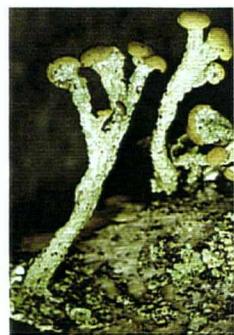
Cladonia rangiferina



Cladina stellaris



Cladonia borealis



Cladonia botrytes



Cladonia carneola



Cladonia cenotea



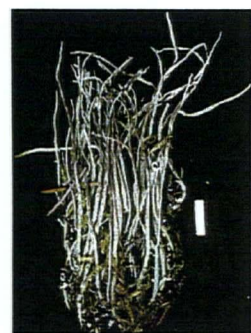
Cladonia cervicornis



Cladonia chlorophaea



Cladonia coniocraea



Cladonia cornuta



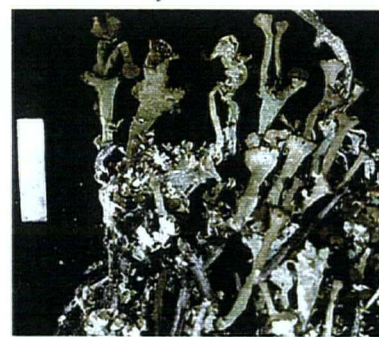
Cladonia deformis



Cladonia ecmocyna



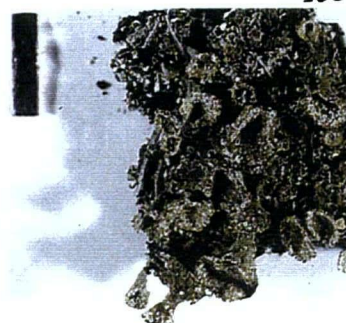
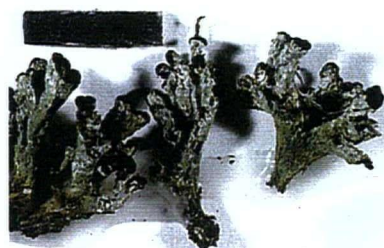
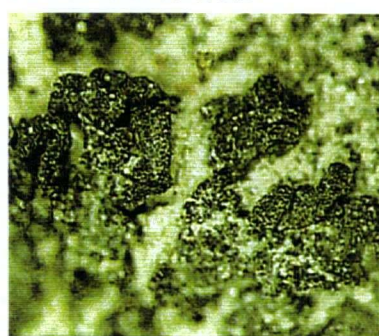
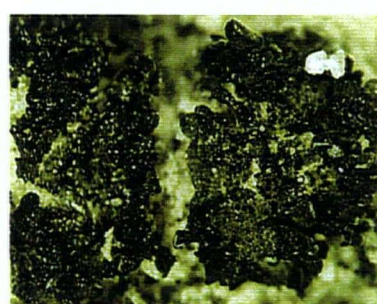
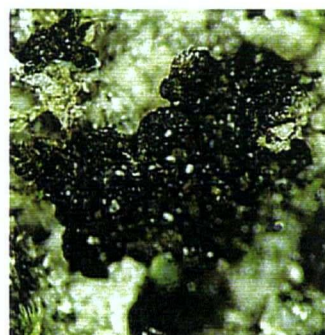
Cladonia fimbriata



Cladonia gracilis

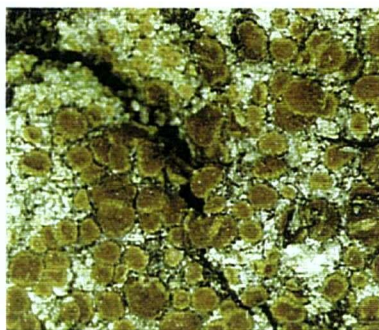


Cladonia multiformis

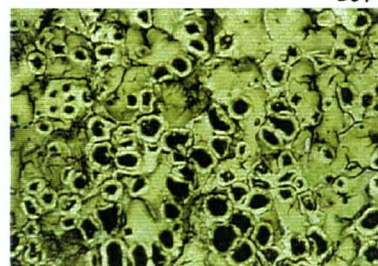
*Cladonia phyllophora**Cladonia pocillum**Cladonia pyxidata**Cladonia rei**Cladonia subulata**Cladonia sulphurina**Cladonia symphyarpa**Cladonia umbricola**Cladonia uncialis**Coelocaulon aculeatum**Collema coccophorum**Collema crispum**Collema tenax* var. *crustaceum**Diploschistes muscorum**Endocarpon pusillum*



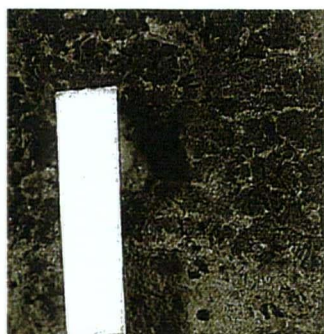
Flavocetraria nivalis



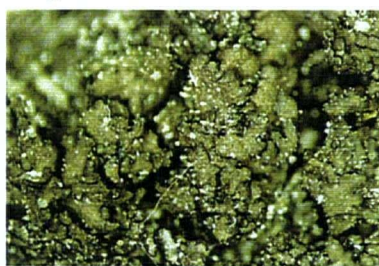
Fulgensia desertorum



Lecanora muralis



Leptogium minutissimum



Massalongia microphylliza



Nephroma parile



Ochrolechia upsaliensis



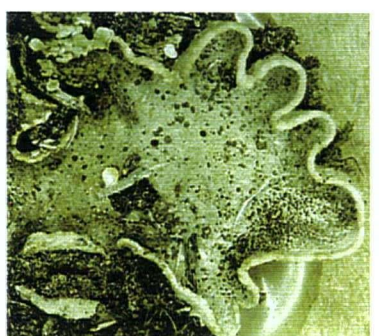
Peltigera canina



Peltigera didactyla



Peltigera didactyla var. *extenuata*



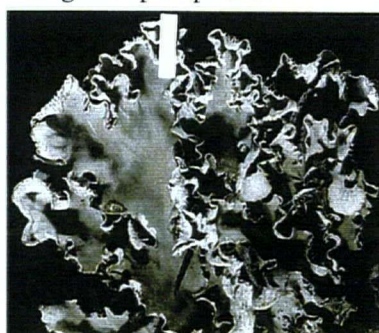
Peltigera lepidophora



Peltigera malacea



Peltigera ponojensis



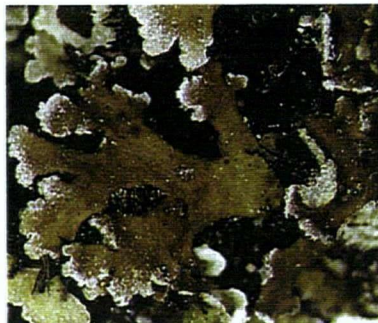
Peltigera rufescens



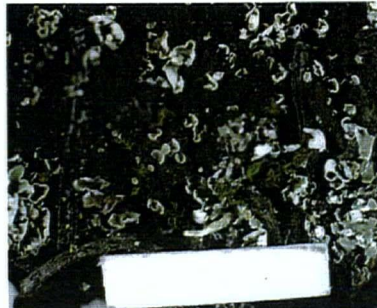
Phaeophyscia constipata



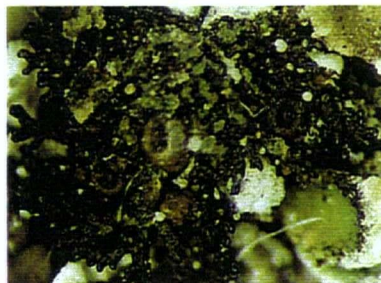
Physconia enteroxantha



Physconia muscigena



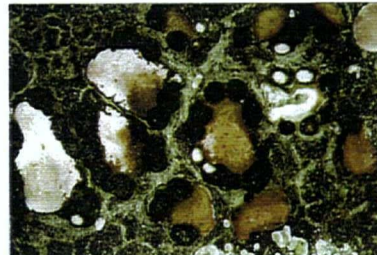
Placynthiella uliginosa



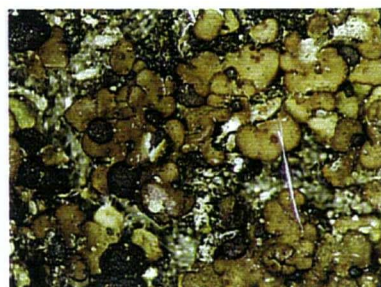
Polychidium muscicola



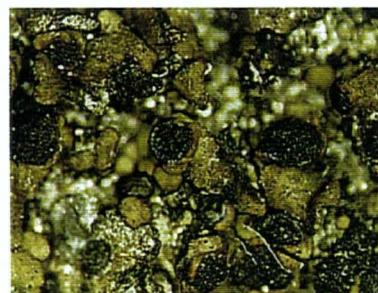
Psora cerebriformis



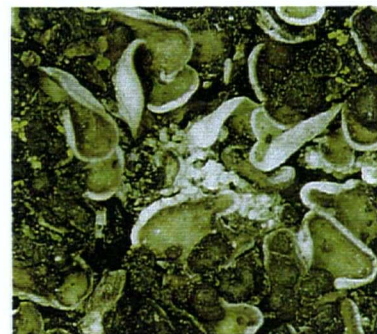
Psora decipiens



Psora globifera



Psora montana



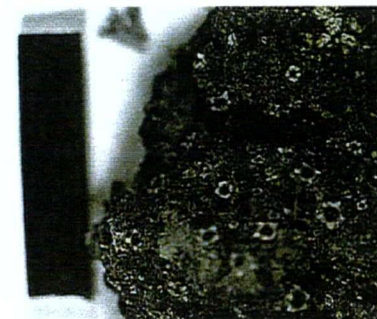
Psora nipponica



Psora tuckermanii



Rhizoplaca melanophthalma



Solorinella asteriscus



Stereocaulon sp.



Xanthoria wyomingica

Site Number

<i>Collema coccophorum</i> Tuck.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Collema crispum</i> (Hudson) F.H. Wigg.	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Collema tenax</i> var. <i>crustaceum</i> (Kremp.) Degel.	+	-	-	-	-	-	-	+	-	+	+	-	-	-	-	-	-	+	-
<i>Diploschistes muscorum</i> (Scoop) R. Scant	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Endocarpon pusillum</i> Hedw.	+	-	+	-	-	-	+	+	-	-	-	+	+	-	-	-	+	+	+
<i>Ochrolechia upsaliensis</i> (L.) A. Massal.	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	+
<i>Peltigera canina</i> (L.) Willd.	-	-	-	-	-	+	-	-	+	-	-	-	-	+	+	-	-	-	-
<i>Peltigera didactyla</i> (With.) Laundon	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	+	+	+
<i>Peltigera didactyla</i> var. <i>extenuata</i> (Nyl.) Goffinet & Hastings	-	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	+	-
<i>Peltigera lepidophora</i> (Vainio) Bitter	-	+	-	+	+	-	-	+	+	+	-	-	+	-	-	-	+	-	+
<i>Peltigera malacea</i> (Ach.) Funck	-	-	-	+	+	+	+	-	+	+	+	+	-	+	-	-	-	-	+
<i>Peltigera ponjensis</i> Gyl.	+	-	-	-	-	+	+	+	-	+	-	-	-	-	+	-	+	-	+
<i>Peltigera rufescens</i> (Weis) Humb.	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+
<i>Phaeophyscia consipata</i> (Nortlin & Nyl.) Moberg.	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Physconia muscigena</i> (Ach.) Poelt	+	+	+	-	+	+	+	+	+	-	+	-	+	-	+	-	+	+	-
<i>Placynthiella uliginosa</i> (Schrader) Coppins & P. James	+	-	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	+	-
<i>Polychidium muscicola</i> (Sw.) Gray	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Psora cerebriformis</i> W. A. Weber	-	-	+	-	-	-	-	-	-	-	-	+	+	+	-	-	-	+	-
<i>Psora globifera</i> (Ach.) A. Massal.	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Psora montana</i> Timdal	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
<i>Psora tuckermanii</i> R. Anderson ex Timdal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Xanthoparmelia wyomingica</i> (Gyel.) Hale	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Lichen Richness

Bryophytes

Mosses

<i>Aloina bifrons</i> (De Not.) Delgadillo	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Aloina brevirostris</i> (Hook & Grev.) Kindb.	-	-	-	-	-	-	-	+	-	-	+	+	-	-	+	+	-	-	+
<i>Barbula convoluta</i> Hedw.	-	+	-	-	+	-	-	-	-	-	-	+	+	-	-	+	+	-	+
<i>Brachythecium albicans</i> (Hedw.) Shimp. in B.S.G.	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Brachythecium collinum</i> (Schleich. ex C. Mull.) Shimp. in B.S.G.	-	+	-	+	+	+	-	+	+	+	-	-	+	-	+	+	-	+	+
<i>Bryum argenteum</i> Hedw.	-	-	+	-	+	-	+	-	-	-	-	-	-	-	+	+	-	+	-
<i>Bryum caespitium</i> Hedw.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ceratodon purpureus</i> (Hedw.) Brid.	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	+	+	+

Site Number

<i>Desmatodon convolutus</i> (Brid.) Grout	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Dicranum polysetum</i> Sw.	-	-	-	+	+	+	-	+	-	-	-	+	-	-	-	-	-	+	-
<i>Dicranum scoparium</i> Hedw.	-	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Didymodon vinealis</i> (Brid.) Zander	-	-	-	-	-	-	+	+	-	-	-	-	-	-	+	+	-	-	-
<i>Encalypta rhaptocarpa</i> Schwaegr.	-	-	+	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-
<i>Encalypta vulgaris</i> Hedw.	-	-	+	+	+	-	-	-	+	-	-	+	+	-	-	+	+	-	+
<i>Fissidens bryoides</i> Hedw.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Funaria hygrometrica</i> Hedw.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Homalothecium aeneum</i> (Mitt.) Lawt.	-	-	-	-	+	+	-	-	+	-	-	+	-	-	-	-	-	-	-
<i>Hylacomitrium splendens</i> (Hedw.) B.S.G.	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hypnum vaucheri</i> Lesq.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Phascum cuspidatum</i> Hedw.	-	-	-	+	+	-	+	+	-	-	-	+	-	-	-	+	-	-	-
<i>Pleurozium schreberi</i> (Brid.) Mitt.	-	-	-	-	-	+	-	-	-	+	-	+	-	-	-	+	-	-	-
<i>Pohlia nutans</i> (Hedw.) Lindb.	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Polytrichum juniperinum</i> Hedw.	-	+	-	-	+	-	-	+	+	+	-	-	+	-	-	+	+	+	+
<i>Polytrichum piliferum</i> Hedw.	-	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	-
<i>Pterygonerum sessile</i> (Brid.) Jur.	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-
<i>Pterygoneurum ovatum</i> (Hedw.) Dix.	-	-	+	+	+	-	+	-	-	-	+	+	+	-	-	+	-	+	-
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhytidiopsis robusta</i> (Hedw.) Broth.	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sanionia uncinatus</i> Loeske	-	-	-	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-
<i>Timmia austriaca</i> Hedw.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Tortula ruralis</i> (Hedw.) Gaertn. et al.	+	+	+	+	+	+	-	+	+	+	+	+	-	+	+	+	+	+	+
<i>Weissia brachycarpa</i> (Nees & Hornsch.) Jur.	-	-	+	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-

Liverworts

<i>Barbilophozia hatcheri</i> (Evans) Loeske	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cephaloziella divaricata</i> (Sm.) Schiffr.	-	-	+	+	-	-	+	+	-	+	-	+	-	+	+	-	+	+	-
<i>Lophozia excisa</i> (Dicks.) Dum.	-	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	-
<i>Ptilidium ciliare</i> (L.) Hampe	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Ptilidium pulcherrimum</i> (G. Web.) Hampe	-	-	-	+	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-
Bryophyte Richness	3	9	11	13	14	17	9	12	9	11	8	19	11	7	11	15	10	10	11

Site Number

<i>Centaurea maculosa</i> Lam.	-	+	-	-	+	+	-	-	-	+	-	+	-	-	+	-	+	+
<i>Chrysothamnus nauseosus</i> (Pall.) Brit.	+	-	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+
<i>Cirsium undulatum</i> (Nutt.) Spreng.	+	-	+	-	+	+	-	-	-	+	-	-	-	-	-	-	-	-
<i>Cirsium vulgare</i> (Savi) Tenore	+	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	+
<i>Collinsia parviflora</i> Lindl.	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Comandra umbellata</i> (L.) Nutt.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Crepis atrabarba</i> Heller	+	-	-	+	+	+	+	+	-	+	+	+	+	+	+	+	+	-
<i>Cynoglossum officinale</i> L.	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	+
<i>Delphinium nuttallianum</i> Pritz.	-	-	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-
<i>Descurainia pinnata</i> (Walt.) Britt.	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-
<i>Descurainia sophia</i> (L.) Webb	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Dodecatheon pulchellum</i> (Raf.) Merrill	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Draba nemorosa</i> L.	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Draba verna</i> L.	-	+	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Elymus cinereus</i> Scribn. & Merr.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Epilobium foliosum</i> (T. & G.) Suksd.	+	-	+	+	+	+	+	+	+	-	+	+	+	-	-	-	-	-
<i>Erigeron compositus</i> Pursh	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Erigeron corymbosus</i> Nutt.	+	+	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+
<i>Erigeron filifolius</i> Nutt.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Erigeron pumilus</i> Nutt.	-	+	+	-	-	+	+	+	+	-	-	-	-	-	-	-	-	+
<i>Eriogonum heracleoides</i> Nutt.	-	-	-	+	+	-	+	+	+	-	-	-	-	-	+	-	-	-
<i>Festuca campestris</i> Rydb.	-	+	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Filago arvensis</i> L.	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fragaria virginiana</i> Duchesne	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Fritillaria pudica</i> (Pursh) Spreng.	+	+	+	-	-	+	+	+	+	-	+	+	+	+	+	+	+	-
<i>Gaillardia aristata</i> Pursh	+	+	+	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+
<i>Geum triflorum</i> Pursh	-	-	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+
<i>Grindelia squarrosa</i> (Pursh) Dunal	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hedysarum sulphurescens</i> Rydb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Heterotheca villosa</i> (Pursh) Shinnars	-	-	+	+	+	-	-	-	-	-	+	+	+	+	-	-	-	-
<i>Heuchera cylindrica</i> Dougl.	-	+	-	-	-	+	+	+	-	-	-	-	-	-	+	+	+	+
<i>Hieracium albiflorum</i> Hook.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hieracium scouleri</i> Hook.	-	-	-	-	-	-	-	-	-	+	+	+	+	+	-	-	-	-
<i>Hieracium umbellatum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Juniperus communis</i> L.	-	-	-	-	-	+	-	+	-	+	-	-	-	-	+	+	-	-

Site Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Shepherdia canadensis</i> (L.) Nutt.	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Silene douglasii</i> Hook.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Silene menziesii</i> Hook.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Sisymbrium loeselii</i> L.	+	+	+	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	+
<i>Solidago canadensis</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Solidago spathulata</i> D.C.	-	+	+	+	-	+	+	+	+	-	+	+	+	+	-	-	+	-	+
<i>Sporobolus cryptandrus</i> (Torr.) Gray	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Stephanomeria tenuifolia</i> (Torr.) Hall	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Stipa comata</i> Trin. & Rupr.	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+
<i>Stipa occidentalis</i> Thurb.	-	-	-	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-
<i>Symphoricarpos albus</i> (L.) Blake	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+
<i>Taraxicum officinale</i> Weber	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+	-	+
<i>Tragopogon dubius</i> Scop.	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Verbascum thapsus</i> L.	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Vulpia octoflora</i> (Walt.) Rydb.	+	-	+	+	+	+	+	+	+	-	+	-	+	+	+	+	+	-	-
<i>Zigadenus venenosus</i> Wats.	-	+	-	-	+	-	-	+	-	-	-	-	+	+	-	-	+	-	+
Richness	44	55	41	35	51	52	33	50	42	36	47	32	50	41	41	39	47	24	53