Distributional Patterns of Terricolous Lichens Occurring Above Treeline At Deer Park, Olympic National Park

by

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Abstract

DISTRIBUTIONAL PATTERNS OF TERRICOLOUS LICHENS OCCURRING ABOVE TREELINE AT DEER PARK, OLYMPIC NATIONAL PARK

By Linda Marie Kunze

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This study investigates distributional patterns of terricolous lichens occurring above treeline at Deer Park in the Olympic Mountains. It identifies environmental and biotic factors affecting their occurrence and determines the environmental scale appropriate for their study.

Twenty-six sites were selected to represent the broadest range of habitat conditions present at Deer Park. Each site was randomly subsampled determining percent cover of lichen and vascular plant species. Twenty-eight species of terricolous lichens were identified. Environmental parameters measured include slope, aspect, elevation, soil type and substrate stability. Percent soil moisture and temperatures at soil surface and at a 6 cm depth were obtained for four dates during the summer of 1979.

Data were analzsed using simple and multiple linear regression, Kendall's nonparametric rank correlations, curve fitting techniques, Path Analysis, RA, PO and PCA.

Lichen species composition is correlated with vascular

plant community type. Lichen cover is related to vascular plant cover. In alpine communities, lichen cover is directly correlated with vascular plant cover. Vascular plants stabilize the substrate allowing the establishment of lichens. Species-rich mats of vascular plants and lichens result. In subalpine meadows, cover of vascular plants and lichens are inversely related. The higher plants are hypothesized to have a competitive advantage over slower growing lichens and to produce a microenvironment of low light and high moisture, conditions which are detrimental to lichen growth. High soil moisture and perturbation by deer or marmots are shown to reduce lichen cover and species richness regardless of other conditions.

Distributional patterns for individual lichen species are determined on the microhabitat scale. *Cladonia chlorophaea*, *C. ecmocyna*, *C. piedmontensis*, *C. verticillata* and *Peltigera canina* occur in cool, moist, shaded microsites. *Cetraria cucullata*, *Cornicularia aculeata*, *Ochrolechia upsaliensis*, *Peltigera canina* var. *rufescens*, *Stereocaulon tomentosum* and *Thamnolia vermicularis* all occur in highly exposed, dry, stable microsites. *Peltigera canina* var. *rufescens* and *Thamnolia vermicularis* also occur on unstable substrates. *Cetraria islandica* and *Cladonia impexa* exhibit a large environmental amplitude, occupying both cool, moist, shaded subalpine sites and xeric exposed alpine sites. *Cladonia cariosa* and *C. polycarpoides* occupy xeric, exposed microsites and areas preturbed by deer and/or marmots.

Vascular plant community type and cover are causally related to lichen establishment and growth. However, the mechanisms by which they are related are still a matter of speculation.

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CHAPTER I: INTRODUCTION

Lichen ecology is a young field of study, frought with myths and generalizations concerning the range and severity of conditions under which lichens grow. Ecological studies of higher plants often lump lichen species into artificial categories which lack any real ecological significance. Lichens are difficult to deal with taxonomically and though any attempt to work with them is admirable, for the most part these studies only further obscure the true relationships between lichens and their environments. Only recently have studies been undertaken to determine the effect of various environmental factors upon individual lichen species. From these studies it is apparent that lichens can no more be viewed as homogeneous in their responses to the environment than can higher plants. Individual species have varied tolerences to ranges of light, moisture and temperature often occupying quite specific positions in the ecosystem.

This study is an attempt to determine first, how terricolous lichen species above treeline are distributed with respect to their environment and second, whether studies of distributional patterns in lichens are more appropriate on a micro- or macrohabitat scale.

The first portion of this study approaches several questions. First, are there lichen species with similar distributional patterns? In ecological studies not specifically carried out on lichens, species are usually 1) lumped into a single category, 2) broken down into recognizable morphological groups or 3) most often, simply ignored. The first choice assumes uniformity of species responses to environmental and biotic factors. The second assumes comparable responses of species with similar morphology and differences between those with dissimilar morphology. It is obvious through recent ecological and physiological studies of lichens that these are unreasonable assumptions. But how individualistic are distributions of species? Does each species have a unique pattern of distribution or are there associations or communities of species with similar distributions? Several vascular plant communities have been delimited. Is there reason to believe that a similar situation might occur with the lichen flora?

Second, how do lichen distributions relate to vascular plants? Are there correlations between community type, overall cover or specific species of vascular plants with either lichen associtions or individual species? How does the vascular plant flora affect lichens?

Third, are there correlations between the distribution of lichens and environmental parameters? Which parameters are significant?

The second portion of this study considers the scale requisite for investigation of lichen species distribution.

By this is meant investigation on the macro- versus microhabitat level. Are there distributional patterns on the microhabitat level which are not apparent on the macrohabitat level? Are distributional patterns found on the macrohabitat level meaningful?

Ecological Considerations of the Lichen Symbiosis

Unlike most other plants, lichens are not single organisms. They are composites, the result of a symbiotic relationship between a fungus and an alga producing a unique structure unlike that formed by either component separately. The interactions of the phycobiont (algal component) and mycobiont (fungal component) are not well known. Simply put, the alga carries out photosynthesis while the fungus provides a structure, protection from desiccation and probably a collection and storage system for nutrients and moisture. Further information on the nature of the lichen symbiosis can be obtained from Ahmadjian (1967), Hale (1967) and Ahmadjian and Hale (1973).

This symbiosis must be kept in mind when studying either lichen physiology or ecology. As obvious as this may sound, it is something which has been and often still is overlooked. For example, until recently, respiration rates were monitored to indicate species responses to different enviromental factors. MacFarlane and Kershaw (1980) point out that the fungus is responsible for most observed respiration in lichens. They also determined that the phycobiont is more sensitive to thermal stress than is the mycobiont. Hence, experiments using respiration to monitor physiological responses of lichens to temperature indicate ranges exceeding those tolerated by the phycobiont. As a result, ranges were determined which exceed the tolerence of the lichen as a whole.

Literature Review

Moisture, temperature and light are the most common parameters dealt with in the lichen literature though substrate, pH, wind effects and available nutrients are also considered briefly.

Moisture. Until recently, it was assumed that the optimal thallus moisture level for lichen growth was saturation. Hence, most physiological studies prior to 1975 were conducted with saturated thalli. Investigators have since discovered that this is not a reasonable assumption, that in fact most lichens tested show sharp declines in photosynthesis when saturated (Harris, 1971; Armstrong, 1976; Farrar, 1976a; Kershaw and Smith, 1978; and Larson, 1979). Optimal thallus moistures are species specific. *Stereocaulon paschale* gives maximum photosynthetic values at 120% thallus moisture (percent of air dry thallus weight) which is equivalent to 24 to 30% saturation (Kershaw and Smith, 1978). Kershaw and FacFarlane (1980) report optimal moisture levels for Peltigera canina var. praetextata at 200% of air dry thallus weight (approximately 40 to 50% saturation). Harris (1971) quotes saturation optima for Umbilicaria pustulata at 65% saturation, U. polyphylla at 75%, Peltigera canina at 90% and an aquatic species, Verrucaria eleaomeleana at 100%. Harris's figures are from Ried (1960) and though they are supposedly photosynthetic optima, it is not clear whether respiration rates or net carbon uptake are used. In comparing net carbon assimilation and respiration rates with thallus moisture, three species of Parmellia show photosynthetic maxima between 35 and 75% saturation and respiration rates which increase nonlinearly to 100% saturation. Respiration rates are typically found to increase sharply with increased moistures levels. The combination of decreasing carbon uptake and increasing respiration with increasing moisture levels leads to depletion of stored photosynthate and eventual death of the lichen.

Moisture, light and temperature have coeffects on net carbon assimilation (Harris, 1972; Kershaw, 1975b; Kershaw and Smith, 1978; MacFarlane and Kershaw, 1980). At lower temperatures, high thallus moisture and low light drasticly reduce net carbon assimilation. Conditions of high temperature, low light and high moisture induce high respiration rates but not photosynthesis hence there is a net loss of carbon. Low temperatures, low light and high moisture reduce respiration and consequently no net carbon assimilation is observed. Low incident light regardless of moisture or temperature conditions produces no net carbon uptake and with increased moisture and temperature combined, give increasingly high respiration rates.

Snow-melt. Flock (1978) and Larson and Kershaw (1975) conducted separate studies on the distribution of lichens with respect to snow-melt patterns. On Niwot Ridge in Colorado, Flock determined that the correlations between lichen cover and abundance and snow-melt patterns are related to moisture. Considering all lichens, she observed the greatest diversity and cover of lichen species in xeric sites with little if any snow cover and soil moistures frequently below the permanent wilting point. There were no lichens observed in late snow-melt sites where soils are at field capacity most of the year. In terms of terricolous lichens, greatest abundance occurs in sites intermediate to the two extremes though they also occur extensively in xeric sites. Larson and Kershaw (1975) obtained similar results in their arctic study. They found the greatest accumulation of lichens on raised beaches where snow cover was slight and a lack of lichen flora in meadow areas with late snow-melt and standing water. The observed distributional patterns from these two studies fit well with the physiological data on the general intolerence of lichen species to extended periods of saturation. But there are further factors to consider here. As Larson and Kershaw point out, late snow-melt areas also have a reduced growing season. Coupled with the typically low temperatures and shaded conditions, this could cause an annual carbon deficit. In early snow-melt sites it is hypothesized that the growing season in extended long enough to allow a net carbon gain. In arctic and alpine regions where growing seasons are short, for plants with low growth rates (i.e. low net carbon fixation), extension of the growing season by a few days or elevation of temperatures one or two degrees can be significant.

Aspect. This parameter is frequently correlated with lichen distribution (Pearson and Lawrence, 1965; Orwin, 1972; Armstrong, 1975; Nash et al., 1977; Pentecost, 1979). Like snow-melt patterns, moisture is directly related to aspect though other factors are also involved. In general, studies have shown a strong correlation between increased abundance and diversity of lichen species with aspects having high moisture, low evaporation rates and reduced wind effects. These studies are primarily carried out on saxicolous or epiphytic lichens in which desiccation is a greater consideration than high moisture levels (Pearson et al., 1965; Orwin, 1972; Sheard et al., 1974; Armstrong, 1975, 1977; Case, 1977; Hoffman et al., 1977; Lindsay, 1978; Pentecost, 1979). Theoretically, aspects with low irradiance and wind effects reduce evaporative processes thereby extending the period of time in which photosynthesis can occur in lichens. Nash et al. (1977), in a study of desert lichens, determined that predawn relative humidity was sufficient to trigger photosyntheisis but within thirty minutes of sun rise, on southern aspects, temperatures could rise 20°C and relative humidity drop to a level at which photosynthesis could not be carried out by representative lichen species. However, on northern aspects, temperatures and relative humidities remained at a level conducive to photosynthesis for a prolonged period of time. If one is dealing with an organism with low annual net carbon fixation, extending each daily period in which photosynthesis can occur is critical.

Orwin (1972), in a study of saxicolous lichens in New Zealand, observed lichens concentrated on the leeward sides of rocks by which she determined a correlation between aspect and wind direction. She hypothesized that wind has a dual effect: 1) desiccation and 2) abrasion, hence aspect is an index of combined evaporative and abrasive effects.

The role of lichens in desert environments has always interested ecologists but there are few studies actually determining conditions under which they grow. As one might expect, moisture is indicated as the major factor correlated with their distribution. Nash et al. (1977) correlated lichen cover with aspect relating it to evaporation rates. Rundel (1978), in a study of desert fog zones, observed lichens concentrated on the windward side of rocks. Here aspect correlated with lichen occurrence is related not with evaporation rates but with interception of moisture in the form of wind blown fog. Epiphytic lichens occurrring on cacti are concentrated on ends of spines where condensation collects.

Wetting and Drying Cycles. A recent issue in lichenology is that of wetting and drying cycles. In nature a given moisture level is seldom maintained for an extended period of time with exception of aquatic or extreme xeric situations. Rather cycles of wetting and drying are observed. Several investigators have since looked at this situation with lichens (Orwin, 1972; Armstrong, 1976; Farrar, 1976; Rundel, 1978; Larson, 1979). Lichens typically respond very quickly to wetting with photosynthesis initiating shortly following moistening. However, if the thallus is dried again after a short elapse of time, the period of activity is detrimental. Briefly, short cycles are quite energy expensive with carbon loss due to elevated respiration exceeding that gained through photosynthesis. Investigators think then that lichens are located in protected sites, not necessarily because of intolerence to dry conditions or high light and temperature but because of reduced evaporation rates which extend periods favorable for photosynthesis and thereby allow a net carbon gain.

Temperature. Temperature has a variable effect on lichens dependent upon conditions of light and moisture. Early studies indicate extreme temperature tolerances for many lichen species. However, these studies monitored respiration rates and often with saturated thalli. As previously discussed, the phycobiont is more sensitive to thermal stress than is the mycobiont (Kershaw and Smith, 1978 and MacFarlane and Kershaw, 1980). Therefore at high temperatures, the mycobiont continues to respire though the phycobiont is no longer photosynthesizing. This condition is compounded at high moisture levels. Hence by monitoring respiration rates, one is led to believe the lichen is functioning well when in fact the alga is being severly stressed.

Recent studies have determined considerable variability in temperature tolerances for different species (Lechowicz and Adams, 1974; Kershaw, 1975b, 1978; Kershaw and Smith 1978; and MacFarlane and Kershaw, 1980). Generally at high temperatures correspondingly high light levels are required for net carbon assimilation. Decreasing temperature broadens the range of light values for which there is net carbon gain. One might predict that higher moisture levels would extend the upper range of temperatures which a species can tolerate. This is not the case. Instead, as temperature increases, the range of moisture and light values under which there is a net carbon gain becomes increasingly narrow (Kershaw, 1978). It has long been known that under dry thallus conditions lichens are more tolerant of extreme temperatures (Ahmadjian, 1967). It would seem that the phycobiont is primarily responding to temperature at the extremes of its range of tolerance. The mycobiont however is relatively unaffected by temperature but rather is affected by moisture. At either extreme of temperature the phycobiont is unable to photosynthesize. If the thallus is dry, the mycobionts metabolism is reduced and in this state the lichen can exist for an extended period of time. However, if the lichen is moist at either temperature extreme, the mycobiont continues to respire eventually depleting all stored photosynthate and the lichen as such dies.

The actual range of temperature tolerence is species specific in lichens. MacFarlane and Kershaw (1980) report thermal stress levels for several species: *Peltigera apthosa*, 45°C; *P. scabrosa*, 25°C; *P. canina* var. *praetextata*, 35°C; *P. canina* var. *rufescens*, 45°C; and *Stereocaulon paschale*, 35°C. These temperature tolerances fit well with their distributions in nature. *Peltigera apthosa* has both sun and shade varieties. MacFarlane and Kershaw tested specimens collected in open meadows with correspondingly high temperature tolerances. *P. scabrosa* is a late successional species in woodlands. *P. canina* var. *praetextata* occurs in woodlands and shaded microhabitats in subalpine meadows. *P. canina* var. *rufescens* occupies open areas with direct radiation. *Stereocaulon paschale* is interesting in that it forms dense mats in boreal-tundra regions but does not appear for 25-50 years following fire. Kershaw (1978) determined that this species and probably *Cladonia stellaris* can not tolerate the thermal stress of these areas bared by fire where soil surface temperatures reach 48°C. Rather they appear in a later successional stage when albedo is increased and temperatures decreased to tolerable levels.

One final consideration in terms of temperature concerns thallus color. Kershaw (1975a and b) suggests that a dark thallus color preadapts lichen species to regions with short growing seasons and cold temperatures. His studies would indicate that a dark thallus color increases thallus temperature in early spring to a degree allowing photosynthesis to occur even when ambient temperatures are too low (Kershaw, 1975a and b; Larson and Kershaw, 1975). In the arctic it is quite conceivable that an increase of a few degrees over a month to three months time could make the difference between net carbon gain or loss.

Light. Very little information is available on this parameter and most of what is available has been presented in conjunction with moisture and temperature effects. Inferences have been drawn to correlations between thallus color and incident light suggesting the presence of various pigments as protection for the phycobiont against high light intensity and particularly against ultra violet radiation (Ahmadjian, 1967). Certainly one may readily observe the predominance of highly pigmented species of saxicolous and terricolous lichens in areas with high incident radiation.

Higher Plant Effects. There is very little data on the interactions of vascular plants and lichens but some observations indicate a negative correlation between higher plant cover and lichen cover. Kershaw (1978) has stated that, "as a direct consequence of the absense or minimization of higher plant competition, a number of lichen communities have developed" following fire in the boreal-tundra zone in Canada. Dey (1978), in a study of Appalachian lichens says, "grassbalds are dominated by grasses, sedges and herbs. This dense herbaceous layer prohibits growth of terricolous lichens." In which ways higher plants compete with or prohibit lichen growth is not clear. Kershaw determined that as spruce became established, Cladonia stellaris and Stereocaulon paschale mats suffered from shading. Though competition for light may be the primary factor in this case, other factors maybe involved as well. Growth rates may be a key factor. From studies of epiphytic lichens, under conditions favorable to both lichens and mosses, moss will dominate and finally over grow slower growing lichens. It may also be speculated that dense herbaceous vegetation produces a microhabitat combining low light, high moisture and low temperature conditions such that most lichens would experience a negative carbon balance.

Disturbance. The final consideration of this review is disturbance or substrate stability. Classically it has been put forth that lichens are able to colonize unstable or disturbed habitats (Shields et al., 1957). This theory grew out of the observance of lichens growing under harsh conditions: On rock surfaces, in deserts and glaciated areas. In fact, lichens are very poorly suited to growing on unstable substrates due to their slow growth rates. Nash et al. (1977), in their study of hot desert lichens state, "Low cryptogam cover values on the bajada is probably a reflection of soil surface disturbance which is well known to limit abundance in arid soil crusts." Lindsay (1978) in a study of antarctic lichen ecosystems says, "In maritime Antarctic, lichens colonize most stable substrata more rapidly than unstable substrata." He found that lichens were the initial colonizers of rock surfaces with shorter colonization times on large immobile rocks and longer times on smaller more mobile rocks. Soils tended to be colonized by mosses. This may relate back to growth rates, the faster growning organisms colonizing the least stable substrates.

CHAPTER II: SITE DESCRIPTION

Deer Park is located on Blue Mountain in the northeast section of the Olympic National Park in Washington State (latitude $47^{\circ}55'$ N, longitude $123^{\circ}15'$) (Figure 1).

Geology

There are three primary rock types at Deer Park; basalt, shale and sandstone (Tabor, 1975). The basalt originated as lava flows on and beneath the ocean floor. The sandstone and shale were laid down as marine sediments 50 to 60 million years ago in the early Eocene. Through time these materials were uplifted and eroded producing a pattern of ridges of resistant basalt connected by saddles of finely eroded sandstone and shale. Proceeding from the saddles to the ridges, progressively courser materials are encountered. Scree composed of shale, coarse sandstone and volcanic breccia are interlaced with more stable finer grained sandstone substrates on the slopes. Coarse sandstone, shale, volcanic breccia and red limestone are predominant on the ridges. For a more complete discourse on the geologic history and composition of the Olympic Range consult Tabor (1955 and 1975) and Belsky (1979).

Logistics

Study sites are located along ridges and saddles from 0.25 km northwest of Blue Mountain to 1.0 km east (Figure 2).

Figure 1. Location of Deer Park in the Northeast Section of the Olympic National Park on the Olympic peninsula

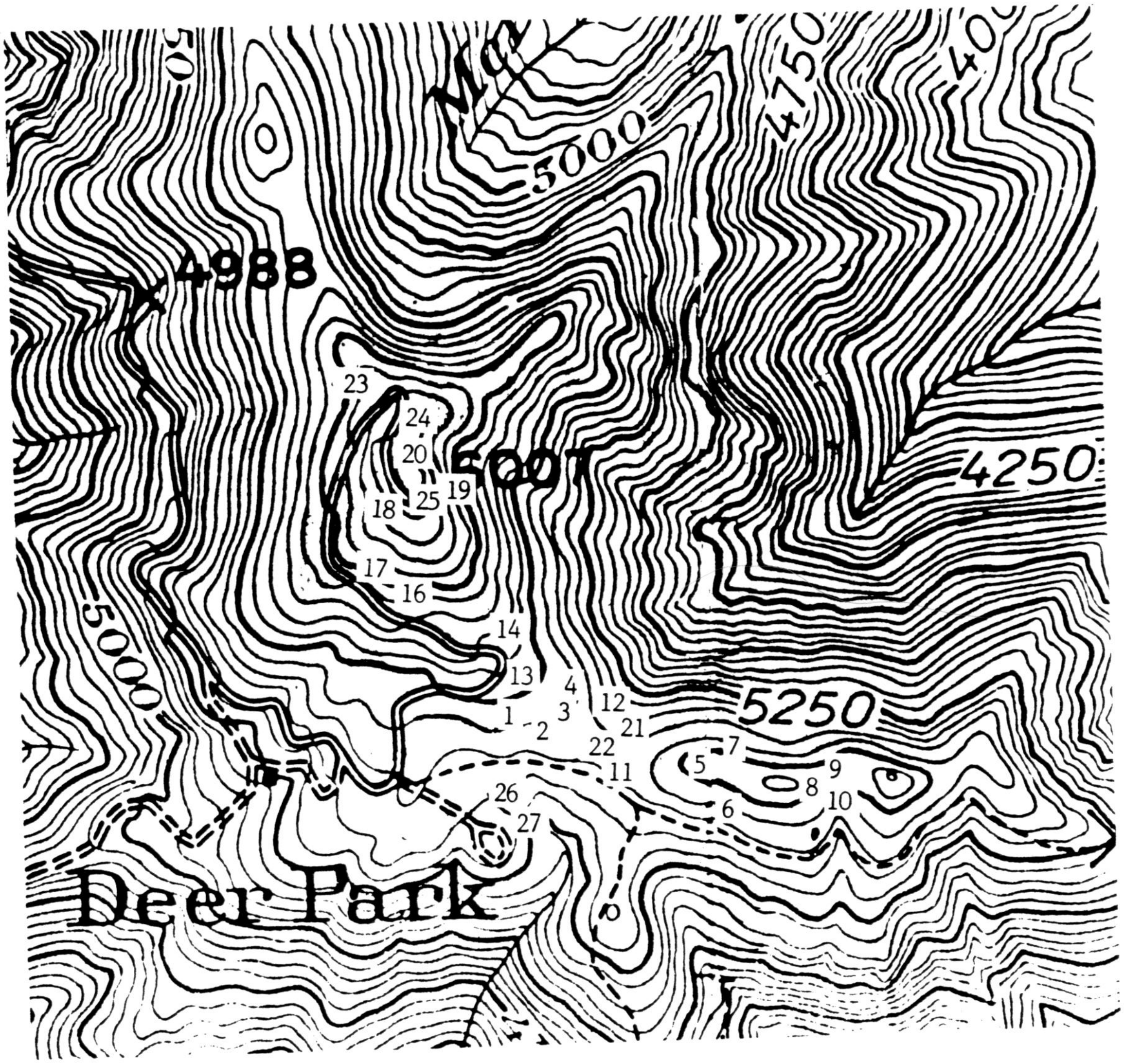

Figure 2. Site Locations

Climate

Climatic data are inferred from two stations: Port Angeles 22 km to the northwest of Deer Park and Sequim 17 km to the northeast. Both stations are located at sea level on the Strait of Juan de Fuca. Both fall within the Olympic rain shadow though Sequim is more heavily affected receiving two-thirds the annual rain fall of Port Angeles (NOAA, compiled data from 1941-1970).

The Olympic Peninsula experiences a temperate maritime climate with cool wet winters and cool dry summers. Air flow is predominately north-northwest in the summer and southwest in the winter (Belsky, 1979). Approximately 75% of the precipitation falls between November and April as snow (del Moral, unpublished).

In studies of bryophytes and lichens, atmospheric moisture can be more significant than precipitation. At Deer Park the dew point is reached nightly during much of the summer with heavy deposition of moisture. The area is subject to frequent late morning and afternoon fogs (0900 to 1800 hours). Temperature inversions cause moisture to collect in river drainages and over the Strait of Juan de Fuca to the south and north of Deer Park. As the air warms during the day, clouds rise and by early to mid-afternoon, engulf Deer Park.

Temperatures for Deer Park can be projected from those recorded for Port Angeles and Sequim (Table 1). Monthly maximum, minimum and means for the two stations are averaged and a factor (0.65°C decrease in temperature for every 100 m increase in elevation) determined from the adiabatic lapse rate formula applied to give projected values for Deer Park.

Table 1. Mean monthly temperature (°C) minima, maxima and means for Deer Park based on Columbia Basin States Climatological Handbook, for 1931-1960.

TEMPERATURE CATEGORY	JAN.	FEB.	MARCH	APRIL	MAY	JUNE	JULY	AUG.	SEP.	OCT.	NOV.	DEC.	ANN. MEAN
MINIMUM	-10.9	-10.3	- 9.3	- 7.1	- 4.7	- 2.3	- 1.0	0.9	- 2.3	- 5.3	- 8.3	- 9.7	- 6.0
MAXIMUM	- 4.2	- 2.8	- 1.0	2.2	5.2	7.2	19.5	19.6	7.6	3.4	- 2.4	- 3.0	2.7
MEAN	- 7.0	- 5.6	- 4.7	- 2.2	0.6	3.1	5.2	4.9	3.2	- 0.5	- 4.7	- 6.2	- 1.2

CHAPTER III: METHODS AND MATERIALS

Site Selection

Sites were selected to represent first, a broad range of environmental conditions and second, visually distinct vascular plant community types. Homogeneous sites 100 m^2 in area were required to allow for subsampling. Twenty-six sites were chosen. Within each, ten 1 m^2 plots were random selected and sampled.

Data Collection

Taxonomic determinations for lichens follow Thomson (1967) for the genus *Cladonia* and Fink (1935) and Hale (1979) for all other species. Taxonomy of vascular plant species follows Hitchcock and Cronquist (1969).

Cover values for both lichen and vascular plant species were collected for each plot. Lichen cover values were recorded in absolute terms while vascular plant cover was recorded on a log scale: "P" indicating cover of less than 1%; 1 = 1-2% cover; 2 = 3-4% cover; 3 = 5-8% cover; 4 = 9-16% cover; 5 = 17-32% cover; 6 = 33-64% cover; and 7 = 65% or greater cover. This scale proved inappropriate for analysis utilized hence values were converted back into mean absolute terms. This introduced considerable error into the analysis. However, Detrended Correspondence Analysis (DECORONA) site ordinations using this floristic data and that of two other investigators, both of whom recorded cover in absolute values, gave reasonably comparable results.

Environmental parameters measured for each site include slope, aspect, elevation, soil type, an index of substrate stability, below-surface soil moisture, soil surface temperatures and temperatures at a depth of 6 cm both for areas free of vegetation and with vascular plant cover. Slope and aspect were measured with a Brunton compass. Elevation was determined with a Thommen pressure-sensitive altimeter. As indicated previously, there are three predominate soil types in the Deer Park area, two of which are important to this study; a sandstone and a loose shale.

Temperatures were determined with a Tele-thermometer (thermister) using two soil-surface disk probes and two metal soil depth probe. Each probe was marked and consistantly used for the same type of reading (i.e. soil surface below herbaceous canapy, soil surface lacking plant cover, etc.) to insure comparability of readings between sites and dates. Two replicates of each temperature were taken. The soil surface probes were shielded from direct radiation and allowed to equilibrate before each reading. Temperatures were recorded four times during the smmer of 1979: July 18, August 4 and 22, and September 11. Readings were taken on clear days at approximately solar noon (between 1200 and 1500 hours). Soil moisture was determined gravimetrically. Two samples per site were collected for each of the four dates on which temperature data were recorded.

An index of substrate stability utilized four categories: 1 = substrate stable, no apparent movement; 2 = substrate fairly stable, with slight movement of substrate surface; 3 = substrate unstable but slight slope with little apparent substrate movement; 4 = substrate unstable, slope steep.

A brief subsidiary study was conducted in July of 1980 to acquire microhabitat data for individual lichen species. For this study, twenty-four of the twenty-six study sites used for the 1979 study were resampled. The distribution of each lichen species was described giving proximity to vascular plant species and microtopography. The same index of substrate stability derived for the macrosite studies was utilized to characterize microsites. An indication of photosynthetically active radiation (PAR) incident to each site was attempted using a Lambda quantum sensor. Weather conditions did not allow for the completion of this study. However, an indication of PAR beneath various herbaceous canopies was acquired.

Data Analysis

Data were analyzed several ways. Indirect ordinations were carried out on mean lichen speices cover for sites using "ORDIFLEX", a Cornell Ecology Program Computing Package. Principal Components Analysis (PCA) (Orloci, 1966), Reciprical Averaging (RA) (Hill, 1973) and Polar Ordination (PO) (Bray and Curtis, 1957) were used on standardized and log transformed data to give site and species ordinations. Twenty-one species and twenty-four sites were included in the ordinations. A second ordination was performed using nineteen species and twenty-four sites. This second ordination excludes all species with fewer than three occurrences.

Simple and multiple linear regressions were performed on percent mean lichen cover, lichen species richness, individual lichen species, percent vascular plant cover and percent graminoid cover against all variables. Simple as well as multiple regressions were performed. Path Analysis was utilized to determine causal relationships for lichen richness and percent cover as well as percent vascular plant and graminoid cover. Curve fitting techniques were used to determine nonlinear correlations between data pairs.

Kendall's test for nonparametric rank correlations was utilized for all possible pairs of data.

CHAPTER IV: RESULTS

Lichen distribution was analyzed on both the macro- and microhabitat scales for lichens as whole and for individual species.

General Distributional Patterns of Lichens

Environmental Parameters: Distribution of lichens as a whole correlates with some of the parameters considered by this study (Table 2). There is a significant linear correlation between percent lichen cover and lichen species richness (r=.59*). Correlations with soil stability (r=.39) and percent cover of graminoid species (r=-.34) are not significant but relatively high. Kendall's nonparametric rank test (Table 2) indicates significant correlations between percent lichen cover and lichen species richness (K=.53**), percent vascular plant cover (K=-.30*), soil type (K=.26*), soil stability (K=.35*), mean soil moisture (K= -.25*), soil moisture values from specific dates throughout the study season (Table 2), percent cover of Carex spectabilis (K= -.35*) and mean graminoid cover (K=-.27*). Lichens are inversely correlated with vascular plant cover, soil moisture, occurrence of Carex spectabilis and graminoid cover.

Vascular Plant Cover: A nonlinear relationship between percent lichen cover and percent vascular plant cover is shown

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*Indicates significance at the 0.05 level
**Indicates significance at the 0.01 level

Table 2. Selected Correlation Coefficients from Kendall's Nonparametric Rank Test and Linear Regression for Lichen cover, Lichen Species Richness, Vascular Plant Cover and Graminoid Cover. * = significance at the 0.05 level; ** = significance at the 0.01 level; NS = not significant.

DEPENDANT VARIABLE	INDEPENDANT VARIABLE	KENDALL'S TAU	LINEAR REGRES.
Lichen Cover	Vascular Plant Cover	-0.30*	-0.29 NS
	Lichen Species Richness	0.53**	0.59*
	Graminoid Cover	-0.27*	-0.34 NS
	Soil Type	0.26*	0.10 NS
	Substrate Stability	0.35*	0.39 NS
	Mean Soil Moisture	-0.25*	-0.25 NS
	7/18 Soil Moisture	-0.25*	-0.10 NS
	8/4 Soil Moisture	-0.28*	-0.28 NS
	9/11 Soil Moisture	-0.25*	-0.29 NS
	Carex _spectabilis_ Cover	-0.35*	-0.51*
Lichen Species Richness	Vascular Plant Cover	-0.41*	-0.58*
	Graminoid Cover	-0.48**	-0.64**
	Soil Type	-.44*	0.53*
	Substrate Stability	0.41*	0.55*
	Mean Soil Moisture	-0.42*	-0.55*
	7/18 Soil Moisture	-0.39*	-0.49*
	8/4 Soil Moisture	-0.34*	-0.58*
	8/22 Soil Moisture	-0.30*	-0.41*

Table 2. Continued

DEPENDANT VARIABLE	INDEPENDANT VARIABLE	KENDALL'S TAU	LINEAR REGRES.
Lichen Species Richness	9/11 Soil Moisture	-0.37*	-0.51*
	Aspect	0.24*	0.39 NS
	Carex _spectabilis_ Cover	-0.29*	
Vascular Plant Cover	Graminoid Cover	0.67**	0.81**
	Soil Type	-0.60**	-0.71**
	Substrate Stability	-0.71**	-0.83**
	Mean Soil Moisture	0.48**	0.69**
	7/18 Soil Moisture	0.36*	0.53*
	8/4 Soil Moisture	0.38*	0.63**
	8/22 Soil Moisture	0.28*	0.47*
	9/11 Soil Moisture	0.63**	0.78**
	Aspect	-0.29*	-0.41*
	Carex _spectabilis_ Cover	0.37*	-----
Graminoid Cover	Soil Type		-0.58*
	Substrate Stability		-0.66**
	Mean Soil Moisture		0.61**
	7/18 Soil Moisture		0.52*
	8/4 Soil Moisture		0.65**
	8/22 Soil Moisture		0.42*
	9/11 Soil Moisture		0.60*

in figure 3. Lichen cover is described as a function of vascular plant cover by the set of equations:

Y= [$1.53e^{0.06x}$ if 20 x 55 and $6419.84e^{-0.09x}$ if x 55].

There are only occassional occurrences of lichens where vascular plant cover is less than 20% (del Moral, unpublished). As vascular plant cover increases between 20 and 55%, percent lichen cover increases exponentially (sites 1, 5, 10, 14, 17, 20, 22 and 23). Percent lichen cover decreases exponentially as vascular plant cover increases from 55 to 100% (sites 2, 3, 6, 7, 9, 12, 16, 18, 19, 22, 24 and 25). Maximum lichen cover values are observed between 45 and 60% higher plant cover. Five sites deviate from this pattern, 4, 8, 11, 13 and 21. Sites 4, 8 and 13 are highly disturbed sites: Site 4 is located on an unstable scree slope (stability value of 4); site 8 experiences a late snow melt and shows signs of soil surface abrasion by snow pack; site 13 is chronically preturbed by marmots from an adjacent colony. Site 13 is also a late snow melt site. Site 21 is an anomoly. It is a cool, moist site with high vascular plant cover that is expected to have low lichen cover yet has both high cover, 9%, and number of lichen species, 7 (Appendix A). A possible explanation is the ready availability of lichens for colonization from site 22. Site 22 is a lichen rich site located adjacent to and above site 21. Site 21 is patchy with less dense areas of vascular vegetation that

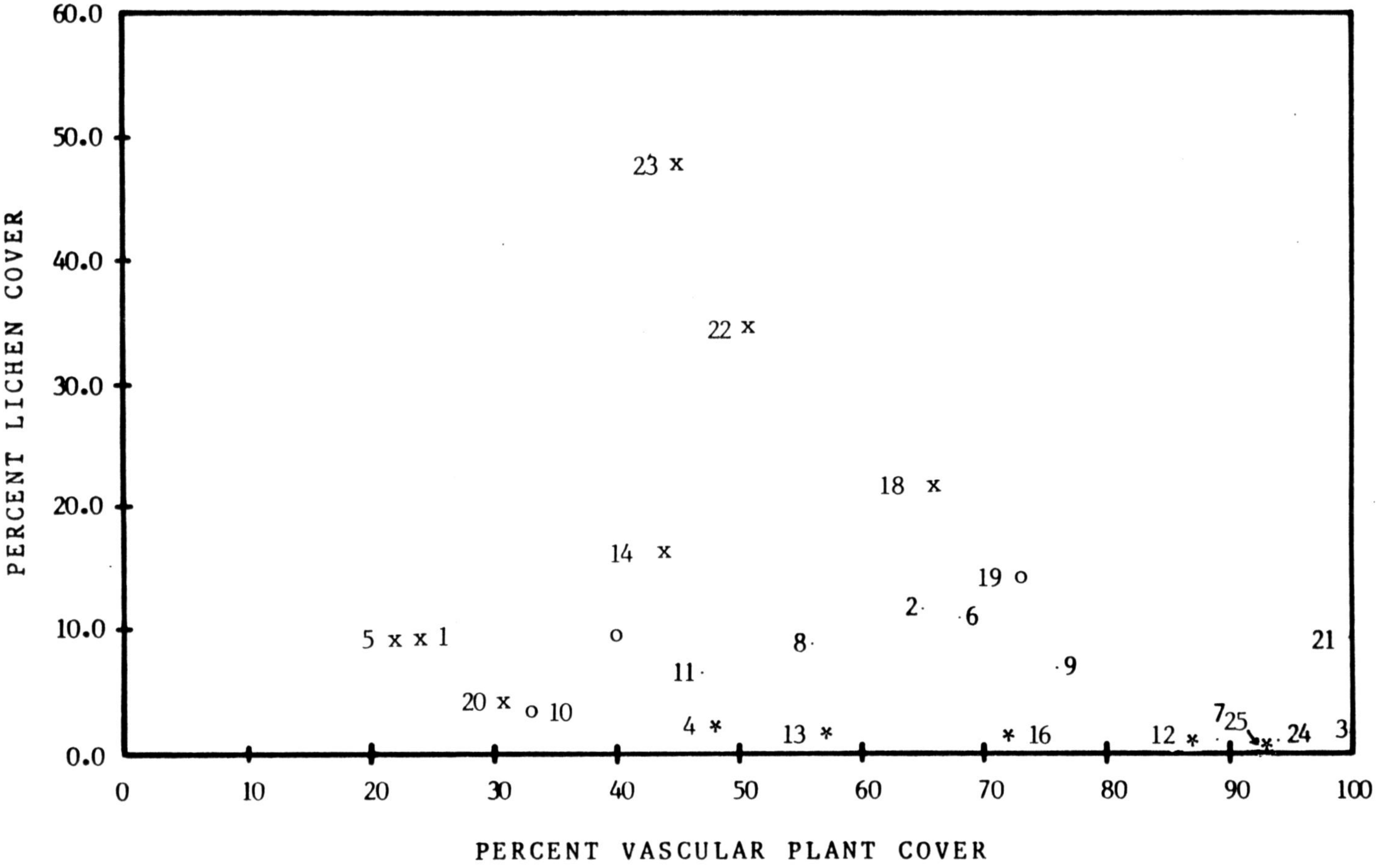

Figure 3. Graph of Sites with Respect to Percent Cover of Lichens and Vascular Plants. x = Alpine; • = Subalpine; o = Mixed Alpine and Xeric Subalpine; * = Disturbed.

are suitable for colonization by lichens (Appendix A).

Lichen cover and vascular plant cover exhibit opposite patterns with respect to other variables tested. Mean lichen cover is lower on sandstone soils, 8.9%, than on shale substrates, 11.1% (Table 3). Vascular cover is lower on shale substrates (40%) than on sandstone soils (75%). Lichen cover increases and vascular plant cover decreases with increased substrate instability (Table 3). Lichen cover generally decreases and higher plant cover increases with increased soil moisture (Figure 4 and 5). Lichen cover decreases and vascular cover increases with increased graminoid cover (Figure 6 and 7).

Site Ordinations: Reciprical Averaging (RA) and Polar Ordination (PO) of sites using percent cover values for individual lichen species identify three groups of sites (Figures 8 and 9). The first consists of mesic, subalpine sites having late snow melts and relatively well developed sandstone soils (sites 7, 8, 9 and 11) (Plate I). The vascular flora is dominated by *Carex spectabilis*, *Lupinus latifolius*, *Antennaria lanata* and *Veronica cusickii*. Lichen species richness and cover values are moderate with *Cetraria islandica*, *Cladonia chlorophaea*, *C. ecmocyna* and *C. piedmontensis* as the predominant species (Table 4).

The second group consists of sites 3, 12, 13, 16, 24 and 25. These sites have few lichen species and low cover

Table 3. Mean values of Percent Lichen Cover, Percent Vascular Plant Cover and Lichen Species Richness for Different Soil Types and Substrate Stabilities. * Value derived from a single site (4).

	SOIL TYPE		SUBSTRATE STABILITY			
	Sand-stone	Shale	1	2	3	4
Mean Percent Lichen Cover	8.9	11.1	3.9	9.3	17.9	2.1*
Mean Percent Vascular Plant Cover	74.7	40.1	88.0	59.9	35.7	48.0*
Mean Lichen Species Richness	6	10	5	8	1	6*

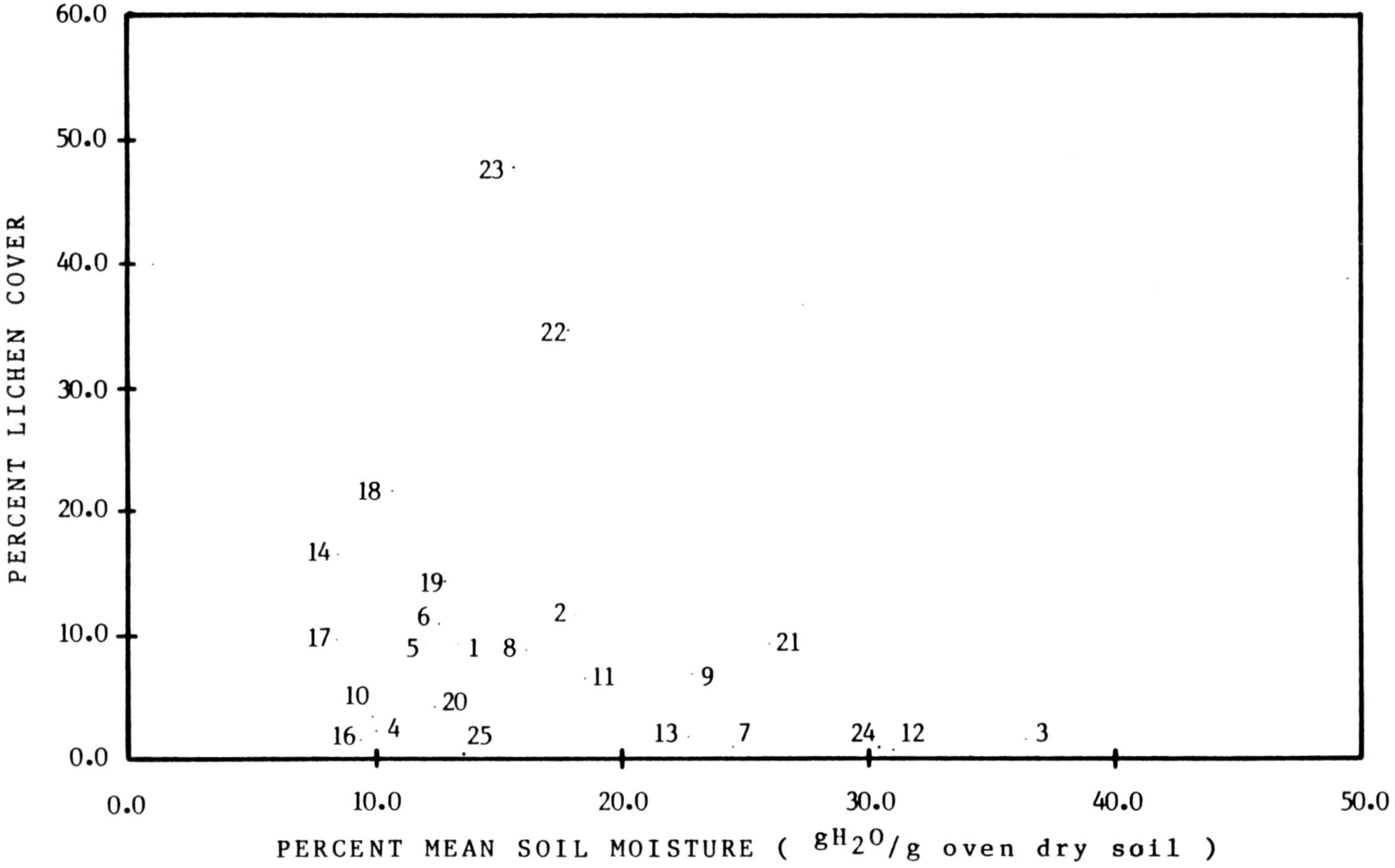

Figure 4. Graph of Sites Indicating Relationships Between Percent Lichen Cover and Mean Soil Moisture.

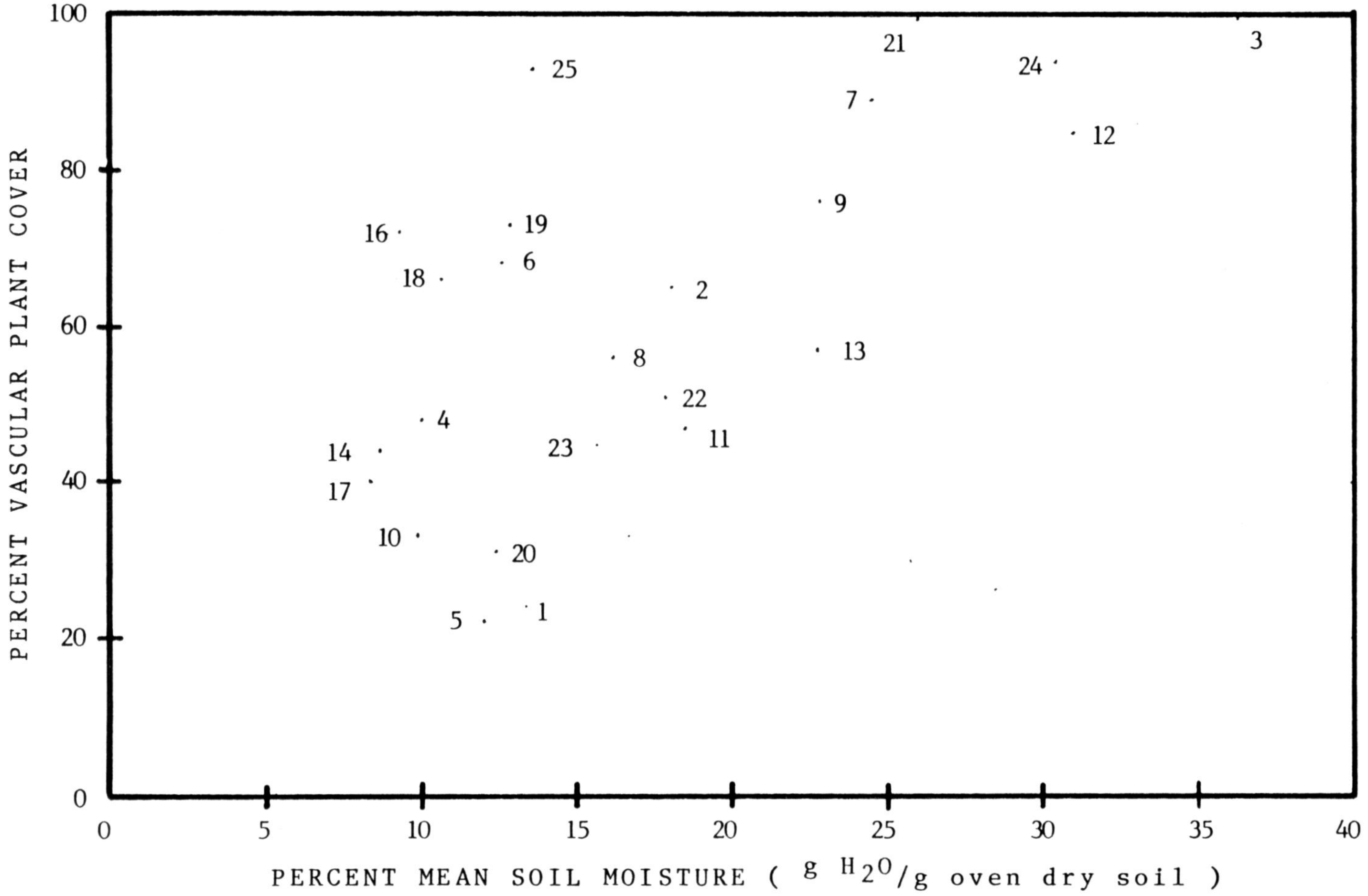

Figure 5. Graph of Sites Indicating a Linear Relationship Between Percent Vascular Plant Cover and Mean Soil Moisture. $Y = 25.6 + (2.1x)$.

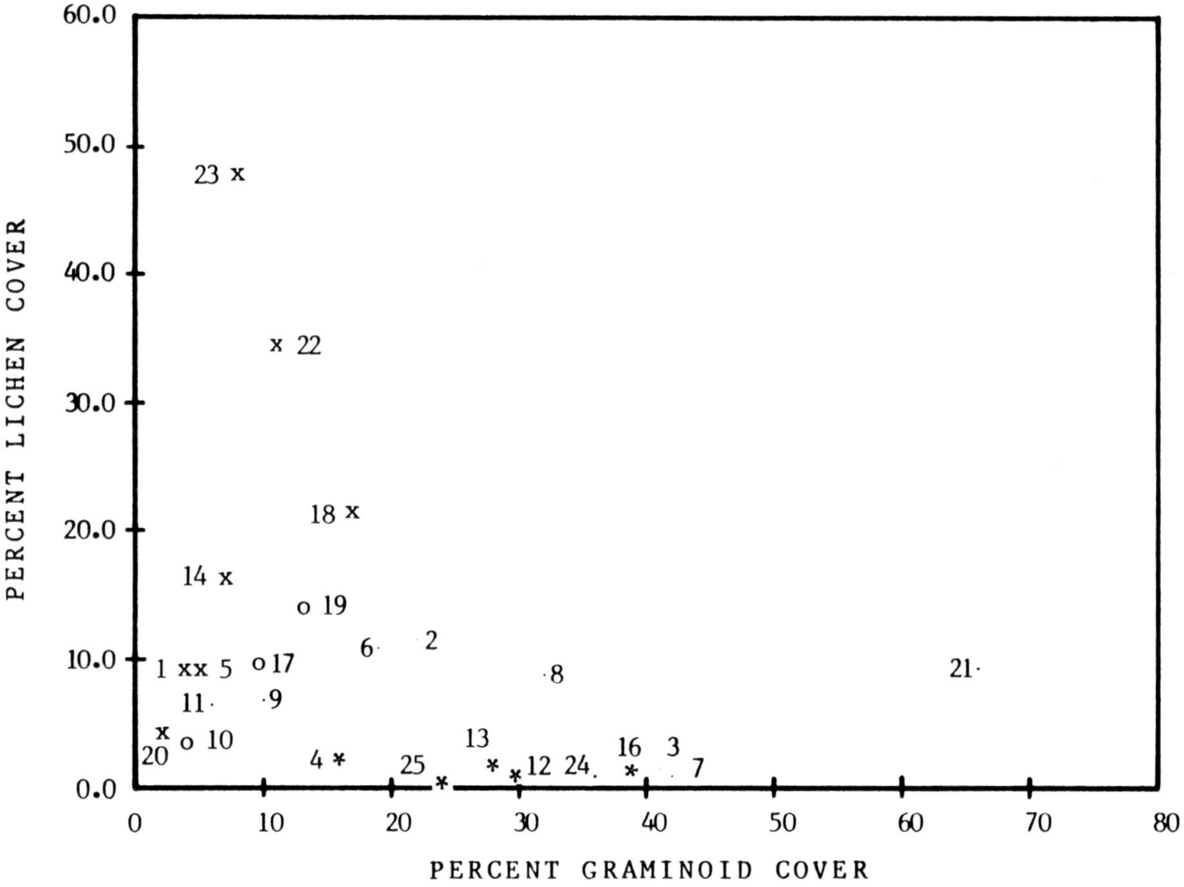

Figure 6. Graph of Sites Regarding Percent Lichen Cover and Percent Graminoid Cover. x = Alpine; • = Subalpine; 0 = Mixed Alpine and Xeric Subalpine; * = Disturbed.

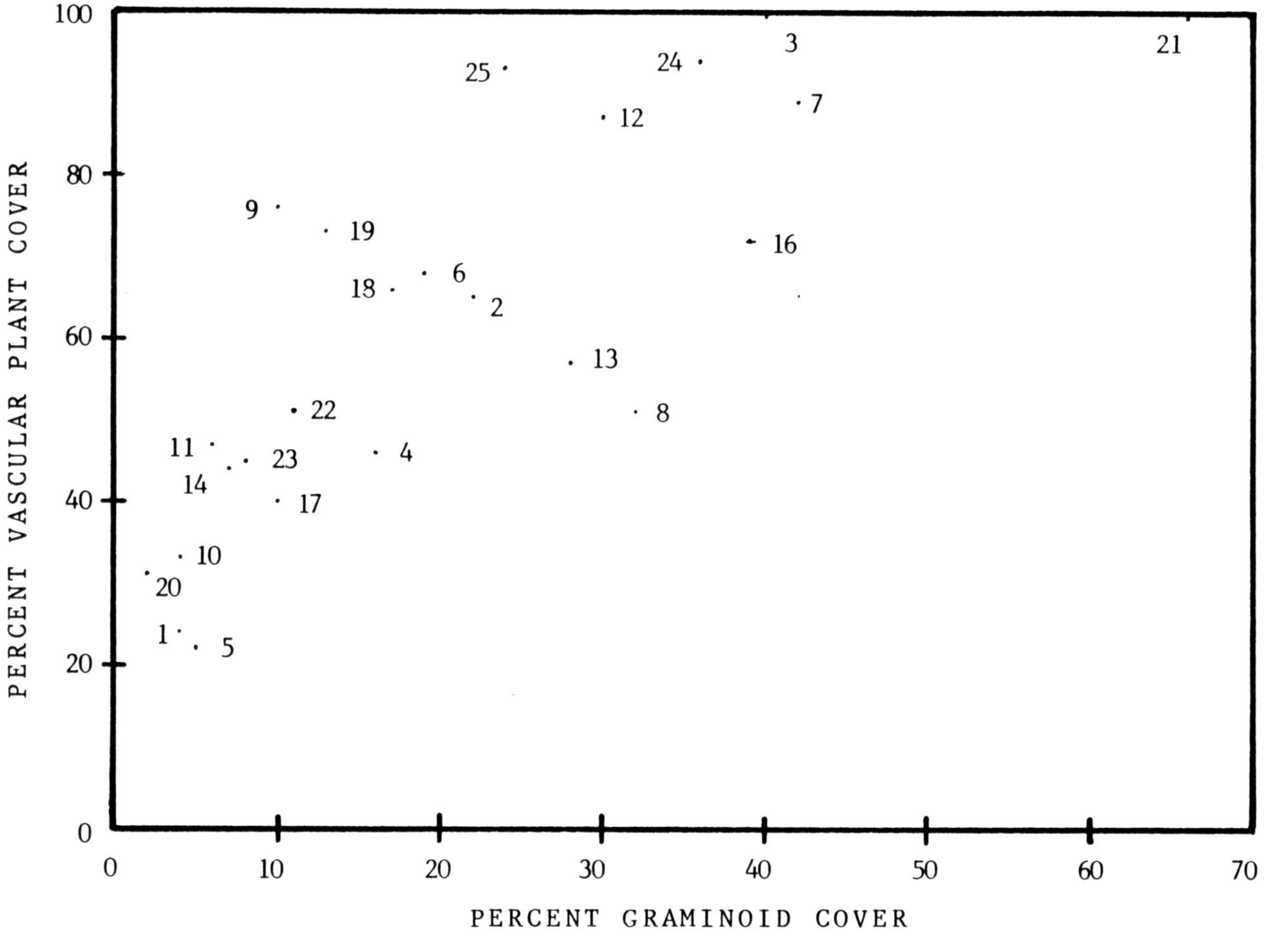

Figure 7. Graph of Sites Indicating a Linear Relationship Between Percent Cover of Vascular Plants and Graminoid Species. Y = 36.95 + (1.21x).

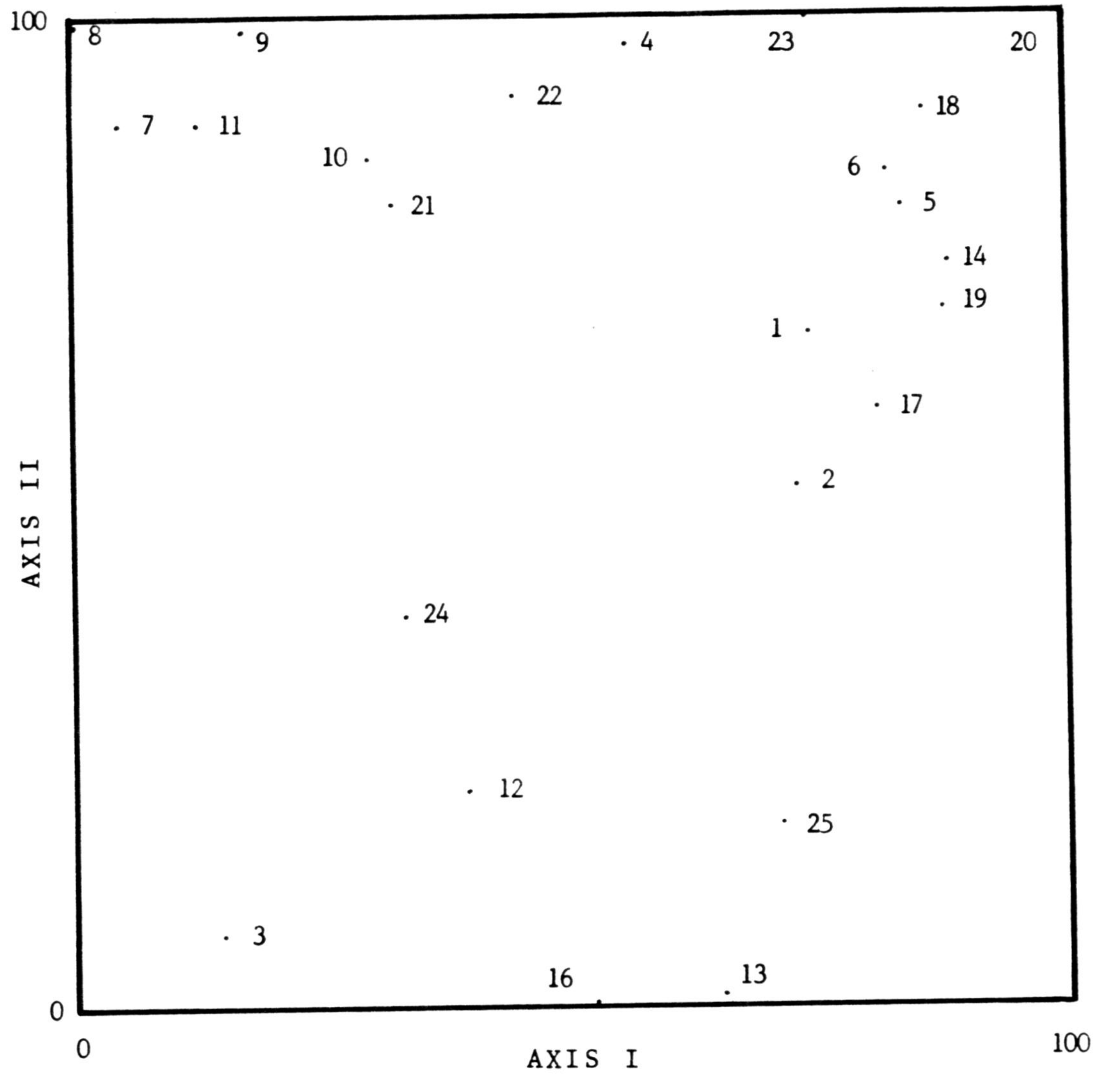

Figure 8. Reciprical Averaging Site Ordination Using Lichen Species Cover Values. Axis I is a complex gradient combining exposure, soil moisture and soil development. Axis II is a complex gradient partially identified as perturbation.

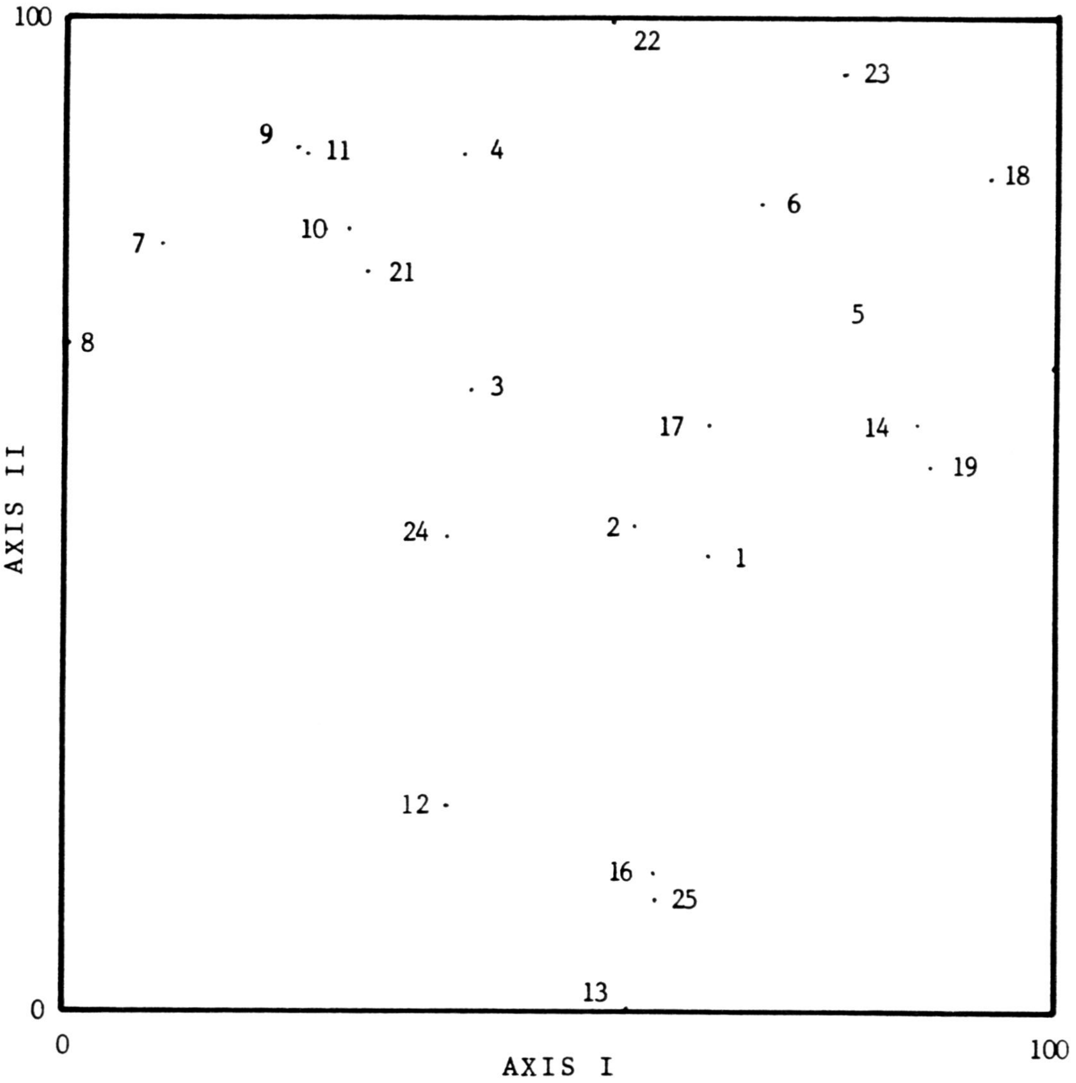

Figure 9. Polar Ordination of Sites Using Lichen Species Cover Values. Axis I is a complex gradient combining exposure, soil moisture and substrate stability. Axis II is a disturbance gradient.

Plate I. Mesic Subalpine Meadow: *Antennaria lanata*, *Carex spectabilis* and *Lupinus latifolius* dominate.

Plate II. Late Snow-melt Site (site 24) in Mid July: *Antennaria lanata*- *Carex spectabilis* meadow.

Table 4. Mean Lichen Species Percent Cover Values for Sites Reflecting Site and Species Rankings from Reciprical Averaging.

SPECIES	SITES																							
	8	7	11	3	9	10	21	24	12	22	16	4	13	25	2	23	1	17	6	5	18	19	14	20
Cladonia ecmocyna	7.7	0.6	3.0		4.2	2.0	3.8	0.1		5.0		0.2			0.1	1.4	0.2	0.1		0.2				
Peltigera canina		0.1	0.4	1.2		0.1		0.1	0.1	0.5	0.3				0.1				0.1		0.1	0.1	0.1	
Cladonia chlorophaea	1.0	0.1	0.4	0.1	0.4	0.1	0.5	0.1	0.1								0.5		0.9	0.1				
Cladonia implexa			2.0		1.1	0.1	0.7	0.1		14.3		0.1				7.0								
Cladonia peidmontensis	0.1		0.1		0.2	0.1	0.3		0.1	0.7		0.2				0.4	0.1			0.1	0.1			
Cetraria islandica		0.1	0.3		0.5	0.1	1.7	0.1		4.8						5.0		0.1		0.1	3.1	0.2		0.2
Cladonia polycarpoides			0.1					0.4	0.2		0.7		0.9	0.1	0.5					0.6	0.1	0.9	1.1	0.1
Cladonia verticillata						0.1				1.3		1.1				2.8		0.1	0.5	0.1			1.8	
Cladonia cariosa					0.1	0.3	1.3		0.1	0.2	0.3		0.8	0.1	1.0		2.5	2.9	0.1	0.1	0.2	0.9	1.2	0.1
Cladonia pixidata				0.1		0.2				3.0		0.4			8.2	4.4	3.3	0.4	2.7	1.8	1.4			
Peltiger can. var. rufescens						0.1	0.9			1.0	0.1	0.1		0.1	1.6	0.3	0.3	3.1	0.5	0.2	1.4	1.3	1.9	0.1
Gray Crust #27			0.1		0.3	0.1										0.8		2.3	1.3	0.1	0.4	3.5	1.2	0.2

Table 4. Continued.

SPECIES	SITES 8	7	11	3	9	10	21	24	12	22	16	4	13	25	2	23	1	17	6	5	18	19	14	20
Stereocaulon tomentosum																0.5				0.6				
Thamnolia vermicularis						0.1				3.9						12.6	1.9	0.1	2.1	4.1	11.6	5.6	5.2	1.2
Ochrolechia upsaliensis																5.3	0.2	0.4	2.0	1.0	0.2	1.3	2.1	
Species #28																		0.1	0.1		0.1	0.2	0.3	
Cornicularia aculeata																1.9	0.3	0.1	0.6	0.2	0.4	0.1	0.8	0.4
Species #37																					0.3	0.1	0.7	0.1
Cetraria cucullata																5.5					2.2			1.6

values. They are stable with relatively good soil development. A number of these sites show evidence of perturbation by marmots (sites 12, 13 and 16) or deer (sites 12 and 25). Sites 13 and 24 are late snow melt sites with snow remaining until late July in site 24 (Plate II). Site 3 is marshy receiving snow melt into July, then drying quickly. The vascular flora is subalpine dominated by *Festuca idahoensis* or, in the case of site 24, *Carex spectabilis* and *Antennaria lanata*. The lichen flora is depauporate, consisting primarily of *Cladonia cariosa* and *C. polycarpoides* (Appendix A, Table 4).

The third group of sites is located on dry, exposed, scree slopes (sites 1, 2, 5, 6, 14, 17, 18, 19, 20 and 23) (Plates III and IV). The vascular plant flora is composed of alpine and xerophytic subalpine species (Appendix A). The lichen flora is rich with high percent cover value. The flora consists of *Cetraria islandica*, *Cladonia impexa*, *Cornicularia aculeata*, *Stereocaulon tomentosum* and *Thamnolia vermicularis* (Table 4).

Several sites hold intermediate positions in these ordinations (sites 3, 4, 10, 21, 22 and 24). Sites 3 and 24 are generally located between the cool moist sites and the wet and/or disturbed sites. Sites 4, 10, 21 and 22 shift between cool moist sites and exposed scree sites. Site 4 is a highly unstable site with a northern aspect. It has

Plate III. Alpine Community

Plate IV. Alpine- Xeric Subalpine Site: Stabilization of substrate by higher plants with secondary establishment of lichens.

elements of alpine and mesic subalpine lichen floras. Site 10 is similar but less unstable and though it has a southern aspect, is located in a protected draw with reduced exposure. Site 21 is a subalpine grassy meadow site with surprisingly high lichen cover (9.2%) and richness (7). Site 22 has a course unstable substrate but very slight slope. The lichen flora is typical of alpine habitats but also contains moist subalpine site elements.

Ordinations using vascular plant species cover data and those using lichen species data produce similar arrays of sites [RA (Figure 8 and 10); PO (Figure 9 and 11)]. Kendall's analysis of first and second axes determined by RA and PO, indicate significant correlations between site rankings determined from these ordinations (Table 5). First axes reflect similarities in environmental gradients from stable, cool, mesic, subalpine sites to highly exposed, unstable alpine sites. There are differences apparent in these rankings. Second axes are not as strongly correlated. Correlations are determined among but not between ordination techniques. Second axes using vascular species cover data are not particularly meaningful adding little information beyond that attributed to the first axes. The second axes using lichen species cover values are complex, representing mean lichen cover and perturbation by marmots and deer. Perturbation is reflected in a shift in and impoverishment

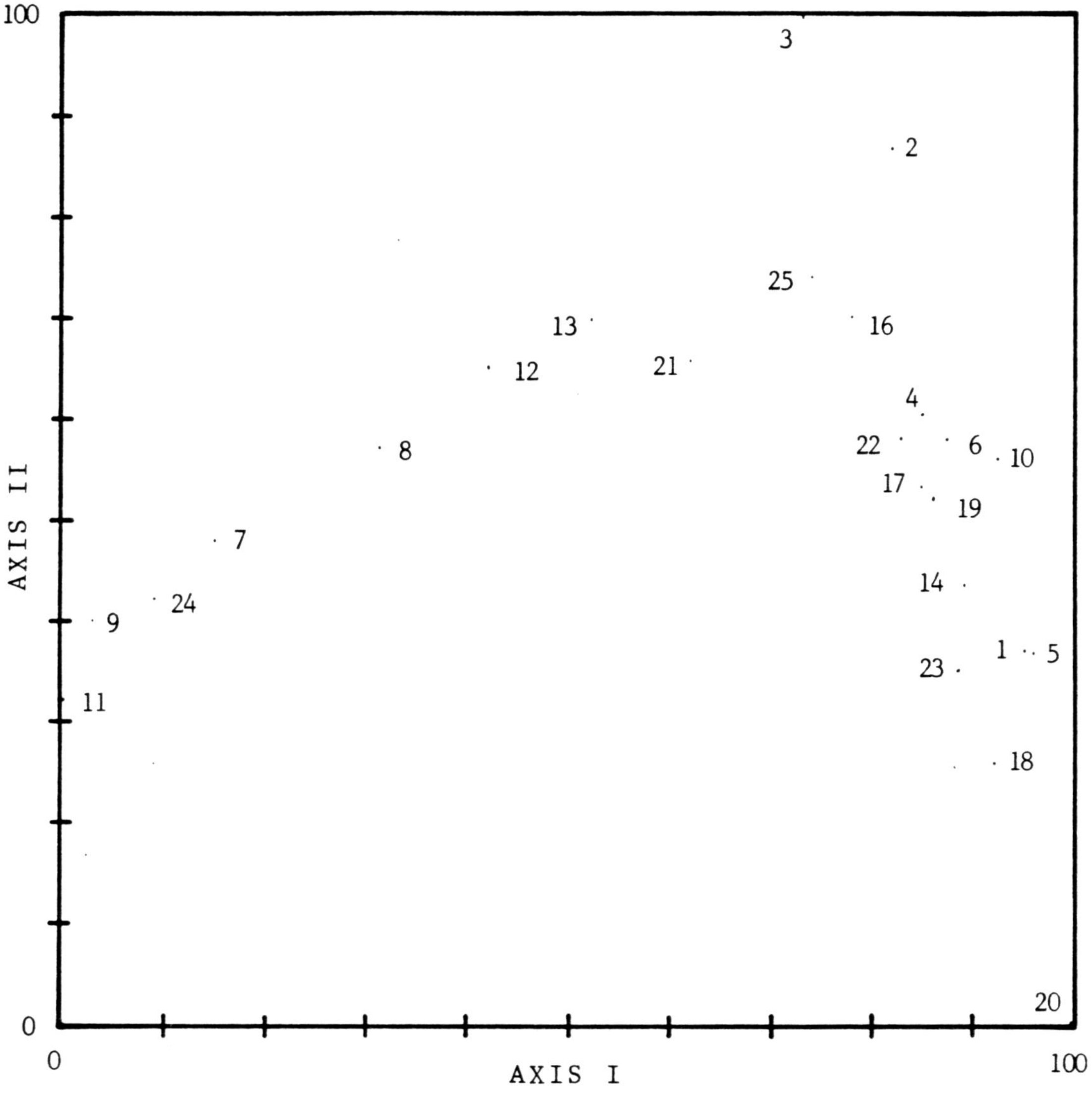

Figure 10. Reciprical Averaging Site Ordination Using Vascular Plant Species Cover Values. Axis I is a complex gradient composed of exposure, soil moisture and soil development. Axis II is uninterpretable.

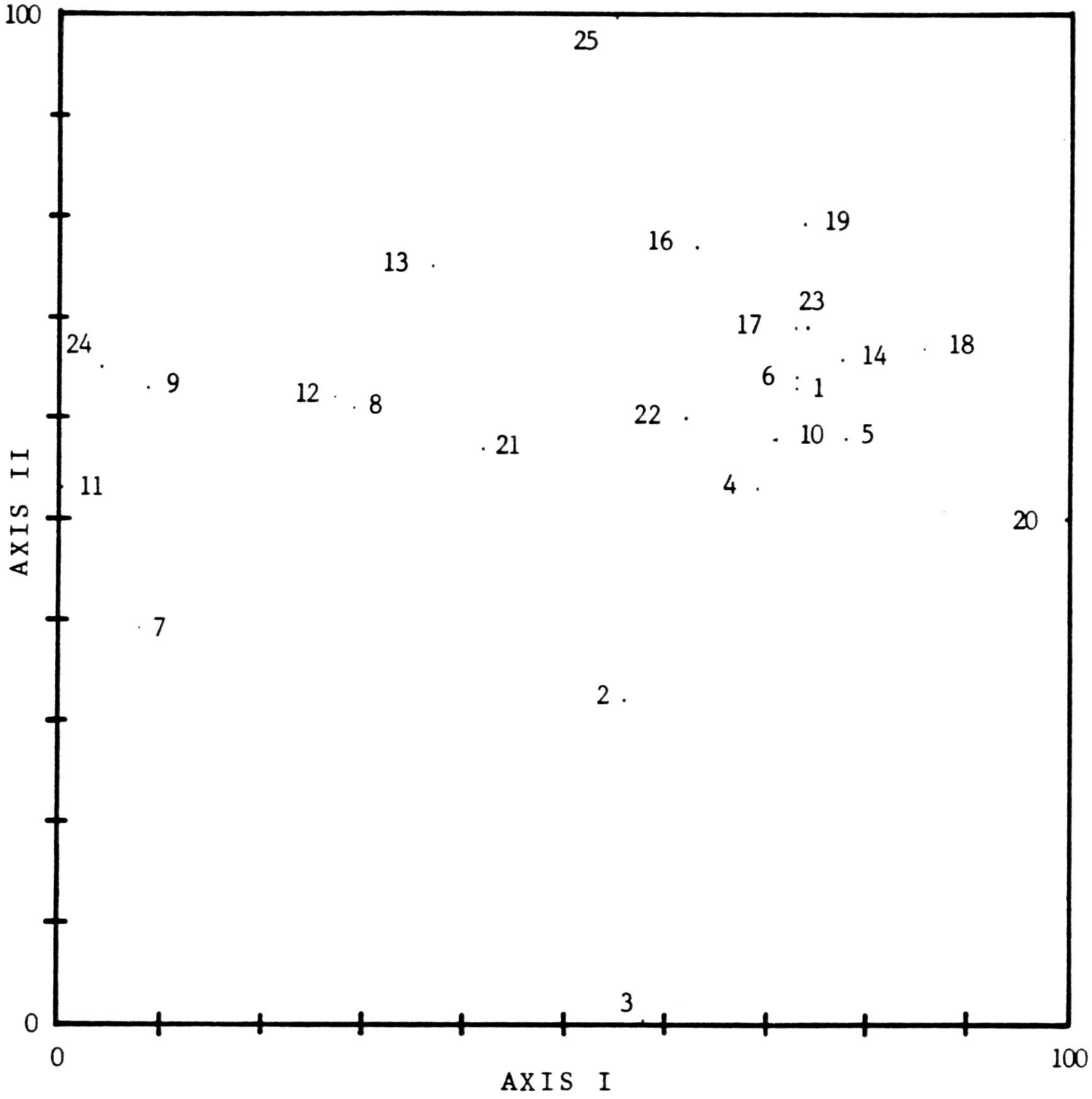

Figure 11. Polar Ordination of Sites Using Vascular Plant Species Cover Values. Axis I is a complex gradient combining exposure, soil moisture and soil development. Axis II is uninterpretable.

Table 5. Comparison of Site Ordinations: Kendall's Correlation Coefficients Comparing Site Rankings from RA and PO Derived from Lichen and Vascular Plant Species Cover Values. * = significance at 0.05 level; ** = significance at 0.01 level.

AXES COMPARED		CORRELATION/ SIGNIFICANCE
RA-1st Axis using Lichens	RA-1st Axis using Vascular Plants	0.61**
	PO-1st Axis using Vascular Plants	0.67**
	PO-2nd Axis using Vascular Plants	0.27*
RA-2nd Axis using Lichens	RA-2nd Axis using Vascular Plants	-0.44*
RA-1st Axis using Vascular Plants	PO-1st Axis using Lichens	0.59**
RA-2nd Axis using Vascular Plants	PO-2nd Axis using Lichens	-0.30*
PO-1st Axis using Lichens	PO-1st Axis using Vascular Plants	0.68**
	PO-2nd Axis using Vascular Plants	0.30*

of the lichen flora and reduction in cover (Appendix A).

Graminoid Cover: Correlations between lichen cover and cover of graminoid species are similar to those of lichen cover versus vascular plant cover (Figure 3 and 6). Percent lichen cover increases exponentially as graminoid cover increases to 10%. As graminoid cover increases above 10%, percent lichen cover decreases as a power function. Site 4 deviates from the observed pattern with 16% graminoid cover and only 2.1% lichen cover. This may be do to the unstable nature of the site (stability index of 4). Site 21 also deviates with high lichen cover, 9%, and high vascular plant cover, 100%.

Substrate: Mean percent lichen cover is similar for sandstone (8.9%) and shale (11.1%) substrates (Table 3). Substrate stability however is linearly related to percent lichen cover (r=.39* Table 2). Stable substrates support a mean lichen cover of 3.9% (Plate V). Mean cover for sites with an index of 2 is 9.3% (Plate VI). Fairly unstable scree slopes have the highest percent cover, 17.9% (Plate III and IV), while highly unstable sites have the lowest value, 2.1%[1] (Plate VII). Though sites with an index of 3 support the highest lichen cover, within this category, as substrate instability increases, lichen cover decreases.

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[1] This figure is derived from a single site (site 4). Further observations indicate 2.1% cover to be high for sites with a stability index of 4 (del Moral, unpub.).

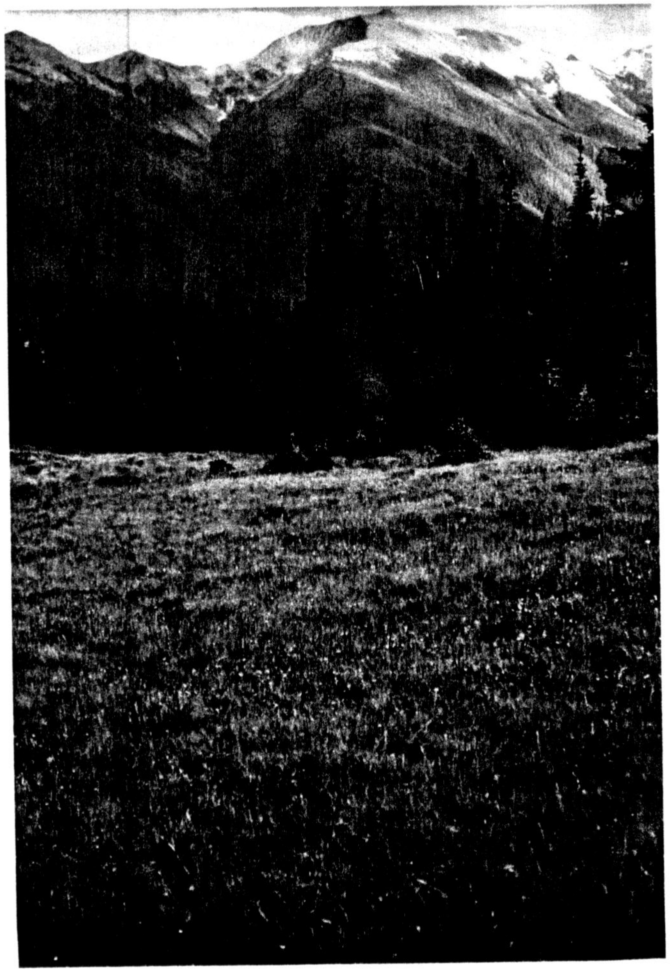

Plate V. Mesic Subalpine Meadow

Plate VI. Xeric Subalpine Meadow

Plate VII. Foreground: Unstable, xeric sugalpine site (4)
Center: Late snow-melt gully (site 11)
Center Left: Alpine- xeric subalpine knoll (site 22)

For example, site 23 with a lichen cover value of 47.9% is more stable than site 10 with a cover of 3.4%.

Soil Moisture: Lichen cover is negatively correlated with soil moisture (Table 2 and Figure 4). Sites which do not fit this pattern (sites 4, 10, 16 and 25) are highly unstable (4 and 10) or chronically disturbed by deer or marmots (16 and 25). There is a strong similarity between this graph and one expressing the relationship between mean vascular plant cover and soil moisture (Figure 5). The array of sites is very similar except vascular plant cover increases rather that decreases with increased soil moisture. This graph also produces a similar array of sites to those comparing percent lichen cover with percent vascular plant cover and percent graminoid cover (Figure 3 and 6).

Lichen cover is not correlated with slope, aspect, elevation, soil surface temperatures or soil temperature at a depth of 6 cm (Table 2).

Patterns of Lichen Species Richness

Environmental Parameters: Patterns of lichen species richness are comparable to those of percent lichen cover. Lichen species richness is significantly correlated with percent lichen cover (K=.52**, r=.59*), percent vascular plant cover (K=-.41**, r=-.59*), substrate stability (K=.41**, r=.55*), soil type (K=.44**, r=.53*), aspect (k=.24*), mean percent soil moisture (K=-.42*, r=-.55*), soil moisture values from specific dates during the study season (Table 2), percent cover of Carex spectabilis (K=-.29*) and percent graminoid cover (K=-.48**, r=-.64**).

Vascular Plant Cover: Lichen species richness and vascular plant cover are linearly and inversely correlated (Figure 12, Table 2). However, there are no occurrences of lichens in sites with less than 15% vascular plant cover (del Moral, unpublished). It is interesting to note that sites with low percent vascular plant cover and concurrent low percent lichen cover have high lichen species richness values (Figures 3 and 12).

Graminoid Cover: A comparison of lichen species richness and mean percent graminoid cover identifies a striking linear correlation (Figure 13). The variables are inversely related with y equal to zero for graminoid cover of 54% or greater (projected from linear regression). Comparing the relationships between percent graminoid cover and lichen species richness and cover, shows sites with low graminoid cover and low lichen cover to have high numbers of species (sites 1, 5, 10, 11 and 20) (Figures 6 and 13).

Substrate: There is a significant correlation between lichen species richness and both soil type and substrate stability (Table 2 and 3). Mean number of species occurring on sandstone soils is 6, those occurring on shale substrates is 10. Highly stable sites have a mean species richness of 5.

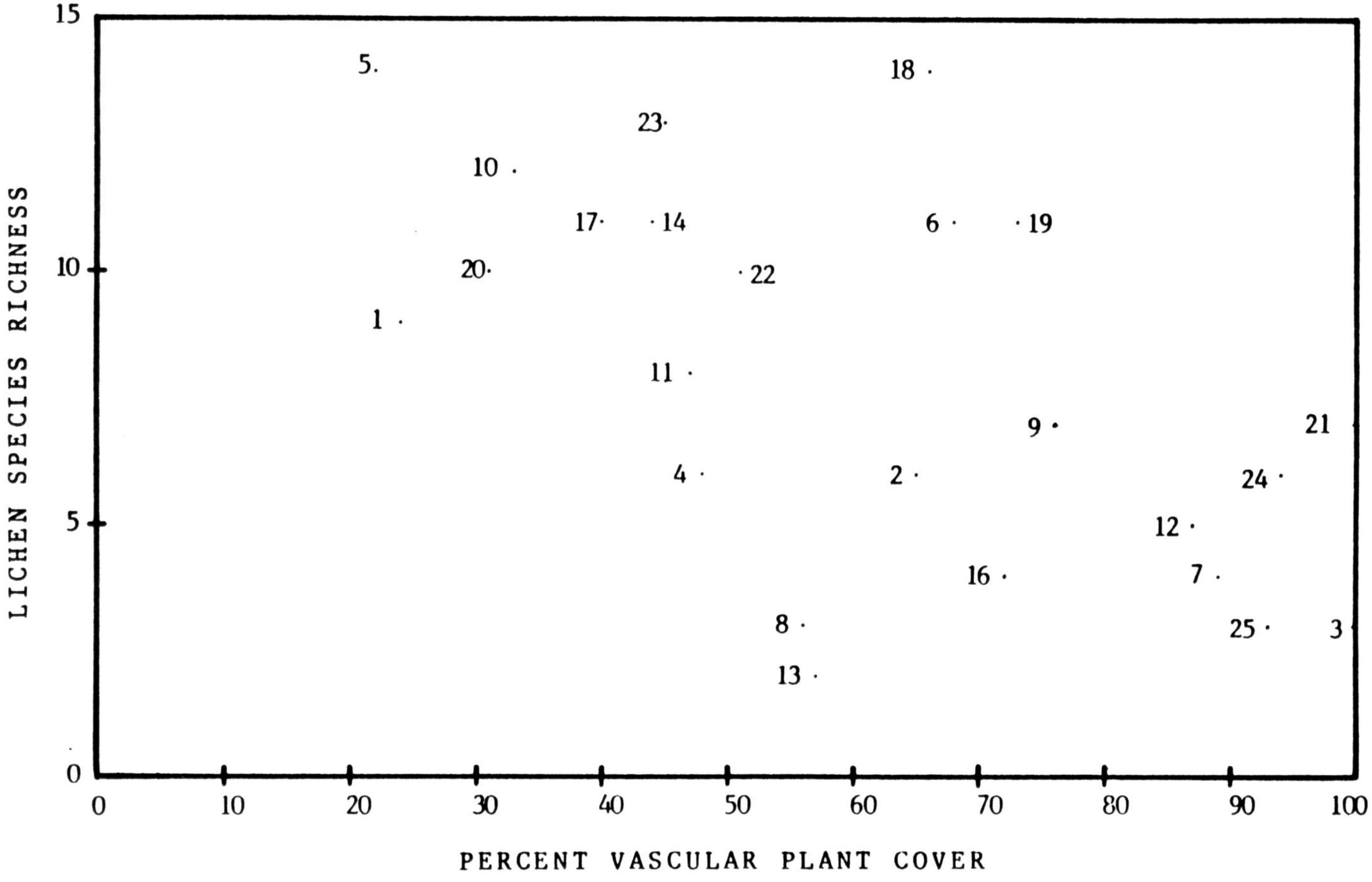

Figure 12. Graph of Sites Indicting Inverse Linear Relationship between Lichen Species Richness and Percent Vascular Plant Cover.

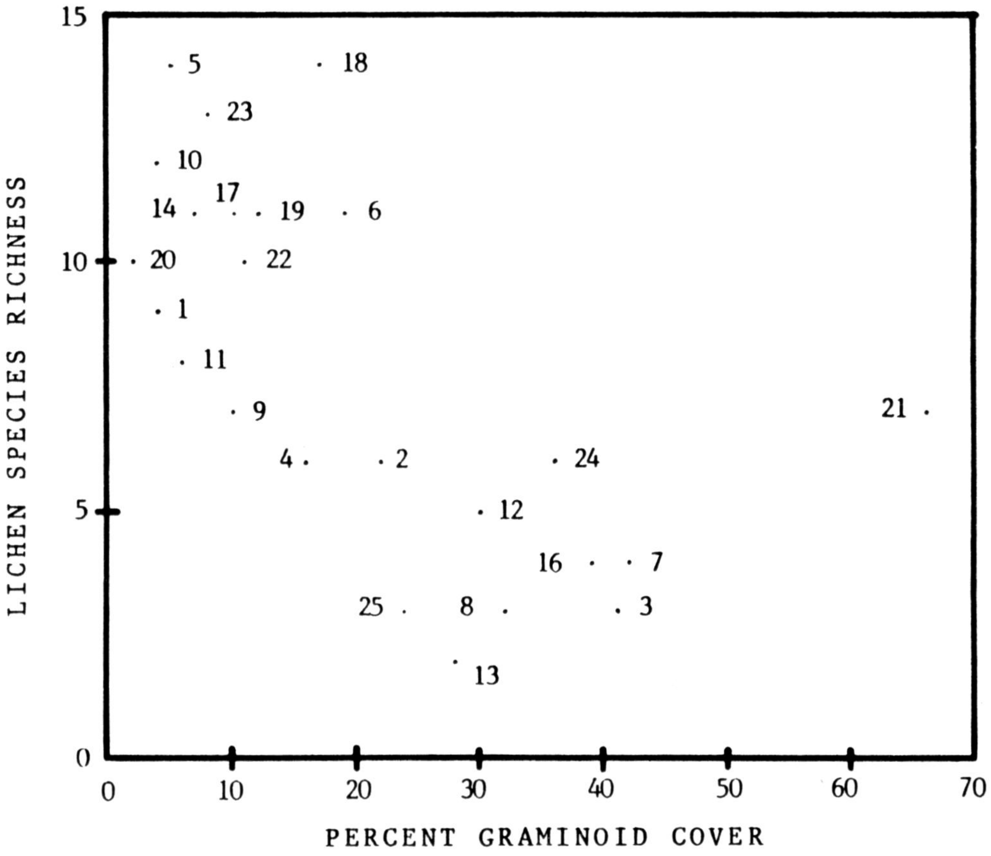

Figure 13. Graph of Sites Indicating an Inverse Linear Correlation Between Lichen Species Richness and Percent Graminoid Cover: $Y = 12.12 - (0.22x)$.

Sites with a stability index of 2 have a mean species richness of 8. Moderately unstable sites have the highest mean number of species, 11 and highly unstable sites have occurrences of 6 or fewer lichen species. Soil type and soil stability are highly correlated (r=.76**): shale substrates are less stable than sandstone soils.

The correlation between lichen species richness and soil moisture is linear and inverse (Table 2, Figure 14). However, there are notable outliers (sites 4, 8, 16 and 25). These outlier sites are all relatively dry with the exception of site 8, and disturbed in one way or another: Site 4 is highly unstable,Sites 16 and 25 are preturbed by deer or marmots and site 8 is abraded by snow pack (Appendix A). A graph of lichen species richness and soil moisture is very similar to one of percent lichen cover and soil moisture (Figures 4 and 14).

Path Analysis

Path Analysis (Li, 1975) can not be performed on lichen cover due to the nonlinear correlations between it and other variables. However, this analysis for lichen species richness indicates graminoid cover, soil moisture and soil type as the primary causal agents:

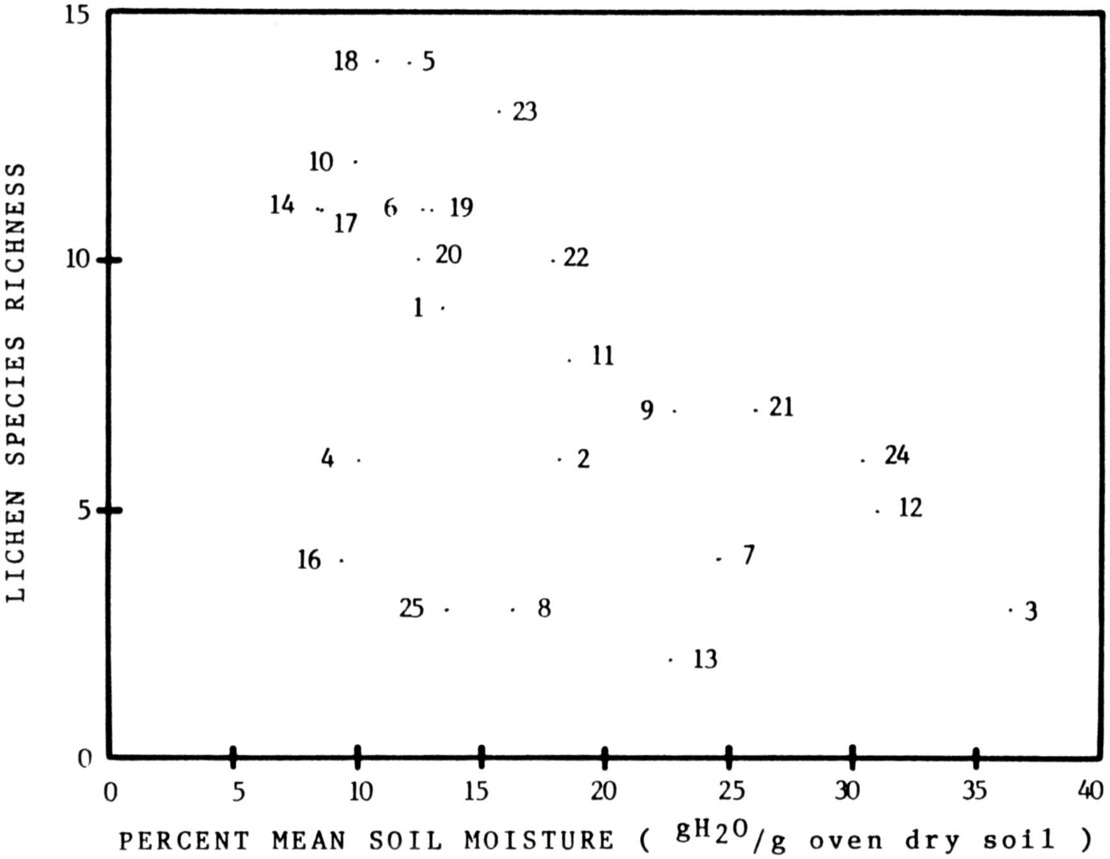

Figure 14. Graph of Sites Indicating Linear Correlation Between Lichen Species Richness and Percent Mean Soil Moisture: Y= 12.5 - (0.25x).

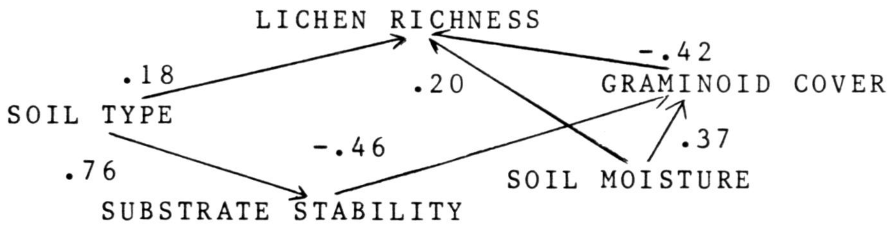

Figure 15. Path Diagram for Lichen Species Richness. Direction and correlation coefficients between causally related variables are indicated. Overall path coefficient = 0.69. Error = 0.72.

Soil type and substrate stability are highly correlated and nearly interchangable in this equation. Graminoid cover is a better indicator of lichen richness than is vascular plant cover. Substituting it for graminoid cover reduces the path coefficient (.61). However, its inclusion reduces the F statistic significantly (2.11 from 6.31) though it does not affect the path coefficient. Graminoid cover is a function of soil moisture and substrate stability:

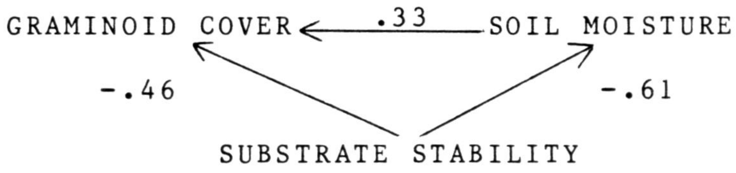

Figure 16. Path Diagram for Graminoid Cover. The path coefficient = 0.71. Error = 0.70.

Vascular plant cover is almost entirely a function of substrate stability (83% correlation).

Lichen Species Distributions

Gradient Analysis: Ordinations of lichen species identify gradients comparable to those of the site ordinations (Figures 8, 9, 17, 18 and 19). PO of lichen species using end points generated from PCA identifies a disturbance (perturbation-substrate stability) gradient (Axis I, Figure 17). *Cetraria islandica*, *Cladonia chlorophaea*, *C. ecmocyna* and *C. impexa* occur in stable unpreturbed sites. *Cladonia cariosa*, *C. polycarpoides* and *Peltigera canina* var. *rufescens* occupy a variety of sites from fairly stable and unpreturbed to highly disturbed. *Cetraria cucullata*, *Cornicularia aculeata*, *Ochrolechia upsaliensis*, *Stereocaulon tomentosum*, *Thamnolia vermicularis* and species #27 occupy sites which as a whole are unstable but are found in microhabitats stabilized by vascular plant cover (Plate III).

A second PO utilizing end points generated from RA (Figure 18) identifies an exposure gradient (Axis I). *Cladonia chlorophaea*, *C. ecmocyna*, *C. piedmontensis* and *Peltigera canina* occur in cool shaded macro- or microsites. *Cetraria islandica* and *Cladonia impexa* are found both in sheltered, cool sites and in more exposed sites. *Cladonia cariosa*, *C. pixidata*, *C. polycarpoides*, *C. verticillata*, *Peltigera canina* var. *rufescens* and species #27 occupy fairly exposed sites though they are also occur in more sheltered microsites. *Cetraria cucullata Ochrolechia*

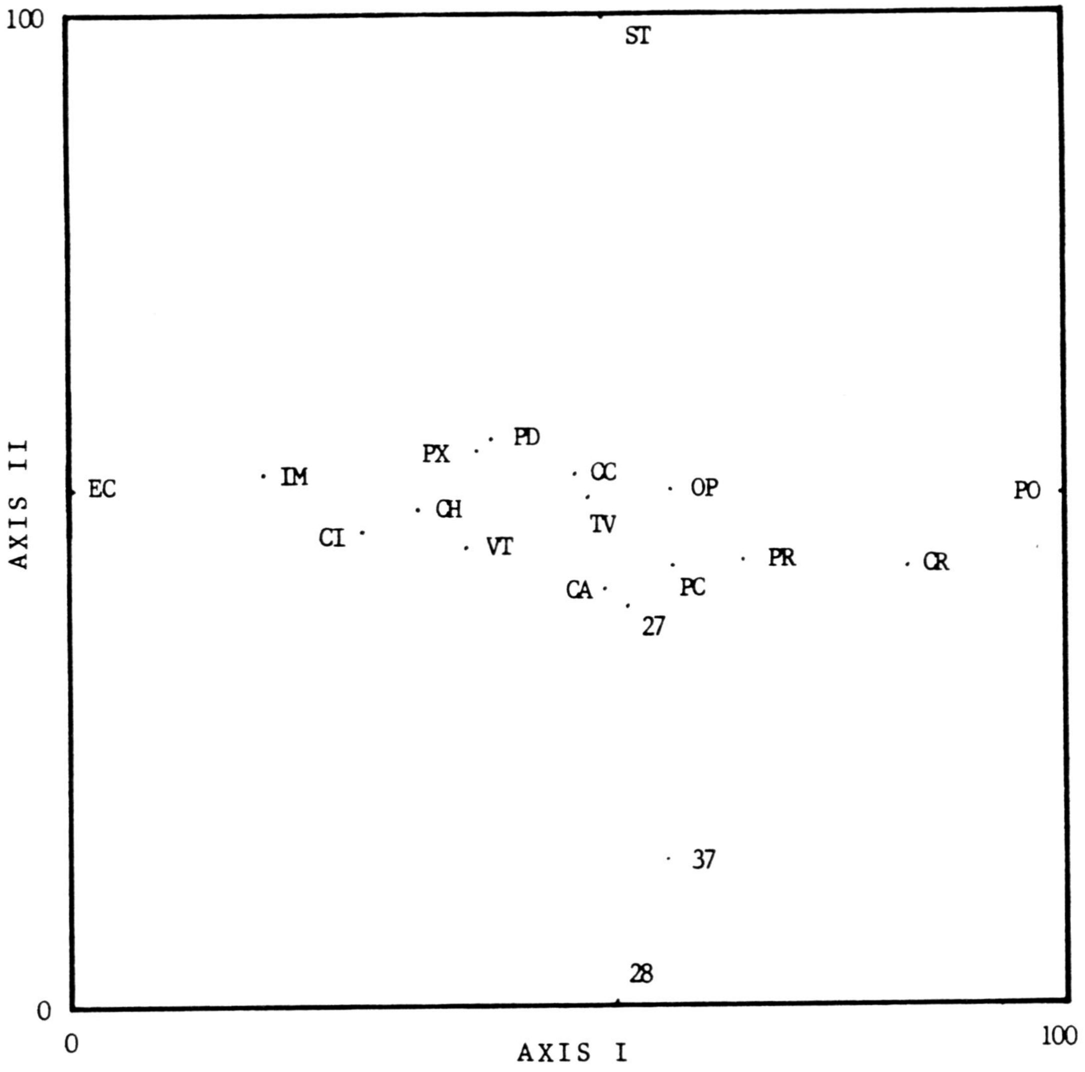

Figure 17. Polar Ordination of Lichen Species. Axis I identifies a substrate stability (disturbance) gradient. Axis I end points were chosen from PCA. Species codes are identified in Appendix B.

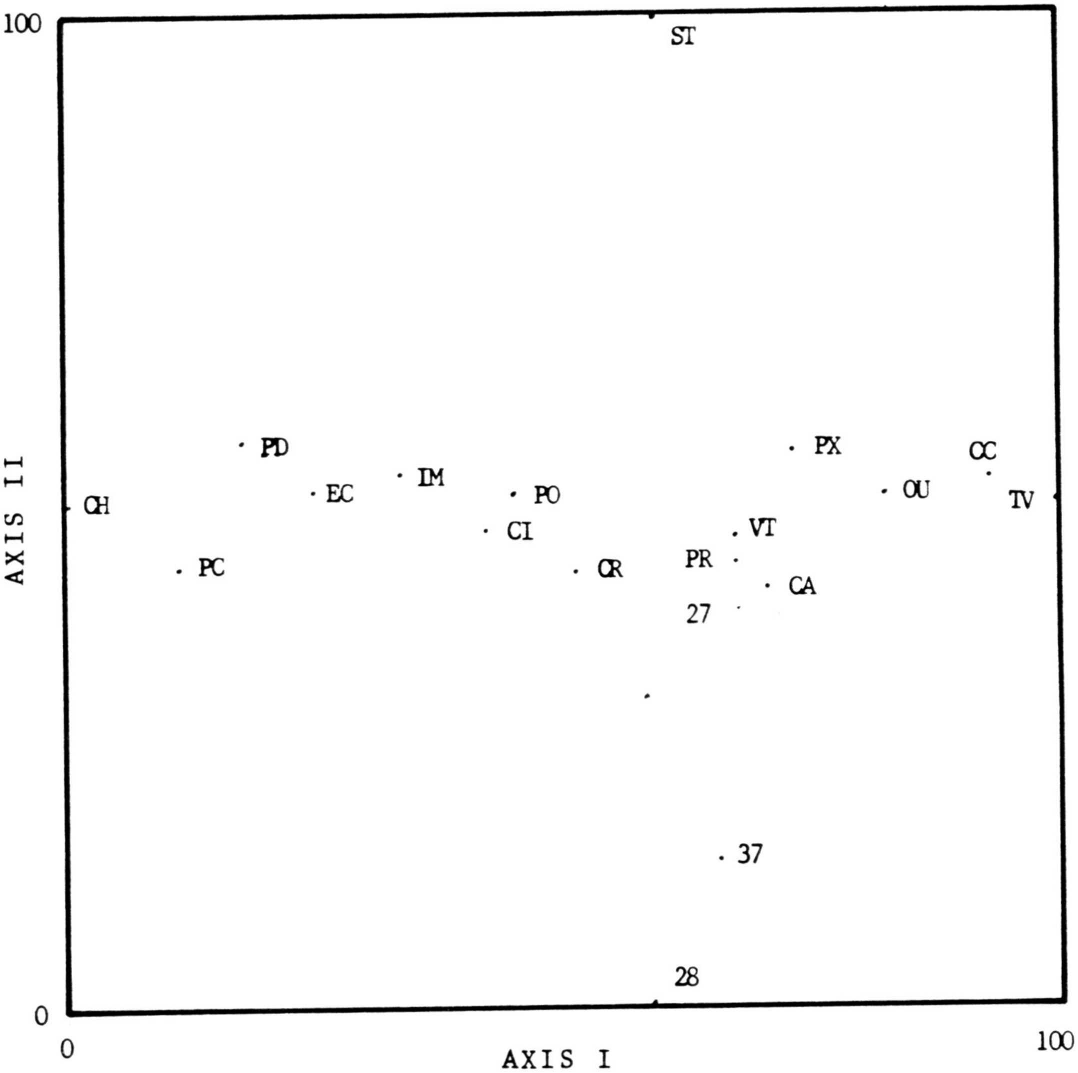

Figure 18. Polar Ordination of Lichen Species. Axis I is a combined moisture-exposure gradient. Axis I end points were obtained from RA. Species codes are identified in Appendix B.

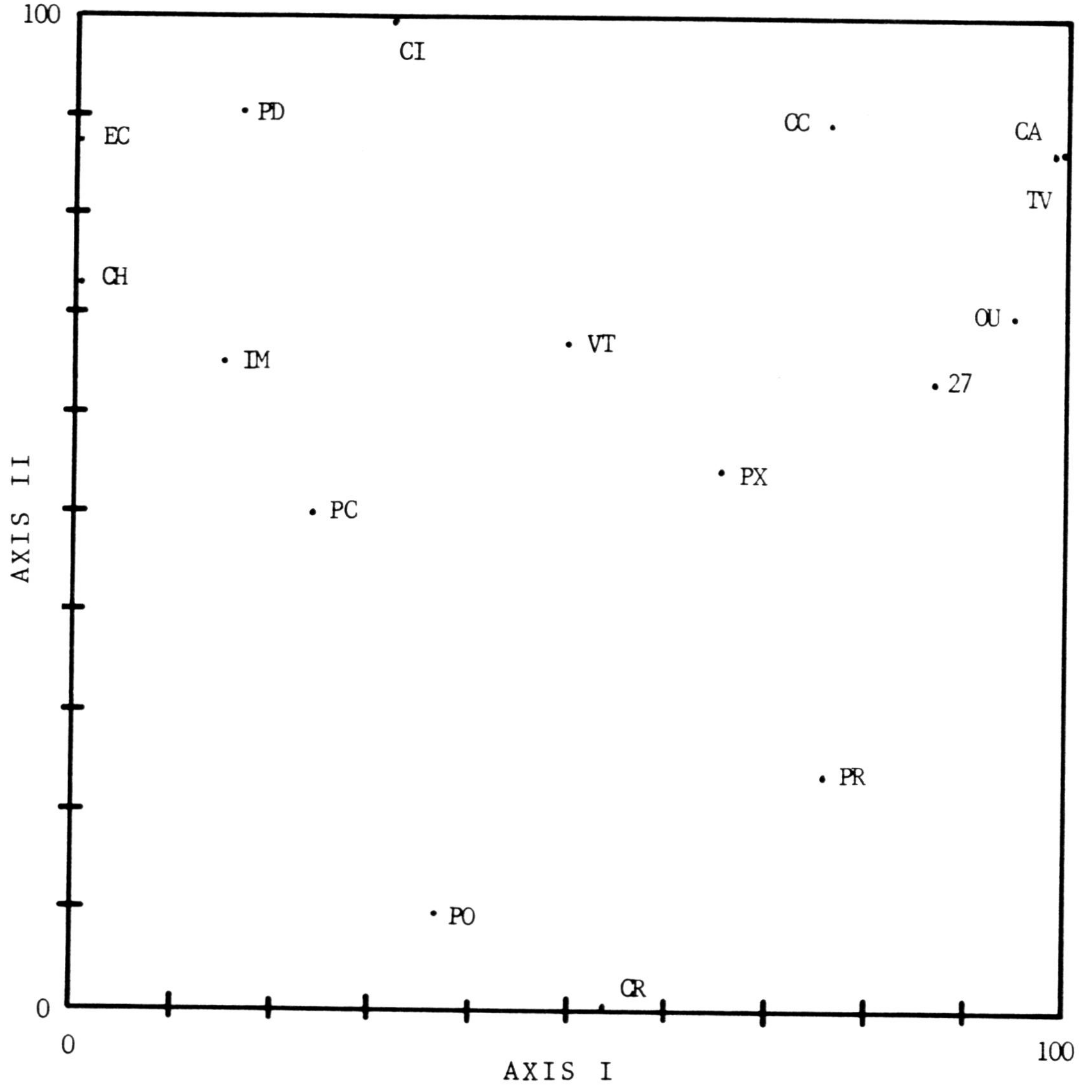

Figure 19. Principal Components Ordination of Lichen Species. Axis I is a complex moisture- exposure gradient. Axis II is a disturbance gradient.

upsaliensis and Thamnolia vermicularis occur in highly exposed sites.

PCA, after removal of Stereocaulon tomentosum and species numbers 28 and 37, produces an interesting array of species (Figure 19). The first principal component is identified as a complex moisture gradient. The second principal component is associated with substrate stability. In the upper left hand quadrant are species occurring in stable shaded, mesic subalpine sites. Species in the upper right hand section occupy exposed, dry sites and stable microsites. Cladonia cariosa and C. polycarpoides are located in the lower portion of the figure. They occupy disturbed sites of moderate exposure and moisture. Peltigera canina var. rufescens occurs in more exposed and slightly less disturbed sites than do the two Cladonia species. These last three species are also the most widely distributed of the lichen species found at Deer Park.

Lichen Species Community Types: Kendall's tau indicates two major categories of lichen species (Table 6). The first group of species (Cetraria islandica, Cladonia chlorophaea, C. ecmocyna, C. impexa, C. piedmontensis and Peltigera canina) inhabit cool wet sites with low incident radiation (Plate I). With the exception of Cetraria islandica and Cladonia impexa which occur in both zones, these are also species which tend to be found in the subalpine rather then

Table 6. Correlations for Lichen Species with Environmental and Biotic Parameters: Correlations Indicated as Positive (+) or Negative (-) with Level of Significance 0.01 (**), 0.05 (*) or 0.05 0.10 (ss). Values from Kendall's Tau.

SPECIES	Vascular Cover	Graminoid Cover	Soil Type	Disturb-ance	Mean Soil Moisture	7-18 Soil Moisture	8-4 Soil Moisture	8-22 Soil Moisture	9-11 Soil Moisture	Aspect	Slope	Elevation	Soil Surface Temp. -cover	Soil Surface Temp. -open	6 cm Soil Temp. -cover	6 cm Soil Temp. -open	Carex spec. Cover
Cladonia chlorophaea				-ss	+*	+*	+*	+ss	+ss	-ss	-*	-*	-*	-*			+*
Cladonia ecmocyna						+ss	+*			-ss	-**	-*	-*	-*		-*	+*
Cladonia piedmontensis				+*		+ss				-*	-*	-*	-*	-*		-ss	
Peltigera canina	+ss								+*	-ss		-ss			-ss	-ss	
Cladonia implexa						+*				-*	-*	-ss	-**	-*	-*	-*	+*
Cetraria islandica													-*	-*	-*	-*	
Cladonia polycarpoides												+ss	+*	+*		+*	
Cladonia cariosa			+*		-*	-*	-*		-*				+*	+**	+*	+*	-*
Peltigera rufescens	-*	-ss	+*	+*	-*	-*	-**	-*	-*	+*	+ss		+*	+*	+*	+*	-**
Cladonia verticillata	-*	-*	+**	+**	-*	-ss	-*	-*	-*						+*	+*	-*

Table 6. Continued

SPECIES	INDEPENDANT VARIABLES																
	Vascular Cover	Graminoid Cover	Soil Type	Disturb- ance	Mean Soil Moisture	7-18 Soil Moisture	8-4 Soil Moisture	8-22 Soil Moisture	9-11 Soil Moisture	Aspect	Slope	Elevation	Soil Surface Temp. -cover	Soil Surface Temp. -open	6 cm Soil Temp. -cover	6 cm Soil Temp. -open	Carex spec. Cover
Species #28			+ss		-*	-*	-**	-*	-ss		+*	+*		+*	+ss	+*	-*
Cladonia pixidata	-*	-ss	+*	+*			-ss		-ss	+*							-**
Gray Crust #27	-*	-*	+*	+*	-*	-*	-*	-*	-ss	+*	+ss	+*					-ss
Species #37		-*		+ss	-*	-*	-*	-ss	-ss		+ss	+*					-*
Ochrolechia upsaliensis	-*	-*	+*	+*	-*	-*	-*	-*	-*	+*	+ss	+*		+ss	+*	+*	-*
Cornicularia aculeata	-*	-*	+*	+**	-*	-*	-*	-ss	-*	+**	+*	+*			+ss	+*	-*
Cetraria cucullata	-ss	-ss		+*						+*	+ss	+*	-*	-ss	-*	-ss	-ss
Thamnolia vermicularis	-*	-*	+*	+**	-*	-*	-*	-*	-*	+*		+*				+ss	-**

alpine zones. The second group of species (*Cetraria cucullata*, *Cladonia cariosa*, *C. pixidata*, *C. polycarpoides*, *C. verticillata*, *Cornicularia aculeata*, *Ochrolechia upsaliensis*, *Peltigera canina* var. *rufescens*, *Thamnolia vermicularis*, and species 27, 28 and 37) occur in warm, dry sites which tend to have unstable substrates (Plates III and IV). They are inversely related to vascular plant cover and cover of graminoid species. *Cetraria cucullata* plays exception being negatively correlated with temperature. However this species occurs in only three of the study sites making in difficult to define its relationship to environmental parameters. Species 28 and 37 occur in five and four sites respectively hence there is some question as to the accurracy of the results for these species as well. *Cladonia chlorophaea* and *Peltigera canina* exhibit positive correlations with vascular plant cover and cover of graminoid species. These two species along with *Cladonia polycarpoides*, are also the only species inversely correlated with substrate stability (i.e. increasing cover values with increased stability).

CHAPTER V: DISCUSSION

The problems in any synecological study are to 1) untangle the complex of environmental and biotic factors affecting a given system, 2) identify those with significant bearing on the question and 3) determine how they affect the system. This study reveals a complex of factors correlated with and presumably affecting the distribution of terricolous lichens found above treeline at Deer Park.

Gradient Analysis

The distribution of lichens and vascular plants are correlated. Ordinations using percent cover of lichen and vascular plant species produce similar arrays of sites (Figures 8, 9, 10, 11; Table 5). The axes identified by RA and PO are complex gradients combing soil moisture, exposure, soil type and substrate stability. However, cover of lichens and vascular plants have opposite responses to these environmental gradients. Lichen cover, on the macrohabitat scale, increases with increased exposure and decreased soil moisture (Figure 4) and is higher on unstable shale substrates (Table 3). Vascualr plant cover increases with increased soil moisture (Figure 5) and is higher on stable sandstone soils (Table 5).

Correlation with Vascular Plants

How are lichens and higher plants related? Is the distribution of lichens a function of vascular plants or are they responding to similar environmental conditions? Their correlation is nonlinear (Figure 3). Three groups of sites can be identified; alpine- xeric subalpine, mesic subalpine and sites which are either disturbed or chronically wet (Figures 8 and 9). Within a given vascular plant community type, changes in lichen species cover are correlated with vascular plant cover values. However, lichen species richness and composition do not shift within a community type (Appendix A; Table 4; Figure 13). In alpine communities, sites have approximatly the same lichen species composition regardless of vascular plant cover (Figure 12; Table 4; Plate III). However, lichen cover increases exponentially with increased vascular plant cover (Figure 3). In both mesic and xeric subalpine community types, lichen cover decreases exponentially with increased vascular plant cover while species composition is generally unchanged (Table 4; Plate I and VI). This suggests 1) that vascular plant cover directly affects lichen cover and 2) that vascular cover does not affect lichen species composition. However, this does not address the question of whether or not the type (i.e. habit and composition) of vascular plant community is directly affecting lichen species composition or whether both are functions of similar sets of environmental conditions.

Path Analysis

Lichen species richness is an index of lichen community type at Deer Park (Figure 13). High richness is correlated with alpine communities (Plate III), moderate richness with subalpine grass meadows (Plate VI) and few species with wet subalpine meadows (Plate I and VIII) and highly disturbed sites (Plate VII and IX). Path analysis indicates that lichen richness is a function of graminoid cover and soil type (Figure 16). Substrate stability and soil moisture are causally related to graminoid cover (Figure 17). Soil temperature at a depth of 6 cm and soil type are causally related to soil moisture. In this area, both vascular plant cover and graminoid cover are partial indexes of community type, however, graminoid cover proves a slightly better index than vascular cover. It is not surprising that lichen species richness and graminoid cover are more highly correlated than lichen richness and vascular plant cover. This analysis suggests that lichen community type is a function of the vascular flora plus environmental parameters most of which are indicated by or mediated through vascular community type.

It may not be fruitful or meaningful to pursue further determination of factors affecting lichen distribution on this scale. It is clear that different groups of lichen species are associated with different vascular plant

Plate VIII. Bog: Site 26

Plate IX. Site 16: Abandoned Marmot Meadow. Patchy vegetation dominated by *Aster foliaceous* and *Festuca idahoensis*.

community types. It is quite likely that species within these community types respond differently to environmental and biotic factors or that they are subject to different factors. Hence, investigation should proceed on a microhabitat scale.

Patterns of Distribution

Alpine. Two patterns of lichen distribution are observed at Deer Park. The first concerns unstable scree slopes and the second, stable subalpine sites. Lichens are slow growing organisms which lack root systems and hence are poorly adapted to highly unstable substrates (Orwin, 1972). Scree slopes are constantly sluffing and are not expected to be surfaces readily colonized by lichens. Such highly disturbed sites for which there is less than 20% cover of vascular plants have limited occurrences of lichens (Figure 3; del Moral, unpublished). The vascular flora that developes in these sites consists of low growing cushion plants. As this cover increases, lichens become established with exponential increase in cover but no increase in richness or shift in composition. The vascular flora acts to stablize the substrate producing microsites favorable for lichen growth (Plate IV). Competition between the cushion plants and lichens is not apparent though no experimental work has been done to test this hypothesis. The culmination of this process is a dense continuous mat of cushion plants and lichens as exemplified by the northeast ridge of Blue Mountain (Plate III). This is the predominant alpine flora at Deer Park developing over scree slopes and basalt outcrops with thin deposites of soil. It is also found over unstable substrates in typically subalpine areas (sites 5, 14 and 22). *Alpine Lichen Species*. There is a typical lichen flora which occupies alpine sites: *Cetraria cucullata*, *C. islandica*, *Cladonia impexa*, *Cornicularia aculeata*, *Peltigera canina* var. *rufescens*, *Thamnolia vermicularis* and *Stereocaulon tomentosum*. These species, with the exception of *Cetraria islandica*, *Cladonia impexa* and *Peltigera canina* var. *rufescens*, are restricted to highly exposed, dry, alpine sites. These lichen species tend to be minimally attached to the soil and often are simply interlaced with the higher plants. Hence, unlike most terrestrial lichens, they are part of the upper canopy, subject to high incident radiation and wind effects. It is interesting that these are all highly pigmented fruticose species. The fruticose habit may be advantageous in highly exposed sites, reducing wind and radiation effects by reducing desiccation, increasing shading and decreasing physical damage caused by wind. Rundel (1978) suggests a similar advantage for fruticose lichens in desert fog zones.

Peltigera canina var. *rufescens* is the only foliose species occurring in this zone. It has a revolute thallus and tomentum which may act to protect it from high light and desiccation. This species occurs closely appressed to the substrate which reduces wind effects.

Several roles have been hypothesized for thallus color. Kershaw (1975a and b) found dark thallus color raised thallus temperatures extending the growing season significantly for boreal-tundra lichens. Ahmadjian (1967) suggests that pigmentation protects the phycobiont from over exposure to the sun. It is also possible that light colored pigments act to increase albedo and reduce thallus temperature. This may be important in alpine areas where incident radiation and thallus temperatures are high. *Thamnolia vermicularis* is white appearing dead until sectioned. *Cetraria cucullata* is bright yellow-green as is *Cladonia impexa*. *Cornicularia aculeata* and *Cetraria islandica* are dark brown almost black in color. *Peltigera canina* var. *rufescens* is dark brown with a layer of white tomentum. When moist, it turns a dark green-brown, when dry, it is a tan color. When wet, the phycobiont may benefit from or tolerate high thallus temperatures and exposure to light hence the dark color and exposure of the algae to radiation may not be deleterious. When dry, the light color would increase albedo reducing thallus temperature and hence metabolic rate. Too, the tomentum would act to insulate against water loss.

Subalpine. Subalpine sites exhibit quite different patterns of distribution. This study suggests that lichen growth is progressively inhibited by development of a dense subalpine flora dominated by graminoids. It is hypothesized that the vascular flora either has a competitive advantage over lichens by virtue of a faster growth rate or produces a microhabitat unsuited for lichens. Dey (1978) found grassbalds in the Appalachian Mountains to be devoid of lichens. He attributes this finding to the dense herbaceous flora though does not speculate how lichen growth is actually inhibited. Preliminary measurements of photosynthetically active radiation indicate a significant decrease in incident light below _Festuca idahoensis_, _Carex spectabilis_, _Lupinus latifolius_ and other dense herbage. At the same time this dense herbaceous canapy is expected to reduce wind and solar effects maintaining a moist microenvironment. It has been shown that prolongation of high thallus moisture in dry environments is beneficial to lichen growth (Orwin 1972; Nash et al. 1977; Rundel 1978; Pentecost 1979). However, it has also been established that a cycle of wetting and drying of the thallus is necessary, that maintenance of saturated conditions is deleterious to most lichens (Armstrong 1975 and 1976; Farrar 1976a, b and c; Larson 1979). Deer Park is subject to frequent heavy dew and fog during May, June and July. It is speculated that the subalpine flora acts to minimize wetting and drying cycles causing maintenance of saturated thallus conditions precluding lichen establishment and growth.

Subalpine Lichen Species. Several lichen species occur in these subalpine sites: *Cetraria islandica*, *Cladonia cariosa*, *C. chlorophaea*, *C. ecmocyna*, *C. impexa*, *C. piedmontensis*, *C. polycarpoides*, *Peltigera canina* and *P. canina* var. *rufescens*. Consideration of microhabitats occupied by these species is necessary to identify and understand factors that affect their distribution.

Cladonia chlorophaea, *C. peidmontensis* and *Peltigera canina* are species generally found in cool, moist, shaded sites. Investigation of their microhabitats indicates that *C. chlorophaea* and *P. canina* occur exclusively under such conditions usually at the base of dense clumps of bunch grass or below undercut terraces with over hanging vascular plants. A few species, which rarely occur in the study area also are found in these microhabitats (*Peltigera malacea*, *P. aphthosa* and *P. venosa*). These are typically woodland species (Kershaw and MacFarlane, 1980) occurring extensively in subalpine forests on Blue Mountain. *Cladonia peidmontensis* is occassionally found in more open microsites in patchy vegetation but still within the range of cool, shaded conditions. *Cetraria islandica* and *Cladonia impexa* occur both in cool, moist shaded habitats and in exposed alpine sites. In subalpine sites, these species occur free of herbs or among low growing vascular plants. Even so, their distributions indicate either a wide tolerance towards environmental conditions or the existence of ecotypes with different physiological or morphological adaptations. Investigations into the physiological responses and niche breadth of these two species would be interesting but beyond the scope of this study. It is noted that thalli of *Cetraria islandica* growing in exposed sites are a darker brown and narrower than those occurring in sheltered sites suggesting adaptations to high incident light and perhaps desiccation.

Cladonia ecmocyna is described by Thomson (1967) as an arctic and alpine species occurring in moist habitats near late snow melts and bogs. This agrees with the species distribution at Deer Park. It should be pointed out that this is a complex of intergrading forms rather than a clearly defined species and that more than one taxon is thought to occur at Deer Park. As a complex, it is observed that *C. ecmocyna* is more vigorous in moist sheltered sites producing extensive mats of branched podetia. The most vigorous mats occur in site 9 which is shaded by surrounding trees. There is a distinct gradient of *C. ecmocyna* cover values within this site from extensive cover in open microsites with low vascular cover to areas with reduced cover dominated by *Antennaria lanata* to few occurrences in *Carex spectabilis* plots (Plate I). The complex is also found in drier sites

(sites 1, 5, 10 and 23) but occurs as sterile squamules with poorly developed podetia. The striking contrast in growth of specimens from the two habitats gives support to the description of this species as a cool, moist, shade species but further work should be done to distinguish forms.

A group of species occurring in dry, exposed sites have broad distribution patterns (*Cladonia cariosa*, *C. pixidata*, *C. polycarpoides*, *C. verticillata* and *Peltigera canina* var. *rufescens*) (Table 4, Figures 7, 8 and 9). *Cladonia pixidata* and *C. verticillata* occur throughout exposed sites but are more vigorous and produce larger more frequent podetia in slightly shaded microsites. These microsites differ from those of *C. chlorophaea* and *Peltigera canina* by being more exposed and drier, among less dense vegetation.

Cladonia cariosa, *C. polycarpoides* and *Peltigera canina* var. *rufescens* are the most widely distributed of the lichen species at Deer Park. These species occupy warm, dry, exposed sites and are noteworthy for occurring in highly disturbed microsites. *Cladonia cariosa* and *C. polycarpoides* occur primarily as sterile squamules, very seldom fruiting. Kershaw (1978) suggests that some Cladonias have unexpectedly high growth rates and thereby are found as colonists in boreal-tundra areas. It is hypothesized that the sterile squamules of these two species have high growth rates which enables them to take advantage of disturbed sites slower growing species can not tolerate. Peltigera canina var. rufescens is widely distributed, occurring in exposed microsites and often on highly unstable substrates. A foliose form is not expected to be advantageous on unstable substrates. This distribution is probably due to soil slumping which carries patches of vascular plants down onto highly unstable slopes. Peltigera canina var. rufescens is noted for its tolerence to high exposure (Kershaw and MacFarlane, 1980) so should not be adversely affected by radiation incident to unvegetated scree slopes. It is suggested that accompanying vegetation protects the Peltegera shielding it from loose substrate material.

Ochrolechia upsaliensis occurs on Selaginella densa (Howard, 1950). Mats of Selaginella act to inhibit growth of other higher plants hence O. upsaliensis is restricted to exposed microsites. The gray crustose species occurs in a similar habitat, growing on old Selaginella or mats of dead vegetation or exposed roots.

Effects of Chronic Saturation

There are two factors which deserve separate consideration in their effects on terricolous lichens. Soil moisture is inversely related to lichen distribution (Figures 4 and 14). Sites with high soil moisture, either seasonally or chronically, support few lichens. As has been pointed out by Larson and Kershaw (1975), Farrar (1976) and Kershaw and

Smith (1978), lichens are intolerant of saturated thallus conditions quickly causing distruction of the lichen. Sites which are chronically saturated (sites 26 and 27) have no occurrences of lichens (Plate VIII). Though the dense cover of vascular plants may be capable of precluding establishment of lichens in these sites, the maintenence of thalli at saturation alone will inhibit their growth. Sites which are seasonally wet as in site 3 with a seasonal spring or sites 7, 8, 11, 13 and 24 with late melting snow banks, support a depauperate lichen flora with low cover values. In these sites, cover of vascular plants appears to play a critical role with soil moisture. Microsites with low vascular cover support what lichens occur there. Microsites with high vascular cover are devoid of lichens. Chronically high atmospheric moisture has the same affect on lichens as does high or saturated soil moisture levels. Dense herbaceous cover is hypothesized to reduce wind effects maintaining high humidity deleterious to lichen growth. Some species appear adapted to moist environments, but most do not occupy these microsites. Those that do are chronically moist having large quantities of deteriorating thallus material. This is probably due to combined effects of low light and high moisture. Only hypotheses can be generated at this point without monitoring microsite conditions and physiological responses of these species to various conditions of light and moisture.

Disturbance

The second factor, disturbance, appears to have a significant effect on the distribution and development of lichen colonies. Substrate instability is hypothesized to enhance lichen growth by maintaining a less dense, patchy cover of higher plants and hence providing niches for lichens. However, due to their slow growth rates, lichens require fairly stable microhabitats (Orwin, 1972). They may benefit from disturbance of the surrounding environment but can not tolerate disturbance of their particular microsite. Lichen cover is found to be low on highly unstable scree slopes (site 4), in sites with substrate disturbance due to snow pack and movement (sites 8, 13 and 24) and in sites which are or have been chronically preturbed by deer or marmots (sites 12, 13, 19, 16 and 25) (Plate IX). This latter category of sites exhibit patchy vascular cover and stable substrates. They are sites in which one would expect to find lichens but where very few occur. The sites visually carry signs of animal activity, deer and marmot trails (sites 12, 13 and 25), deer wallows (site 25), neighboring marmot meadows (sites 12, 13 and 16), compacted substrate, grazed vascular species and occurrence of so called "disturbance species" (Sackett, 1980) of vascular plants. Distinct colonies of lichens are seldom observed rather there are sparse patches of sterile squamules. Squamules appear fractioned with unattached portions lying loose over the substrate. Infrequent disturbance and fractioning aid in dispersal of lichens. Howerer, chronic disturbance inhibits the establishment and maintenance of lichen colonies (Orwin, 1972). These findings suggest that lichens are good indicators of perturbation by animals including humans. There are species which are characterestic of preturbed sites, _Cladonia_ _cariosa_ and _C._ _polycarpoides_. Lack of cover and scattered appearence of colonies serves as an excellent indicator of disturbance.

CHAPTER VI: CONCLUSIONS

Generalizations about patterns of lichen distribution must be approached with caution. However, above treeline at Deer Park, vascular plant cover, soil moisture and substrate stability are strongly correlated and causally related to terricolous lichen species composition and cover. How these factors actually affect lichen distribution is still a matter of conjecture.

Several different vascular plant communities exist at Deer Park. Correlated with these communities are three different groups of lichen species. It is apparent that within different community types, different factors are prevalent. Two distinct patterns of lichen distribution are identified. On scree slopes with alpine vegetation, a characteristic group of lichen species occur (Cetraria cucullata, C. islandica, Cladonia impexa, Cornicularia aculeata, Ochrolechia upsaliensis, Peltigera canina var. rufescens, Stereocaulon tomentosum and Thamnolia vermicularis). Cover of these species is directly related to vascular plant cover which is hypothesized to stablize the substrate allowing establishment and growth of the lichens. With continued stablization of the substrate, a dense mat of lichens and cushion plants developes.

Subalpine community types have a very different effect on lichens. As vascular cover increased, lichen cover decreases. Concurrently, there is an increase in soil moisture and reduction in exposure. Within this general pattern, a shift in lichen species is observed from *Cladonia cariosa*, *C. pixidata*, *C. polycarpoides*, *C. verticilata*, *Ochrolechia upsaliensis*, *Peltigera canina* var. *rufescens* and other species occupying exposed sites to *Cetraria islandica*, *Cladonia chlorophaea*, *C. ecmocyna*, *C. piedmontensis* and *Peltigera canina* which occupy moist shaded woodland meadows. In both of these subalpine communities, lichen cover is hypothesized to be negatively affected by microclimatic conditions created by and competition with the vascular flora. This dense herbaceous flora is thought to have a competitive advantage over slow growing lichens. It also acts to reduce wind effects and incident radiation creating microenvironments with low light and chronically high humidity. This set of conditions has proved deleterious to lichen growth in a number of studies (Farrar, 1976; Kershaw and Smith, 1978). A few species are found to marginally occupy these microsites (*Cladonia chlorophaea*, *C. ecmocyna* and *Peltigera canina*). Other species are conspiciously absent.

Two factors cut across habitat type in their effect on lichens; pertrubation and very high seasonal or chronic moisture conditions. Both result in severe reduction in lichen species richness and cover. Perturbation by fauna or abrasion is typified by scattered occurrence of sterile squamules of Cladonia cariosa and C. polycarpoides. Seasonal or chronic high moisture results in a reduction of the lichen flora. This environmental effect is observed in late snow melt sites, sites with seasonal or continual springs and also beneath dense canapies of herbaceous vegetation where atmospheric moisture is chronically high.

The scale on which investigations are made is crucial in determining patterns of lichen distribution. Individual species are shown to have quite different tolerences to environmental and biotic factors even within proported community types. Consideration of microenvironmental conditions is highly important in determining the ecology of these organisms. Until better methods of maintaining lichens in the laboratory are devised, these studies must be carried out in the field. This makes it difficult to control single factors making analysis of environmental effects more complex. However, it is clear that these types of studies need to be done.

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APPENDIX A: SITE DESCRIPTIONS

Site 1. Aspect: 165 ; Slope: 8 ; Elevation: 1664m; Soil Type: shale; Substrate Stability: 3; Soil Moisture*: 13.3, 14.9, 4.3, 22.8, 11.3; Lichen Cover: 9.3%; Lichen Richness: 9; Vascular Cover: 24% Graminoid Cover: 4%. This is a dry hot site located on course scree. The Vegetation is patchy, dominated by xeric subalpine and alpine vascular plant species (*Festuca idahoensis*, *Phlox diffusa*, and *Selaginella densa*).

Site 2. Aspect: 147 ; Slope: 17.3 ; Elevation: 1646m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 18.1, 15.8, 5.1, 15.8, 36.0, Lichen Cover: 11.5%; Lichen Richness: 6; Vascular Plant Cover: 65%; Graminoid Cover: 22%. This is a subalpine grass meadow. Soil is fairly well developed. It is dominated by *Dodecatheon jeffreyi* *Festuca idahoensis* *Eriophyllum lanatum* and *Selaginella densa*.

Site 3. Aspect: 112 ; Slope: 14.2 ; Elevation: 1648m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 36.3, 31.4, 19.0, 40.9, 54.1; Lichen Cover: 1.4%; Lichen Richness: 3; Vascular Plant Cover: 100%; Graminoid Cover: 41%. This is a seasonally wet, lush, subalpine meadow that becomes dry the end of July. There is an accumulation of peat in the soil. Vegetation is dominated by *Dodecathion jeffreyi*, *Festuca idahoensis* and *Potentilla diversifolia*.

Site 4. Aspect: 48 ; Slope: 15 ; Elevation: 1657m; Soil Type: shale; Substrate Stability: 4; Soil Moisture: 10.0, 15.9, 3.1, 8.0, 12.8; Lichen Cover: 2.1%; Lichen Richness: 6; Vascular Plant Cover: 48%; Graminoid Cover: 16%. This is a cool, xeric site which is terraced. Vegetation is patchy, established along the terrace edges. Dominate species are, *Festuca idahoensis*, *Pholx diffusa* and *Selaginella densa*.

Site 5. Aspect: 158 ; Slope: 8.9 ; Elevation: 1681m; Soil Type: shale; Substrate Stability: 4; Soil Moisture: 12.0, 12.9, 5.4, 16.9, 12.8; Lichen Cover: 9.3%; Lichen Richen: 14; Vascular Plant Cover. 22%; Graminoid Cover: 16%. This is a scree site very similar to site 1. Soil is poorly

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* Percent soil moisture values = mean, 7-18-79, 8-4-79, 8-22-79 and 9-11-79

developed. Vegetation is patchy, dominated by *Festuca idahoensis*, *Phlox diffusa* and *Selaginella densa*.

Site 6. Aspect: 170 ; Slope: 26 ; Elevation: 1670m; Soil Type: shale and sandstone; Substrate Stability: 2; Soil Moisture: 12.6, 10.3, 3.2, 13.4, 23.8; Lichen Cover: 10.9%; Lichen Richness: 11; Vascular Plant Cover: 68%; Graminoid Cover: 19%. This is a dry, highly exposed, subalpine meadow. The soil is shallow and course. Vegetation is not dense. *Arenaria capillaris*, *Festuca idahoensis*, *Selaginella densa* and *Phlox diffusa* are dominant.

Site 7. Aspect: 340 ; Slope: 14.0-15.7 ; Elevation: 1667m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 24.5, 25.9, 13.7, 17.3, 41.4; Lichen Cover: 0.9%; Lichen Richness: 4; Vascular Plant Cover: 89%; Graminoid Cover: 42%. This is a cool, mesic site located on the north side of a ridge encircled by trees. Soil is well developed with high organic content. Vegetation is subalpine dominated by *Antennaria lanata* and *Carex spectabilis*.

Site 8. Aspect: 53 ; Slope: 7.9 ; Elevation: 1678m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 16.2, 23.4, 9.8, 12.1, 19.6; Lichen Cover: 8.8; Lichen Richness: 3; Vascular Plant Cover: 56%; Graminoid Cover: 32%. This is a late snow melt site on a terraced slope. The substrate surface is abraded. Vegetation is subalpine and sparse dominated by *Antennaria lanata*, *Juncus ensifolius* and *Lupinus latifolius*.

Site 9. Aspect: 341 ; Slope: 3.7 ; Elevation: 1695m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 22.8, 22.5, 11.4, 25.0, 32.2; Lichen Cover: 6.8; Lichen Richness: 7; Vascular Plant Cover: 76%; Graminoid Cover: 10%. This is a cool, mesic site located on the north side of a ridge encircled by trees. The southeast portion of the site is dominated by two pine trees. This area has low vascular plant cover and high lichen cover. The major portion of the site is similar to site 7 with an *Antennaria lanata*- *Carex spectabilis* community.

Site 10. Aspect: 174 ; Slope: 13.3 ; Elevation: 1672m; Soil Type: shale; Subsrate Stability: 3; Soil Moisture: 9.8, 7.3, 4.7, 12.3, 15.1; Lichen Cover:

3.4%; Lichen Richness: 12; Vascular Plant Cover: 33%; Graminoid Cover: 4%. This is a dry, scree site with high exposure. The vegetation is patchy, xeric subalpine to alpine in character. Arenaria capillaris, Festuca idahoensis and Phlox diffusa are dominant.

Site 11. Aspect: 20 ; Slope: 11.4 ; Elevation: 1634m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 18.5, 26.3, 8.8, 16.0, 22.3; Lichen Cover: 6.4; Lichen Richness: 8; Vascular Plant Cover: 46%; Graminoid Cover: 6. This site is located on the south slope of a gully which has an east-west aspect. Incident light and temperatures are low. Snow-melt is late. The vegetation is mesic subalpine dominated by Carex spectabilis and Lupinus latifolius.

Site 12. Aspect: 35 ; Slope: 18.1 ; Elevation: 1634m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 31.0, 48.8, 14.3, 22.9, 38.2; Lichen Cover: 0.6%; Lichen Richness: 5; Vascular Plant Cover: 87; Graminoid Cover: 30. This site is located in a mesic, north facing swale. It is preturbed by deer and marmots. The substrate is compacted. The vegetation is subalpine and sparse, dominated by Festuca sp., Lupinus latifolius and Poliginum bistortoides. This site is also rich in Composite species (11).

Site 13. Aspect: 117 ; Slope: 7.5 ; Elevation: 1695m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 22.7, 28.8, 12.5, 30.0, 19.4; Lichen Cover: 1.7%; Lichen Richness: 2; Vascular Cover: 57%; Graminoid Cover: 28%. This site is located in a swale with late snow-melt. It is ajacent to a marmot meadow with apparent perturbation by them and snow pack. Vegetation is dominated by Arenaria capillaris, Festuca idahoensis and Juncus ensifolius.

Site 14. Aspect: 65 ; Slope: 8-10 on upper and 20.6 on lower portion; Elevation: 1713m; Soil Type: shale; Substrate Stability: 3; Soil Moisture: 8.5, 7.8, 3.2, 13.0, 9.9; Lichen Cover: 16.4%; Lichen Richness: 11; Vascular Cover: 44%;. Graminoid Cover: 7%. This site is located on the northeast side of a large rock outcrop. Soil is very shallow over a basalt base grading into a scree slope. It is terraced with vegetation occurring along the terrace edges. The vegetation is dominated by *Festuca idahoensis*, *Phlox diffusa* and *Selaginella densa*.

Site 16. Aspect: 170 ; Slope: 25 ; Elevation: 1731m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 9.3, 8.8, 3.3, 10.6, 14.5; Lichen Cover: 1.4%; Lichen Richness: 4; Vascular Plant Cover: 72%; Graminoid Cover: 39%. This site is located in a deserted marmot meadow. The vegetation is distinctly different from that of adjacent areas (see site 17). Soil is well developed. Vascular plant growth is lush dominated by *Aster foliaceous* *Carex* sp., *Festuca idahoensis* and *Vicia* sp.

Site 17. Aspect: 170 ; Slope: 25 ; Elevation: 1731; Soil Type: shale and sandstone; Substrate Stability: 2; Soil Moisture: 8.4, 7.8, 2.4, 9.8, 13.5; Lichen Cover: 9.7%; Lichen Richness: 11; Vascular Plant Cover: 40%; Graminoid Cover: 10%. This site is located below a basalt outcrop and scree slope. It is rocky with poor soil development. Vegetation is low and patchy. The dominant species are *Arenaria capillaris*, *Festuca idahoensis*, *Phlox diffusa* and *Selaginella densa*.

Site 18. Aspect: 273 ; Slope: 23.7 ; Elevation: 1812m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 10.7, 9.7, 3.9, 10.1, 19.2; Lichen Cover: 21.6%; Lichen Richness: 14; Vascular Plant Cover: 66%; Graminoid Cover. 17%. This site is steep but stable. It has large particle size with poor soil development. Vegetation is alpine and xeric subalpine. The dominant species are *Cerastrium arvense*, *Festuca idahoensis* and *Phlox diffusa*.

Site 19. Aspect: 102 ; Slope: 13.3 ; Elevation: 1804m; Soil Type: sandstone; Substrate Stability: 2; Soil Moisture: 12.8, 11.2, 3.4, 15.4, 21.0; Lichen Cover: 14.2%; Lichen Richness: 11; Vascular Plant Cover: 73%; Graminoid Cover: 13%. This site is similar to site 18. Soil is more developed but still rocky. It is located on the north ridge of a small gully. Vegetation is alpine- xeric subalpine dominated by *Cerastrium arvense*, *Festuca idahoensis*, *Geum triflorum*, *Phlox diffusa* and *Selaginella densa*.

Site 20. Aspect: 270 ; Slope: 15.6-20.4 ; Elevation: 1823m; Soil Type: shale; Substrate Stability: 3; Soil Moisture: 12.4, 9.3, 4.1, 21.2, 15.3; Lichen Cover: 4.1%; Lichen Richness: 10; Vascular Plant Cover: 31%; Graminoid Cover: 2%. This site is located on a terraced scree slope. Soil is poorly developed. Vegetation is patchy on the terrace edges. Vegetation is alpine, dominated by Phlox diffusa and Synthyris pinnatifida var. lanuginosa.

Site 21. Aspect: 12 ; Slope: 11.1 ; Elevation: 1640m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 26.0, 31.3, 14.6, 28.1, 30.0; Lichen Cover: 9.2%; Lichen Richness: 7; Vascular Plant Cover: 100%; Graminoid Cover: 66%. This is a mesic site located at the upper end of a swale. Soil is well developed. It is dominated by grasses, Festuca idahoensis and Festuca sp. and by Arenaria capillaris. It is also rich in Composite species (8).

Site 22. Aspect: 8 ; Slope: 6.8 ; Elevation: 1640m; Soil Type: shale; Substrate Stability: 3; Soil Moisture: 17.8, 24.6, 8.5, 19.6, 18.4; Lichen Cover: 34.7%; Lichen Richness: 10; Vascular Plant Cover: 51%; Graminoid Cover: 11%. The site is located on a slight knoll. Soil development is poor. Vegetation is patchy, xeric subalpine to alpine in nature. It is dominated by Arenaria capillaris, Festuca idahoensis, Geum triflorum, Phlox diffusa and Selaginella densa.

Site 23. Aspect: 237 ; Slope: 17.1 ; Elevation: 1780m; Soil Type: sandstone; Substrate Stability: 3; Soil Moisture: 15.7, 24.6, 5.2, 15.5, 17.5; Lichen Cover: 47.9%; Lichen Richness: 13; Vascular Plant Cover: 45%; Graminoid Cover: 8%. This is a highly exposed alpine site. The soil is poorly developed. Vegetation is patchy and dense, dominated by Carex sp., Lupinus lepidus and Phlox diffusa.

Site 24. Aspect: 305 ; Slope: 22 ; Elevation: 1804m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 30.4, 37.3, 13.4, 35.1, 36.0; Lichen Cover: 0.9%; Lichen Richness: 6; Vascular Plant Cover: 94%; Graminoid Cover: 36%. This is a late snow-melt site. It is terraced and densely vegetated. Antennaria lanata and Carex spectabilis are codominants. Lichens are absent in areas dominated by C. spectabilis. This site contains lichen species not found elsewhere in the study area (Peltigera apthosa, P. venosa and P. malacea).

Site 25. Aspect: 128 ; Slope: 18.9 ; Elevation: 1804m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 13.6, 11.6, 4.5, 16.2, 22.1; Lichen Cover: 0.3%; Lichen Richen: 3; Vascular Plant Cover: 93%; Graminoid Cover: 24%. This is a mesic subalpine site located on the southern slope of a gully abreast of site 19. The site includes a deer wallow hence is chronically preturbed. It is dominated by Arenaria capillaris, Aster foliaceous and Festuca idahoensis.

Site 26. Aspect: 50 ; Slope: 11.3 ; Elevation: 1612m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 327.8, 148.5, 287.3, 120.4, 249.0; Lichen Cover: 0%; Lichen Richness: 0; Vascular Plant Cover: 155%; Graminoid Cover: 63%. This is a chronically saturated site. Soil is high in organic matter. Grasses and Aster foliaceous are dominant.

Site 27. Aspect: 50 ; Slope: 4 ; Elevation: 1609m; Soil Type: sandstone; Substrate Stability: 1; Soil Moisture: 504.3, 382.1, 357.5, 637.4, 640.0; Lichen Cover: 0%; Lichen Richness: 0; Vascular Plant Cover: 97%; Graminoid Cover: 37%. This is a spring feed bog. There are no lichens. Aster foliaceous, Caltha lepida, graminoid sp. and moss are dominate

APPENDIX B: LICHEN SPECIES LIST

CLASS ASCOMYCETES

Order Lecanorales

Suborder Lecanorineae

Alectoriaceae
  Cornicularia aculeata (CA), (Schrad.) Ach.

Cladoniaceae
  Cladonia cariosa (CR), (Ach.) Spreng.
  Cladonia chloraphaea (CH), (Florke) Spreng.
  Cladonia ecmocyna (EC), (Ach.) Nyl.
  Cladonia furcata, (Huds) Schrad.
  Cladonia grayi, Merr.
  Cladonia impexa (IM), (Harm) Lesd.
  Cladonia piedmontensis (PD), Merr.
  Cladonia polycarpoides (PO), Nyl.
  Cladonia pyxidata (PX), (L.) Hoffm.
  Cladonia verticillata (VT), (Hoffm.) Schaer.

Diploschistaceae
  Diploschistes sp.

Lecanoraceae
  Ochrolechia upsaliensis (OU), (L.) Mass. Ricerch. Auton.
  Ochrolechia sp.

Parmeliaceae
  Cetraria cucullata (CC), (Bell.) Ach.
  Cetraria islandica (CI), (L.) Ach.
  Xanthoparmelia sp.

Stereocaulaceae
  Stereocaulon tomentosum (ST), Fr.

Usneaceae
  Thamnolia vermicularis (TV), (Sw.) Schaer.

Suborder Peltigerineae

Peltigeraceae
  Peltigera apthosa, (L.) Willd.
  Peltigera canina (PC), (L.) Willd.
  Peltigera canina var. rufescens (PR), (Weiss) Humb.
  Peltigera malacea, (Ach.) Funck
  Peltigera venosa, (L.) Baumg.
  Solorina crocea, (L.) Ach.

APPENDIX B: CONTINUED

Unknowns

- #27 gray crustose species (27)
- #28 yellow crustose species (28)
- #37 (37)