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ANALYSIS OF THE BOREAL FOREST-TUNDRA ECOTONE:
A TEST OF AVIRIS CAPABILITIES IN THE EASTERN CANADIAN SUBARCTIC

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Principal Investigator
Dr. Samuel N. Goward

Co-investigator
Dr. Donald E. Petzold

Department of Geography
University of Maryland
College Park, Maryland

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Introduction

In the fall of 1986 Dr. Samuel N. Goward and Dr. Donald E. Petzold submitted a competitive grant application to the NASA AVIRIS Investigators Program. The intent of this study was to conduct a simple comparison between ground reflectance spectra collected in Schefferville, Canada and imaging spectrometer observations acquired by the AVIRIS sensor in a flight of the NASA ER-2 Aircraft over the Schefferville, Quebec region. The high spectral contrasts present in the Canadian Subarctic appeared to provide an effective test of the operational readiness of the AVIRIS sensor. We had found in previous studies carried out in this location that various land cover materials possess a wide variety of visible/near infrared reflectance properties. Thus this landscape would serve as an excellent test of the sensing capabilities of the newly developed NASA AVIRIS sensor. An underlying hypothesis in this study is that the unique visible/near infrared spectral reflectance patterns of Subarctic lichens could be detected from high altitudes by this advanced imaging spectrometer developed by NASA. Secondly we proposed to investigate the relation between lichen occurrence and as a predecessor to the use of lichens as an indicator of the boreal forest-tundra ecotone dynamics.

The original grant only requested funds for the summer of 1987, to support field studies in Schefferville, Quebec. This grant was accepted for funding and research activities were initiated in June of 1987. During the summer of 1987 a field team of three researchers travelled to Schefferville and remained in residence for approximately a month. Considerable ground spectra and related microclimatic measurements were collected during this time. Unfortunately, technical and operation problems with the AVIRIS sensor and the ER-2 NASA aircraft prevented collection of AVIRIS data over the selected study site. In an effort to accomplish the research objectives additional funds were sought for 1987-88 to continue the study, which were granted in the fall of 1987. Again, in the summer of 1988, a team of two researchers travelled to Schefferville and spent approximately one month carrying out field studies. Again, technical difficulties prevented the operation of AVIRIS over the Schefferville region. In 1988 we requested a no-cost time extension to December 1989 and we delayed final reporting throughout the summer of 1990, with the hope that AVIRIS operations would be rectified prior to that time. This has not occurred. It has therefore not been possible to test the basic hypothesis of this study. There were however several steps accomplished in the ground studies that have established the basis for such a data comparison, if the AVIRIS observations are ever collected. These results are discussed in the following sections

Research Activities

The field studies in Schefferville focussed on two primary objectives: collection of ground spectra to compare with the AVIRIS observations and analysis of lichen/microclimate relations to ascertain the indicator role of lichen species in the SubArctic environment.

Spectroscopy

The spectral reflectance measurements were carried out the a Spectron Engineering SE-590 Visible/Near Infrared spectrometer. This sensor collects contiguous spectra at a nominal 3 nanometer resolution (15 nanometer precision) in 240 spectral band passes extending from 0.38 μm to 1.1 μm . The operational procedures included calibration against a barium sulfate panel. Measurements were collected from a tripod approximately 1 meter above the land surface. The instrument optics were always oriented at 90° from the principle plane of the sun and at 45° from Nadir. This configuration closely approximates near nadir measurements as long as the sun is above 60° solar zenith angle. In the second year, we also experimented with the ultraviolet Spectron sensor but produced inconclusive results. We had hope to employ the Shortwave Infrared sensor (1.1 μm - 2.5 μm) but it was not available for use during this time period.

A summary report of the field spectroscopy was published in *Remote Sensing of Environment* in 1988 (Petzold and Goward, 1988). We were able to document the high spectral contrast present in this subarctic environment. In particular, lichen species display a VIS/NIR reflectance spectra which is relatively unique to these unusual life forms. The unique spectral pattern may be of great value in future global-scale studies of the Northern Hemisphere Boreal Forest-Tundra Ecotone.

Microclimate

If lichen species might provide a useful indicator of growth conditions in the subarctic, the manner in which they vary with microclimate must be better understood. A series of transects were observed in the Schefferville area to characterize the the variations in plant species mix as a function of altitude and aspect in the Schefferville region. Meter quadrants were periodically sampled across the transects. In particular, the proportionate contributions of lichens, mosses and vascular plants under these variable conditions was of fundamental interest.

It was found in general that proportion lichen presence increased with increasing altitude and/or exposure (to wind). This observation confirms that lichen presence is indicative of more "tundra-like" environments. However, observations of north-facing versus south-facing slopes found that lichens are in greater abundance on south-facing slopes whereas mosses increase in north-facing conditions. This suggests that lichen presence is also indicative of more moisture-limited environments under these SubArctic conditions. Thus the role of of lichens as an indicator of the Boreal Forest-Tundra Ecotone is convolved with local to regional soil moisture conditions. This material served as the basis for a Master's Thesis for Ms. Theresa Mulhern and has been published in *Arctic* in 1987 and the *Proceedings of the Eastern Snow Conference*, June 1988.

Conclusion

The combination of the microclimate analysis with the field spectroscopy data provided an excellent basis to examine the AVIRIS observations and assess the potential of using the unique lichen spectra to characterize the local and regional variations in environments which define the Boreal Forest-Tundra Ecotone. Unfortunately the AVIRIS observations were never forthcoming during this study and it was therefore not possible to assess the ultimate objective of this study. We hope that some time in the future acquisition of the requisite imaging spectrometer observations will be possible over the Subarctic vegetation systems present in the Schefferville, Quebec region.

Late in the study period, we did acquire the JPL imaging spectrometer processing software and have implemented it on a HP Unix workstation. We have been prepared for sometime, to process and reduce the AVIRIS observations from Schefferville. We would still take advantage of this opportunity if it presented itself.

One more positive outgrowth of this study has been the funding of Ms. Theresa Mulhern's doctoral work under a NASA Research Fellowship to investigate the potential of using Coastal Zone Color Scanner observations to map the extent and position of the Northern Hemisphere Boreal Forest-Tundra Ecotone. That study was fundamentally stimulated by the research carried out under this grant. As is often the case it is difficult to predict exactly where a particular research study will direct future investigations.

*Final Technical Report - NASA Grant NAGW-1142
Goward/Petzold AVIRIS Investigation*

Appendix A

**Publications and Presentations of Studies
carried out, in part, under NASA Grant NAGW-1142**

ASSOCIATION OF AMERICAN GEOGRAPHERS ANNUAL MEETING PROGRAM

Compiled by Rose Fabia Roberts

Association of American Geographers



**April 21-26, 1987
Portland Marriott and Hilton Hotels
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SUBARCTIC LICHENS: ACHIEVING EQUILIBRIUM WITH THEIR MICROCLIMATIC-TOPOGRAPHIC ENVIRONMENT by Theresa Mulhern, University of Maryland, College Park, Maryland 20742.

De-voicing lichen interactions with climatic/terrestrial environments will contribute to climate-vegetation modelling and encourage studies of lichens as climatic indicators. This research focused on determining relationships between (1) microclimate/topography and lichen distributions; and (2) lichen spectral reflectances and lichen ecology. (*Cladonia stellaris*, in size and water content, reflect microclimatic differences induced by slopes of opposing aspect. *Stereocaulon paschale* and *Cladonia rangiferina* prefer sheltered, mesic sites created by topographic irregularities. High reflectance of *Cladonia* may be a protective mechanism against overheating in exposed environs.

THE ROLE OF CLIMATIC INDICES FOR EVALUATION OF RECENT LOUISIANA FLOODING VARIABILITY. Robert A. Muller and John M. Grymes, Louisiana State University, Baton Rouge, Louisiana, 70803.

Is repetitive regional flooding during recent years in Louisiana associated with landuse and river-basin management or climatic variability? Streamflow data for regional rivers rarely extend back 50 years, but data sets clearly show much higher floodpeaks in recent years. Climatic data sets for the climatic divisions of the National Climatic Data Center have been extended back to the late 19th century. Water-budget modeling suggests that recent flooding is associated with the wettest period of this century. The divisional data sets do not index specific floods on the regional rivers very closely, but they provide additional information for policy and management.

WIND VELOCITY GRADIENTS MEASURED ON A TRANSVERSE DUNE by Kevin R. Mulligan, 2606-C North Tustin Avenue, Santa Ana, California 92705

Vertical and horizontal velocity gradients measured on a transverse dune show that flow acceleration strongly affects the turbulence structure of wind. These findings suggest that calculated values of shear velocity are largely dependent upon the height and location of wind speed measurements, as well as the strength of the prevailing wind. Moreover, if Bagnold-type transport equations are used to calculate rates of sand transport on a dune, wind speeds measured above a height of 0.2 m may underestimate transport on the windward face and overestimate transport near the brink.

THE ROLE OF PLANNERS IN FOSTERING INDUSTRIAL GROWTH FROM WITHIN THEIR LOCAL COMMUNITIES by John R. Mullin, University of Massachusetts (Amherst), 01003 and Jeanne H. Armstrong, President, LandUse, Inc., Hadley, Massachusetts, 01035

The authors' research and action recommendations focus on the pressing need for planners to work for industrial growth from within their communities through aiding the development of "incubator industries", small industrial firms with growth potential. Planners are urged to identify local small industrial firms, to examine their specific problems and prospects, and to initiate economic development strategies that foster growth of small firms that have taken root in their communities. Findings of Incubator Industry Surveys in three Massachusetts communities are summarized, and the link between the gathering of detailed local data and effective action strategies is examined.

RADIOACTIVE WASTE MANAGEMENT POLICY AND THE POTENTIAL FOR LOCATIONAL CONFLICTS IN CANADA. by G. Tomas Murauskas, University of Oklahoma, Norman, Ok. 73019.

The purpose of this paper is to examine radioactive waste management policy in Canada and to assess the potential for locational conflicts given current policy. In the Canadian context procedures for public participation in the siting process have not been carefully contemplated, and procedures for resolving siting conflicts and coping with external effects have not been anticipated. This paper explores the possibility of developing such procedures.

THE EARLY EVOLUTION OF THE HACIENDA IN THE BAJIO REGION OF COLONIAL MEXICO by Michael E. Murphy, University of Texas at Austin, Austin, Texas 78751.

In the Bajio region of colonial Mexico, an early landscape of small, irrigated agricultural properties evolved into a pattern of haciendas similar to that of other parts of Central Mexico with very different early histories. A common denominator may be found in the culture of the Spanish settler, specifically in the fact that the culture lacked an agrarian ethic and was pervaded by a dynamic of class exploitation. One may plausibly infer that the hacienda system took form because it represented a form of landholding consistent with these cultural patterns.

THE STRUCTURE OF MAORI TERRITORY IN NEW ZEALAND by Brian Murton, University of Hawaii, Honolulu, Hawaii 96822

The concept of existential space is used to visually interpret the way in which the Maori of New Zealand structure territory. Emphasis is placed on the location and the spatial layout of the *marae*, a complex which includes a meeting house, dining hall, and an open area. *Marae* are primary centers of meaning in Maori culture and society. Symbolism in the landscape of the *marae* is related to concepts of importance in contemporary Maori society.

BLACK SUBURBANIZATION AND THE METROPOLITAN OPPORTUNITY STRUCTURE by Holly Myers-Jones, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

With the movement of jobs, retail services and other activities from the central city, suburbanizing blacks are moving into a re-structured metropolitan environment. This environment is considerably different from that which existed during the era of widespread white suburbanization. The opportunity structure of a metropolitan region can no longer be defined in terms of a simplistic central city/suburban dichotomy. Black suburbanization is analyzed in a sample of twelve SMSAs with respect to the existing metropolitan opportunity structure. Attention is focused on the relationship between the location of suburban jobs and the selection of particular suburbs by black households.

LAND USE TRANSITION IN THE KANSAS HIGH PLAINS by M. Jerome Noll, Kansas State University, Manhattan, Kansas 66506.

In the Kansas High Plains, intensive cropland agriculture has been strongly influenced by the availability of water for irrigation. Since surface sources are negligible, groundwater from the Ogallala Aquifer is the critical source for irrigation water. Resulting significant depletion of the Aquifer has led to several adjustments by resource managers. In conjunction with implementation of institutional forces associated with passage of the Kansas Groundwater Management District Act, land use strategies are changing. Although there is a trend toward using land for more water efficient crops, this practice does not include abandoning irrigation as a resource conservation space adjusting technique.

MICROCLIMATIC CHARACTERISTICS OF VEGETATION HABITATS ACROSS A BOREAL FOREST-TUNDRA ECOTONE by D.E. Petzold, University of Wisconsin, River Falls, WI 54022, and T. Mulhern, University of Maryland, College Park, MD 20742.

Detailed vegetation and microclimatic surveys of two slopes of opposing aspect across the boreal forest-tundra ecotone of central Quebec-Labrador revealed the existence of four distinct vegetation habitats which were determined by exposure to wind and solar radiation. These exposure conditions affected the distribution of lichens and vascular plants across the ecotone. It appeared that lichen growth was not related to edaphic factors such as soil pH, moisture, and organic content on these slopes. Cetraria nivalis, Alectoria ochroleuca, and Cetraria nigricans reached their maximum density in the most exposed habitat of minimal shrub growth. There, snow depths were less than 30 cm, there was no attenuation of the solar beam, and the aerodynamic surface roughness averaged 1.2 cm. Cladina stellaris ("caribou moss") was ubiquitous and a generalist in habitat preference. Moderately exposed habitats exhibited the greatest species diversity. In that habitat birch shrubs and spruce trees began to dominate the surface vegetation. Their canopy depleted the solar beam by 32% and increased surface roughness to 20.3 cm. The most protected habitat was characterized by the growth of dense birch and alder thickets which reduced solar radiation receipts at the ground surface by 47% and increased surface roughness to 50.2 cm. These conditions promoted the luxuriant growth of mosses while limiting the growth of lichens to openings in the thicket. The data further indicated that slope aspect was a significant factor in determining vegetation growth patterns. Compression of habitats was observed upon contrasting the NNE-facing slope with the SW-facing slope.

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VEGETATION-SNOW DEPTH RELATIONSHIPS IN THE BOREAL FOREST-

TUNDRA ECOTONE OF EASTERN CANADA

by
Donald E. Petzold*
and
Theresa Mulhern

Department of Geography
University of Maryland
College Park, MD 20742

ABSTRACT

Snow depth was found to influence the morphology of plants and species diversity and predominance along a vegetation gradient between a forested valley bottom and the adjacent exposed ridgetop. Upland habitats, with maximum snow depths less than 30 cm, produced the most exposed vegetation communities. These were dominated by a lichen-heath association, stony earth circles, and an absent or poorly developed shrub layer. Strong winds were responsible for snow removal from these sites. At the other extreme, woodland snow depths exceed 100 cm, drifting is common, and snowpacks may persist until early summer. In this most protected environment, vascular plants, particularly well-developed black spruce trees and dense birch thickets, predominate and lichens are virtually absent.

Snow depth variations provide differing microhabitats in which competing vascular and non-vascular plants may develop. In addition to common climatic data, snow depths and distribution are useful tools for the biogeographer and plant ecologist for understanding vegetation dynamics in high latitude environments.

INTRODUCTION

The impact of snow on the earth's surface includes physical, biological and geographical components. The presence of snow on the landscape influences the interaction between the biotic and abiotic realms. Two important characteristics of snow cover are depth and distribution. Snow distribution helps determine the annual energy budget of the

*Present address: Department of Geography, University of Wisconsin-River Falls, River Falls, WI 54022

earth due to its reflectivity of solar radiation; it influences the presence or absence of
1980); and it controls photosynthetic activity and
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earth due to its reflectivity of solar radiation; it influences the presence or absence of certain types of vegetation (Hiltunen, 1980); and it controls photosynthetic activity and seed germination (Richardson and Salisbury, 1977). The depth of snowcover controls the degree of protection provided to plants and animals from harsh winter conditions; it regulates the light environment of underlying vegetation (Richardson and Salisbury, 1977); and it provides insulation from extreme temperature fluctuations by limiting heat losses from the earth's surface.

Snow controls the climatic environment of the subarctic and high latitude regions of the world because it covers the surface for six to ten months of the year. Yet, topographic variations introduce variability in both the distribution and depth of snowcover over a small area. In the eastern Canadian subarctic, the regular ridge and valley topography of the Labrador Trough leads to an observable change in vegetation from wooded valley bottoms to barren tundra ridgetops. During winter, an equally obvious snow depth gradient is evident from ridgetop to valley bottom where the crests are often blown free of snow while the woodlands may be blanketed by as much as 2 m of snow. Such a gradient may occur over a 1 km transect with an elevational drop of only 200 m.

We believe that the correspondence between the observed vegetation gradient and the snow depth gradient in this region is not coincidental. It appears that physiognomic variations, as well as species composition, of the natural vegetation along these topographical transects are related to the presence and depth of wintertime snowcover. Such relationships have been studied in Finno-scandia since the late nineteenth century (Clark et al., 1985) and recent interest has focussed on remote sensing applications to snowmelt hydrology. Relatively little discussion has centered on North American alpine and high latitude regions. Thus, the objective of this paper is to discuss the relationship between vegetation type, species distribution, and snow depth along topographic gradients in the eastern Canadian subarctic. We will also attempt to identify snow depths which are associated with the development of distinct vegetation habitats and species dominances along the vegetation gradient.

DATA AND METHODS

Detailed vegetation surveys were conducted along two slopes of opposing aspect of a ridge located approximately 30 km WNW of the Schefferville, Quebec townsite (54° 48' N, 66° 49' W). The study area is devoid of anthropogenic influences and there was no evidence of recent fire. The vegetation surveys were compiled from five random throws of a 1 x 1 m quadrat at 5 m elevational intervals along the slope transect. The NW-facing slope had 21 sample levels (100 m elevational decrease) along a 600 m transect. The SW-facing slope had 15 sample levels (70 m elevational decrease) along a 400 m transect. The ridgetop was characterized by tundra vegetation (lichens, heaths) and stony earth circles (periglacial features) while open lichen woodland comprised the valley bottoms (see Figure 1). Soils along these slopes are young, poorly developed, acidic, and have a low organic content (Mulhern and Petsold, 1988).

The climate is considered to be continental subarctic and is characterized by low monthly mean temperatures (-22.2° C in January; +12.5° C in July, at Schefferville), a three month growing season, and a mean annual precipitation of 785 mm, of which half falls as snow (Petsold, 1982). Strong and persistent winds prevail over the region, blowing predominantly from the NW in every season.

Surrogate snow data were obtained from two sources: average birch shrub heights and scar levels on spruce tree trunks. Chernov (1985) stated that the tops of birch, willow and alder shrubs growing on the tundra are "trimmed off" due to snow abrasion such that "when the thickness of the snow is measured, ... it reaches exactly the same height as that of the bushes" (p. 57). Thus, we measured the heights of five to ten birch shrubs (based on their abundance) at each sample level to produce an average surrogate snow depth value. A similar effect is observed in the growth habit of mature spruce trees at the

treeline. There, wind blown snow and ice particles completely remove foliage at and immediately above the snow surface, resulting in the development of an elongated scar along the trunk (Marchand, 1987), facing the direction of prevailing wintertime winds (see Figure 2). Foliage below the snow level remains lush and healthy, while unprotected needles exhibit greatest mortality rates (Hadley and Smith, 1986) and bud and branch damage is greatest immediately above the snow level (Scott et al., 1987). It appears, therefore, that the edge of the trunk scar closest to ground level represents the average minimum long-term level of snow cover at each tree. These lower scar levels were measured for every tree growing at the treeline, at elevations upslope from the wooded valley bottoms. There were, however, only 13 mature trees to measure at 9 sample levels along these transects.

Figure 1. Tundra-dominated ridgetop, elevation 705 m a.s.l. (foreground) which grades downslope to a wooded valley bottom, elevation approx.

Figure 2. Abrasion scar on black spruce tree at the treeline in subarctic Quebec. Note the healthy branches at the lower level of the trunk.

RESULTS

1. Correspondence of Surrogate Snow Data Types

Two purposes are served by discussing the relationship between birch shrub heights and tree scar levels as surrogate snow depth data. First, the small number of trees exhibiting abrasion scars produced the need for further evidence of their viability as snow depth indicators. Second, by using two different sources of natural evidence to obtain surrogate snow depth, we can be more certain of the appropriateness of applying these surrogate data to understand vegetation dynamics along these slopes. To assess the correspondence between the two surrogate data sets, a simple linear regression was performed on matched pairs of data for the sample levels where both tree scar and birch height measurements were available. Figure 3 indicates a very close, direct relationship between the two snow depth indicators. The slope of the regression equation suggests an exact correspondence at all levels along these slopes, but there is a constant 5.5 cm growth differential in the birch shrub heights. It appears that both snow depth indicators are comparable and interchangeable; however, the results must be used with caution because of the small number of data pairs used to establish this relationship.

Figure 3. Relationship between mean birch heights (BH) and the lower level of trunk scars (TSL) on trees growing at the tree line between tundra ridgetop and adjacent wooded valley bottoms.

2. Snow Depth Variations Along the Slopes

Average surrogate snow depths are plotted in the scattergrams of Figure 4 for each slope. As expected, snow depths generally increased downslope toward the valley bottom. Birch shrubs did not grow on the crest of the ridge, hence we assume that the ridgetops are blown free of a protective snow layer throughout much of the winter season. A short distance downslope, however, prostrate birch hug the surface, finding complete protection under a snow layer as shallow as 10 cm. Mean annual snow depths approach 1.5 m at the base of the slopes, affording the highest degree of protection to the underlying vegetation.

Generally, snow depths along the NNE-facing slope were less than those along the SW-facing slope. This was particularly evident at mid-slope elevations. Slope orientation with respect to the prevailing NW winds appears not to be a contributing factor because the

Figure 4a. Mean snow depths along the SW-facing slope, derived from birch height and spruce trunk scar data.

Figure 4b. Mean snow depths along the NNE-facing slope, derived from birch height and spruce trunk scar data.

ridge is oriented NW-SE, thus winds generally blow parallel to the ridgecrests in this region. The NNE-facing slope exhibited many more local variations in topography with several terraces occurring along the transect. The step-like terraces triggered snow drifting which introduced noise in the general snow depth-elevation relationship of Figure 4b. We have observed deep, extensive snow packs on the lee side of these terraces, near the bottom of the NNE-facing slope, as late as early-July.

3. Snow Depth-Vegetation Relationships

The distribution of surface cover types and constituent lichen species is presented by Petzold and Mulhern (1987). These data were grouped further by considering the protection afforded by wintertime snowcover/summertime birch canopy development. Four distinct vegetation associations emerged from this grouping. The first category is predominantly a lichen-heath association of upslope-ridge crest locations. This includes a total of nine sample levels along both transects. There, snow depths averaged less than 30 cm and birch shrubs constituted less than 5% of the surface cover. Spruce trees were not observed in this vegetation association. In such an exposed habitat, a mixed lichen mat dominates the surface with 60-70% coverage. Minimal protection from the strong, desiccating, and often abrasive winds is afforded the existant vegetation. Low snow depths and their corresponding lichen-heath vegetation cover are not restricted to upslope locations. Terrace lips along the NNE-facing transect also exhibited similar characteristics, for example at elevations of 660, 670 and 685 m a.s.l., as can be seen in Figure 4b. Such a displacement is not observed on the SW-facing slope.

The second category, low shrub tundra (as defined by Bliss (1981)), is characterized by average snow depths of 20-60 cm. The surface is still dominated by mixed lichens (65-75% coverage); however, birch shrubs and krummholz (dwarfed) spruce are more evident on the landscape. Nine sample levels at mid-slope elevations comprised this category. Although the protective snow cover is deeper and the birch are taller, the surface remains relatively exposed to strong winds and intense solar radiation. The birch-spruce cover, being only 10-15% of the surface, is not sufficient to ensure a stable snow cover from year to year. We believe that this vegetation association may be blown free of snow during part of the winter season. This is based on our observation of an unusually high incidence of branch and bud tip abrasion of the birch shrubs found in this habitat.

Forest tundra (Bliss, 1981), commonly called open lichen woodland, constitutes the third grouping of vegetation-snow depth characteristics. Here, tall birch and mature spruce trees become a dominant component of the landscape, such that the development of a woodland is apparent (tree densities are greater than 10% and shrubs constitute 10-20% of the surface cover). On these slopes, 13 sample levels were included in this category. Snow depths average between 60 and 100 cm and the snow pack persists longer than in any other vegetation association. Because the structure and density of the woodland produces a more protected environment, bud abrasion of the shrub layer is not common. Lichens comprise a smaller (35-60%), but still significant component of the surface cover. These lichens have adapted to more protected, mesic habitats and are dominated by the "reindeer mosses" (i.e., lichens of the genus, Cladonia). The relatively moist, shaded surface beneath trees and shrubs allows the development of a moss carpet which constitutes approximately 25% of the surface vegetation.

The last category, tall shrub tundra (Bliss, 1981), is a relatively small component of the vegetation gradient along these slopes and includes five sample levels. Slope terraces induce drifting which produce mean snow depths of greater than 100 cm. As a result of this protection, vascular plant species predominate and shrubs grow in dense thickets. Such dense shrub growth attenuates solar radiation and prevents ventilation of the surface, thus reducing evaporation. This results in the development of a moist habitat conducive to extensive moss growth and effectively eliminates lichens. Shrub thickets may be associated with spruce woodlands or may develop independent of tree growth.

DISCUSSION

Snow is a climatic agent which is active for half of the year in this subarctic environment; yet, its effects may be experienced by the vegetation throughout the growing season as well. Many of these effects are immediately apparent after a snowfall (i.e., bud abrasion, trunk scarring). Others may be less noticeable, because they are internalized with other climatic and edaptive factors by the vegetation. In this article we are assuming that that birch shrub heights and minimum tree scar levels are a manifestation of both the internal and external impacts of snow on the vegetated surface. Despite the limited sample size of our data set, it appears that both snow depth surrogates contain the same information and are in agreement.

Based on our results, snow depth variations contribute to the competition between vascular and non-vascular (lichen) plant growth. An average wintertime snow depth of less than 30 cm, associated with an unstable snow pack, provides an apparent advantage to non-vascular plants because they are better able to survive the effects of a persistent exposure to abrasive, desiccating winds and to greater fluxes of solar radiation.

There is a dichotomous relationship between snow depth/distribution and the vegetation which grows beneath it. Initially snow benefits the vegetated surface, acting as a protective cover which allows plants to reach their maximum height and development. Once the vegetation achieves equilibrium with the snow microenvironment, the vegetation plays an active role in the depth and distribution of the snow. Trees and dense thickets serve to trap snow and trigger drifting. Such a mutual interrelationship also has been suggested by Clark et al. (1985) for subarctic vegetation in Finland.

This study has implications at the macroscale as well. The changes in vegetation that we observed along these 400 and 600 m transects may be considered analogous to an observable latitudinal-vegetation gradient from the spruce woodlands of Sept-Isles, Quebec (50° N), to the subarctic tundra found on southern Baffin Island at 62° N (Aleksandrova, 1980). In snow-dominated environments of the world, the certainty of surface-based snow measurements is diminished, because of the increased frequency of drifting in treeless or sparsely-treed environments. Therefore the use of surrogate snow data is an additional means of assessing snow and vegetation dynamics in northern latitudes of the world.

ACKNOWLEDGEMENTS

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Reflectance Spectra of Subarctic Lichens

DONALD E. PETZOLD AND SAMUEL N. GOWARD

Department of Geography, University of Maryland, College Park, Maryland 20742

Lichens constitute a major portion of the ground cover of high latitude environments, but little has been reported concerning their *in situ* solar spectral reflectance properties. Knowledge of these properties is important for the interpretation of remotely sensed observations from high latitude regions, as well as in studies of high latitude ecology and energy balance climatology. The spectral reflectance of common boreal vascular plants is similar to that of vascular plants of the midlatitudes. The dominant lichens, in contrast, display variable reflectance patterns in visible wavelengths. The relative reflectance peak at 0.55 μm , common to green vegetation, is absent or indistinct in spectra of pervasive boreal forest and tundra lichens, despite the presence of chlorophyll in the inner algal cells. Lichens of the dominant genus, *Cladonia*, display strong absorption of ultraviolet energy and short-wavelength blue light relative to their absorption in other visible wavelengths. Since the *Cladoniae* dominate both the surface vegetation in open woodlands of the boreal forest and the low arctic tundra, their unusual spectral reflectance patterns will enable accurate monitoring of the boreal forest-tundra ecotone and detection of its vigor and movement in the future.

Introduction

Spectral measurements of reflected solar radiation are becoming an important means of studying terrestrial phenomena (Goetz et al., 1985). The contribution of these measurements to vegetation research is particularly significant, with implications for both mapping vegetation patterns and analyzing the biophysics of vegetation (Kumar and Monteith, 1981; Goward et al., 1985; Asrar et al., 1984). The value of vegetation spectral measurements occurs as a result of the unique spectra that photosynthetically active green vegetation produce. Most earth surface materials display ramplike reflectance spectra, either increasing reflectance with wavelength for soils and common manufactured materials or decreasing reflectance with wavelength for ice, snow, and water (Krinov, 1947; Swain and Davis, 1978). The photosynthetically active components, primarily leaves, of vascular plants (green vegetation) produce steplike reflectance

spectra with low reflectance in the visible spectrum (0.4–0.7 μm), high reflectance in the near infrared (0.7–1.3 μm), and moderate reflectance in the shortwave infrared (midinfrared) wavelengths (1.3–2.5 μm).

At latitudes greater than 50° in the northern hemisphere, lichens, an autotrophic life form based on a symbiotic relation between fungi and algae, become a significant component of vegetation communities and terrestrial land cover. In open lichen woodlands of central and northern Canada, lichens constitute 70% or more of the ground cover observed from above the woodland canopy (Lechowicz et al., 1984). The unusual visual appearance of lichens, ranging from off-white and pale green to grey and black, suggest that lichen reflectance spectra may differ from those of green vascular plants (Petzold and Renee, 1975) and thus affect interpretation of vegetation patterns at high northern latitudes with multispectral observations. Spectra of unspecified crustose rock lichens have

been presented by Satterwhite et al. (1985), and laboratory spectra of lichens have been discussed by Gauslaa (1984). However, the paucity of *in situ* lichen reflectance spectra reported in research literature and their marginal quality (Krinov, 1947; Steiner and Guterman, 1966) led us to carry out field measurements in the Canadian subarctic during the summers of 1984-1985.

Field Site and Measurement Technique

Measurements were taken in the vicinity of Schefferville, Quebec (54°48'N, 66°49'W) with the support of the McGill University Subarctic Research Station. Sampled vegetation communities range

from closed canopy spruce woodlands to open tundra, depending on the elevation and exposure of the site (Hare, 1958; Petzold and Mulhern, 1987).

Two instruments, provided by the Earth Resources Branch, NASA/Goddard Space Flight Center, were used to obtain measurements: a Barnes Model 12-1000 Modular Multiband Radiometer (MMR) and a Spectron Engineering SE-590 Spectrometer. The MMR instrument is an eight-band spectral radiometer (sensing seven reflected and one emitted spectral radiance bands), configured for this experiment with filters matching the spectral bandpasses on the Landsat Thematic Mapper (TM) instrument, as well as one additional spectral bandpass

TABLE 1 Mean and Standard Deviation (SD) of Spectral Band Reflectance (%) of Selected Subarctic Surface Types. Recorded by a Barnes Model 12-1000 Modular Multiband Radiometer

SURFACE TYPE	BAND WAVELENGTH (μm)						
	0.45-0.52	0.52-0.60	0.63-0.69	0.76-0.90	1.15-1.30	1.55-1.75	2.08-2.35
Black spruce							
Mean	2.8	4.7	4.2	15.7	23.5	16.1	9.4
SD	0.3	0.7	0.6	4.0	2.9	4.1	3.8
Dwarf birch							
Mean	3.2	5.6	5.9	30.8	40.9	26.1	12.4
SD	0.1	0.8	1.1	5.4	2.2	1.3	1.0
Exposed soil							
Mean	7.2	9.9	12.2	13.2	16.2	17.0	17.1
SD	0.7	0.8	0.9	0.7	1.1	1.4	1.5
Airport runway							
Mean	7.9	9.4	10.6	11.3	13.6	11.9	16.1
SD	0.6	0.7	0.7	0.8	0.9	1.1	1.3
Mixed lichen mat							
Mean	10.2	12.4	13.9	29.7	45.0	37.4	24.1
SD	1.2	1.2	1.1	2.5	1.5	1.3	1.7
<i>C. stellaris</i>							
Mean	16.4	20.3	23.4	39.4	48.1	36.9	24.4
SD	2.7	2.9	2.8	5.1	4.9	3.1	2.0
<i>S. paschale</i>							
Mean	5.0	10.1	10.8	27.6	38.3	27.4	15.7
SD	0.9	0.7	1.2	1.2	0.5	1.8	1.6
<i>C. cinctatum</i>							
Mean	3.6	5.0	6.7	22.4	44.4	38.0	23.0
SD	0.8	1.2	1.2	2.2	0.9	1.1	0.5

REFLECTANCE SPECTRA OF SUBARCTIC LICHENS

at 1.20–1.30 μm (see Table 1 for band wavelengths). The SE-590 instrument measures 240 contiguous spectral bands, with a nominal bandwidth of 3 nm, from 0.38 μm to 1.1 μm . Since the radiant sensitivity of the silicon detector degrades rapidly past 1.0 μm , reflectance data past that point have not been presented in this analysis. Each instrument was fitted with a 20° field of view lens. [For further instrument description, see Williams et al. (1984).] Measurements were taken under clear sun conditions between the hours of 1000 and 1500 local time. Instrument calibration was achieved by successively viewing a panel of BaSO_4 of known reflectance and the target of interest. Completion of one measurement pair (calibra-

tion plus target) required less than 1 min for each instrument. The instruments were tripod-mounted, raised 2 m above the target, and oriented 90° from the azimuth position of the sun and 45° from the target surface. Once a target was selected, five measurement pairs were collected with variance introduced by shifting the instruments 0.5–1.0 m laterally across the surface, between each measurement. By visual assessment, only sites with complete vegetation cover were selected for sampling. The MMR and SE-590 instruments were positioned such that they viewed similar, but not precisely the same targets. Thus, there may be minor discrepancies between the corresponding data of Figs. 1–8 and Table 1.

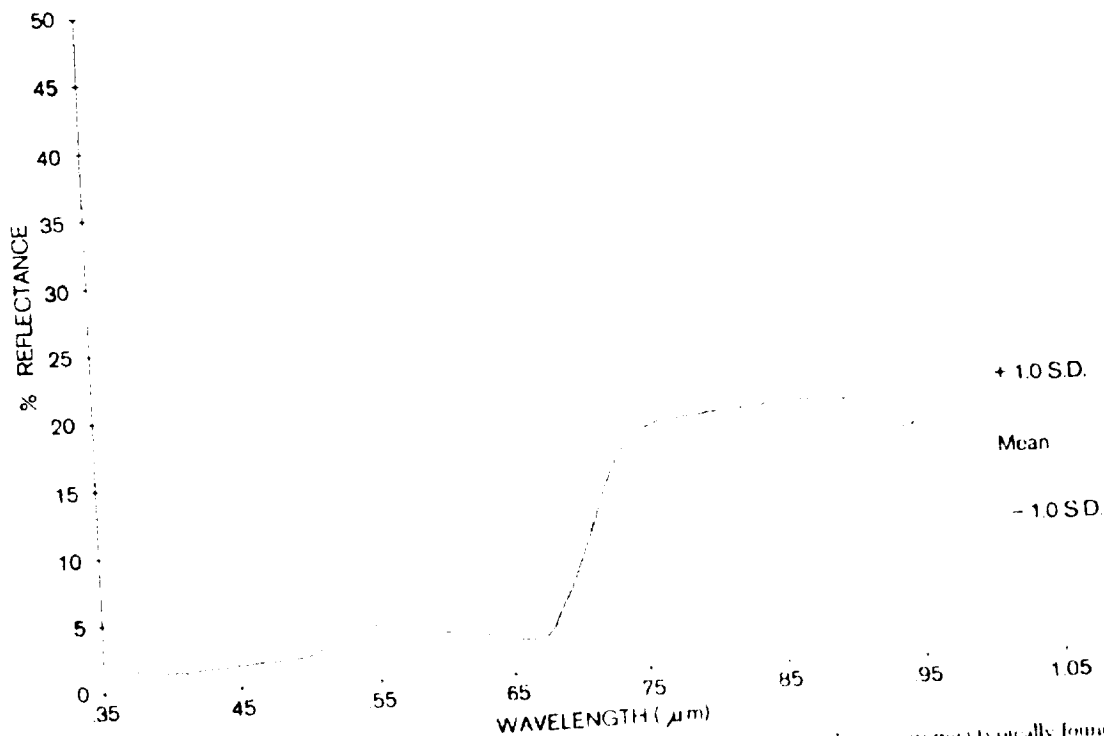


FIGURE 1. Mean and standard deviation of five reflectance spectra of black spruce (*Picea mariana*) typically found in subarctic woodlands of eastern Canada.

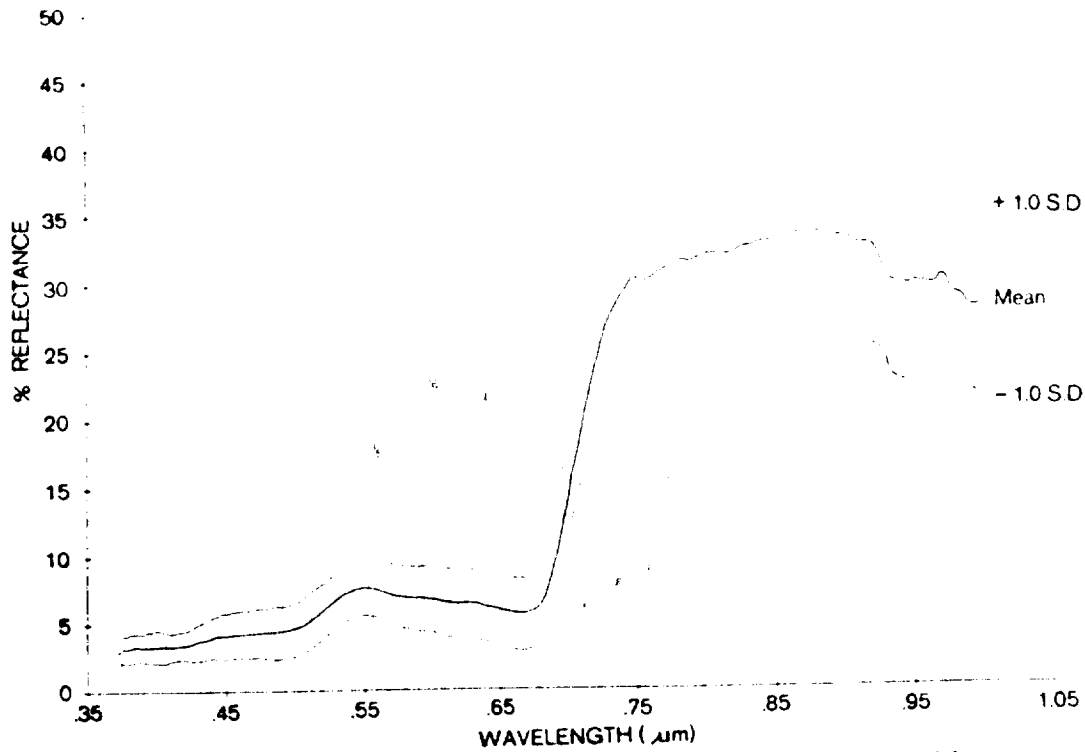


FIGURE 2. Mean and standard deviation of five reflectance spectra of a birch shrub (*Betula glandulosa*) growing on the tundra.

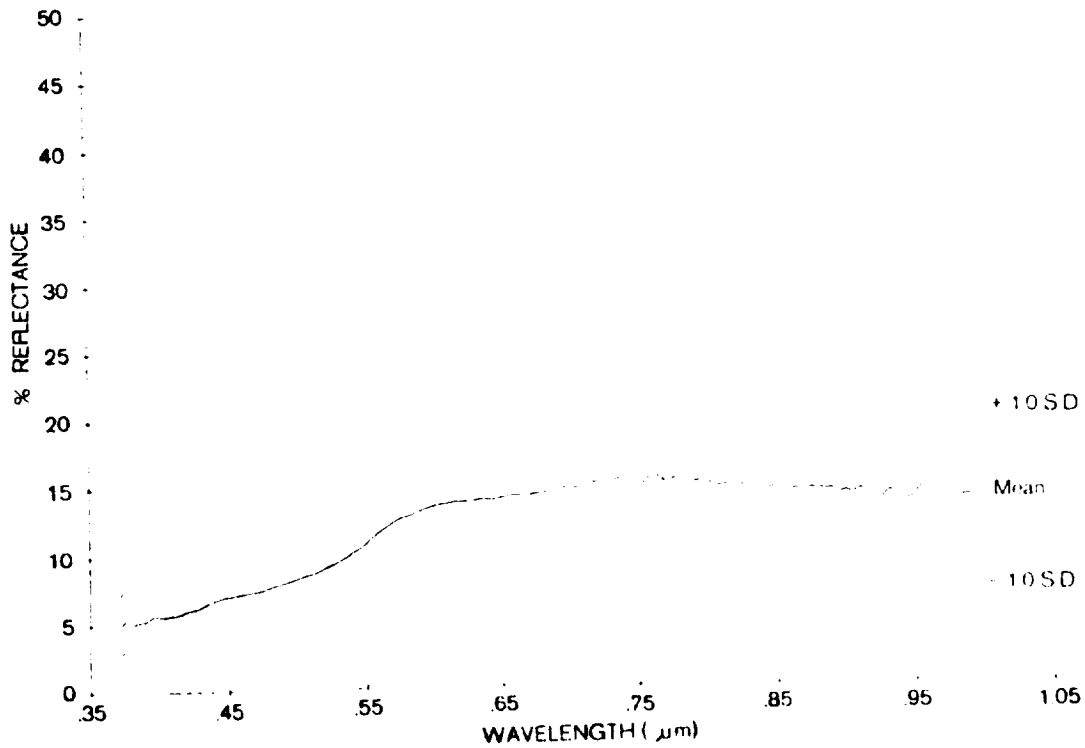


FIGURE 3. Mean and standard deviation of five reflectance spectra of exposed tundra soil of stoney earth circles (Munsell color 5YR3/4-dark reddish brown).

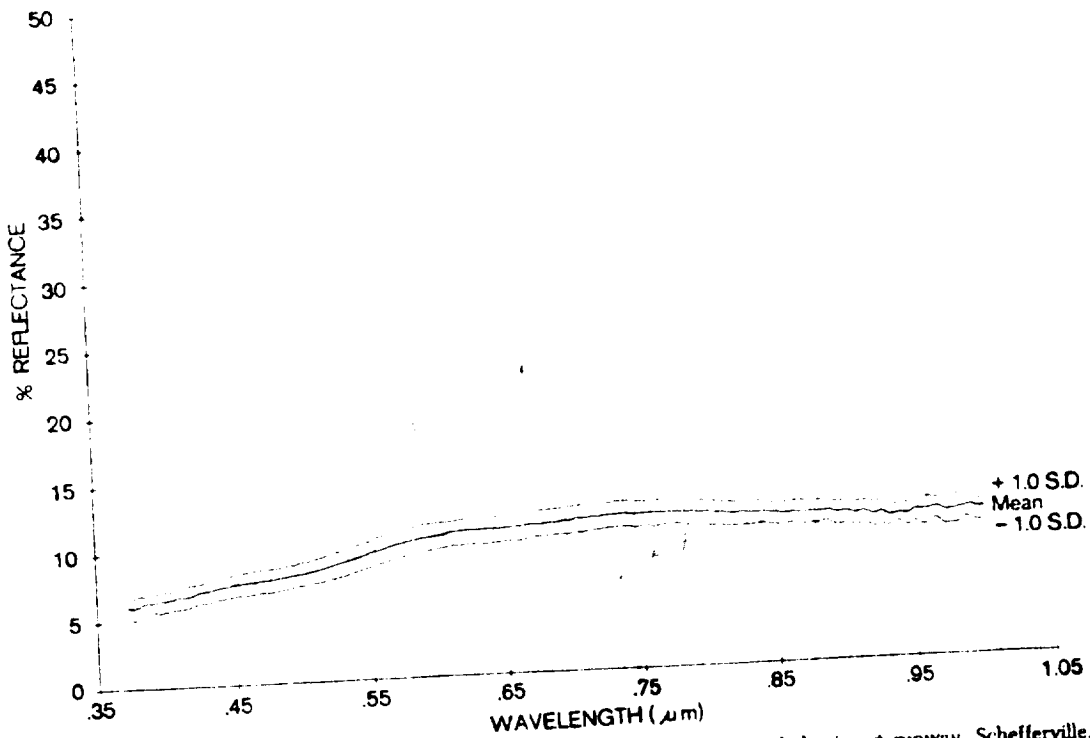


FIGURE 4. Mean and standard deviation of five reflectance spectra of an asphalt airport runway, Schefferville, Quebec.

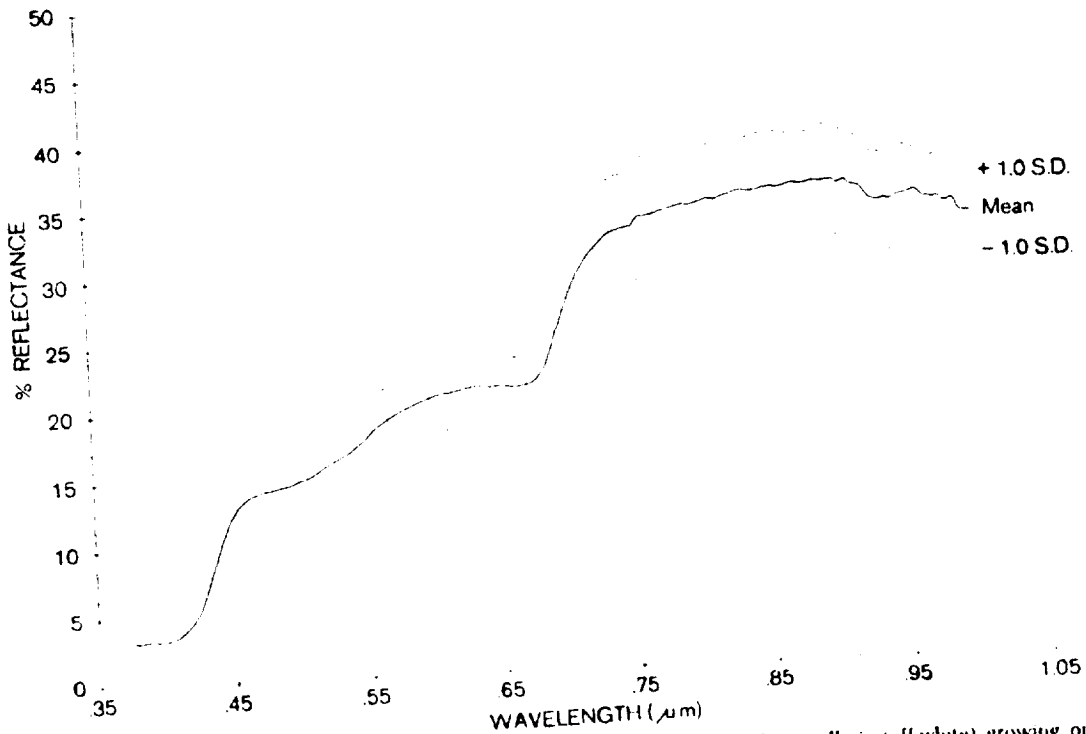


FIGURE 5. Mean and standard deviation of five reflectance spectra of *Cladonia stellaris* (off white) growing on subarctic woodland floors.

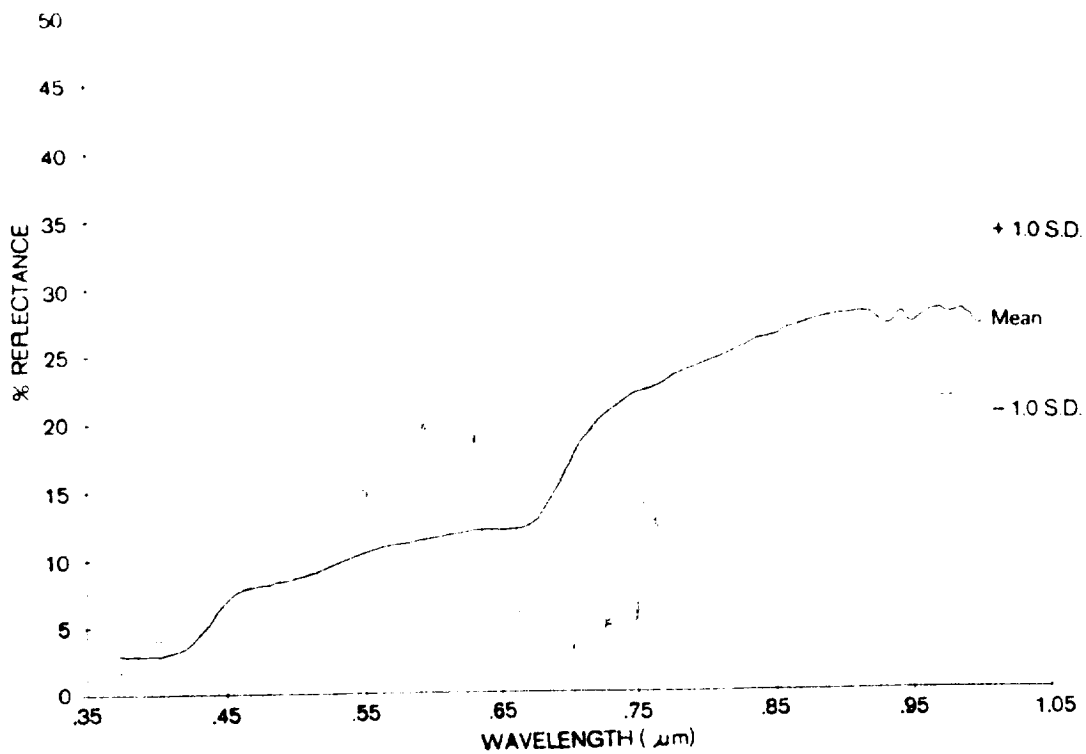


FIGURE 6. Mean and standard deviation of five reflectance spectra of a mixed lichen mat (pale green-yellow) comprised primarily of *Cladonia stellaris*, with scattered *Cetraria nivalis*, and *Alectoria ochroleuca* growing on an exposed tundra ridgetop.

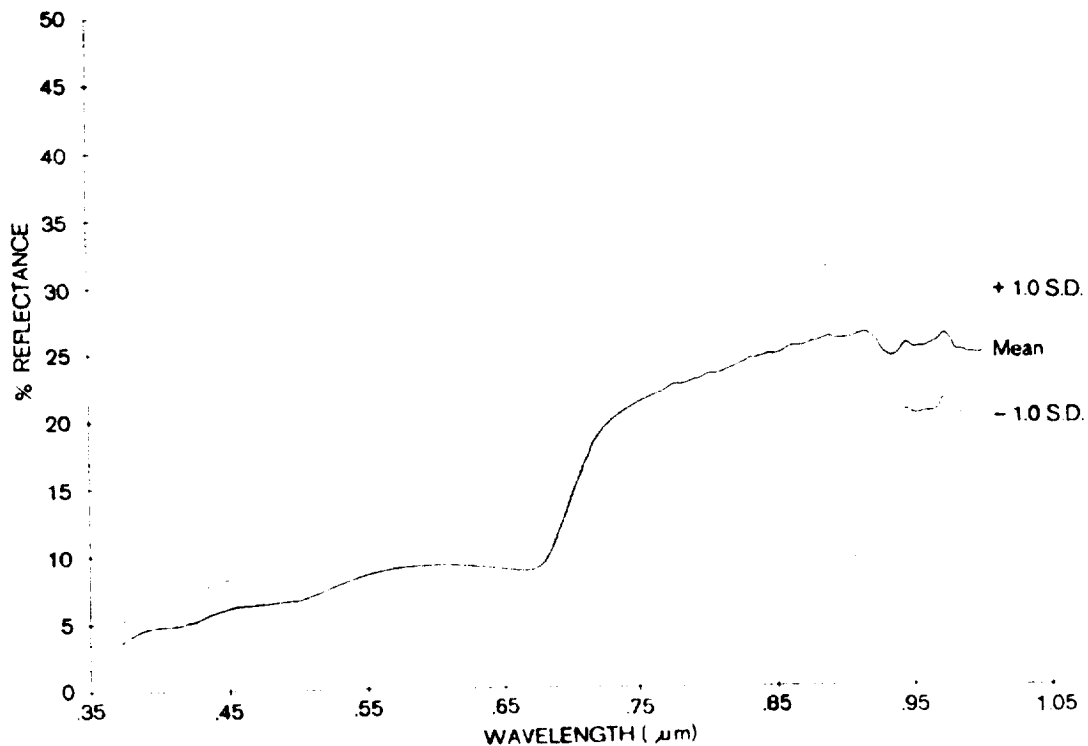


FIGURE 7. Mean and standard deviation of five reflectance spectra of *Stereocaulon paschale* (gray) growing on the tundra in moderately exposed habitats.

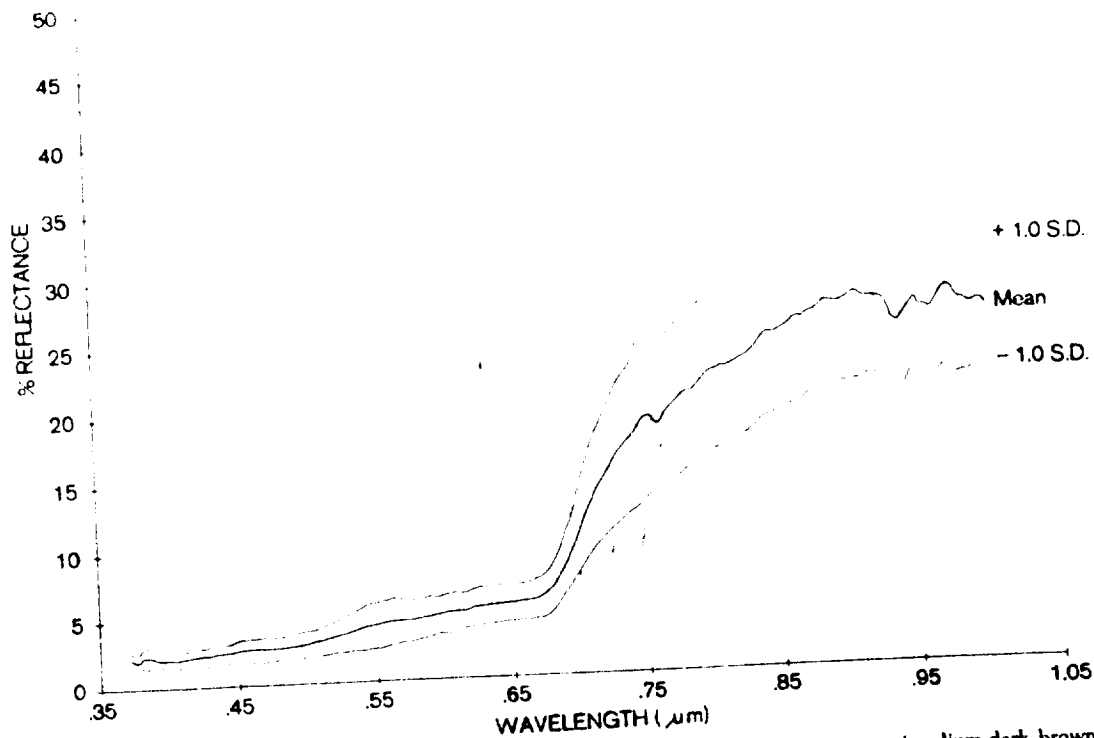


FIGURE 8. Mean and standard deviation of five reflectance spectra of *Cetraria ericetorum* (medium-dark brown) growing on the tundra.

Surface Reflectance Characteristics

Representative SE-590-derived spectral reflectance patterns of major surface covers of the eastern Canadian subarctic, as well as an asphalt runway for reference, are presented in Figs. 1-8. Corresponding spectral band reflectances, observed by the MMR radiometer, are listed in Table 1. Reflectance patterns of typical green vegetation, soil and the Schefferville airport runway (Figs. 1-4) are representative of what has been typically observed in most other landscapes (Ungar et al., 1977; Swain and Davis, 1978; Williams et al., 1984). The only difference among spectra of the sampled green plants is the magnitude of the re-

flectance, not the general pattern of reflectance.

In contrast, the dominant lichens of the genus *Cladina* (Reindeer Moss) are characterized by greater reflectance in the visible wavelengths and a more gradual reflectance increase at 0.7 μm (9-12% increase for lichens compared to a 25% increase for dwarf birch and a 16% increase for black spruce). From 0.7 to 0.9 μm , both *Stereocaulon paschale* and the mixed lichens exhibit similar reflectances, while *Cladina stellaris* reflects a greater proportion of the near-infrared irradiance. However, there is stronger absorption of longer ultraviolet (UV-A) and short wavelength blue energy, as compared to the other visible wavelengths, by the off-

white colored *C. stellaris* (Fig. 5) and the pale green-yellow mixed lichens (Fig. 6), which is predominantly *C. stellaris* with scattered thalli of *Cetraria nivalis*, and threads of *Alcortoria ochroleuca*. The gray lichen, *S. paschale* (Fig. 7), does not display as strong an ultraviolet radiation absorption band, suggesting physiological contrasts between species that may be a function of habitat. A less common but visually distinct tundra lichen, *Cetraria ericetorum* (medium-dark brown), exhibits strong absorption of all visible wavelengths and a gradual reflectance increase at 0.7 μm . However, reflectance in the near and middle infrared wavelengths increases markedly to a level equivalent to or higher than that of the light-colored lichens (Fig. 8, Table 1). For all lichens, the water absorption band at approximately 0.95 μm is less distinct than in vascular plants, indicating lower intercellular reserves of water in lichen thalli growing in a natural air-dried state. This is a common state for most ground lichens. They have no roots and cannot draw soil moisture, so that they dry rapidly after a rainfall.

Discussion

The reflectance patterns of common lichens of the eastern Canadian subarctic are unique; they absorb photosynthetically active portions of the solar spectrum in a manner unlike vascular plants common to environments of lower latitudes. Reflectance differences among common subarctic lichens are due in part to the variable pigmentation of the lichen thallus which we believe to be related to the ecological niches which they occupy in the boreal forest-tundra ecotone. The pigments responsible for coloration are

secondary metabolic byproducts of the fungal component (Hale, 1983); however, most pigments have not yet been identified and their physiological and climatic significance has not been determined (Hale, 1985, personal communication).

Lichens of the shaded woodlands and exposed tundra environments should have different light responses to maintain optimal levels of photosynthesis. It appears that the density of pigmentation of the outermost cell layer of the thallus is inversely related to the level of light energy which is transmitted to the inner algal cells in which photosynthesis occurs (Laudi et al., 1969; Hale, 1983). That is, high levels of pigmentation are an adaptive and protective response of the lichen to high levels of incident solar radiation. A general correlation of heavily pigmented lichens with open habitats has been suggested, although no evidence has been presented to support this (Laudi et al., 1969; Richardson, 1974). Visual inspection of the pervasive *C. stellaris* supports this idea. This species grows equally well in the open tundra as in spruce woodlands of the boreal forest (Petzold and Mulhern, 1987). It appears to be darker, more yellow in color and more compact in structure in exposed habitats, while its podetia (erect, bulblike structure bearing the fungal fruiting bodies) are larger and its color is visibly brighter and pale green in more protected habitats. Certain lichen acids and pigments have been found to increase the opacity of the outer fungal layer, thereby reducing intensities reaching the light-sensitive algal layer (Ertl, 1951). The algal component, *Trebouxia*, of the *Cladinae* may benefit from higher fungal opacity since this alga species seems to tolerate lower light intensities better than nonlichenized algae

(Hale, 1983). This inverse relationship between pigment density and ambient light intensity is supported by results reported by Petzold and Rencz (1975) as well as by the results reported herein.

The *C. stellaris* measurements, exemplified by the patterns shown in Figs. 5 and 6, indicate that they utilize an additional strategy beyond low pigment density for adaptation to low light habitats of boreal woodlands. The *Cladinae* absorb a high proportion (96-98%) of the ultraviolet radiation striking their surfaces. Rao and LeBlanc (1965) found that atranorin, a colorless, fluorescent substance produced by the fungal component, emits energy at a peak of 0.425 μm , corresponding to the absorption component of chlorophyll in the blue wavelengths. This fluorescence is not, however, absorbed by pigments of the outer fungal layer. Thus, this substance appears to support lichen algal photosynthesis by providing fluoresced light in blue wavelengths from intercepted ultraviolet radiation, which is more frequently available in diffuse low light intensities of woodland habitats, as well as under moderate snow covers (Caldwell et al., 1980).

The light-colored *S. paschale* reflects more than twice the ultraviolet radiation of the *Cladinae* (compare Figs. 5 and 7). This may be attributed to the less protected heath-lichen tundra community in which *S. paschale* flourishes. Its habitat is characterized by higher incident fluxes of direct and global solar radiation since it grows near sparsely foliated *Betula glandulosa* (a birch shrub) of less than 1.0 m in height on the treeless tundra; however, it rarely grows completely unprotected by a vascular plant canopy.

Dark pigmented lichens of the open tundra exhibit low albedos (Petzold and

Rencz, 1975). These habitats are subject to perhaps the most severe climatic stress found in the boreal zone. Between latitudes 52°N and 56°N tundra is confined generally to barren ridgetops and is subject to lower temperature, high solar radiation intensities, and strong winds, which effectively remove protective snowcover. The extremely low reflectance, and thus strong absorption of *C. ericetorum*, in the visible and near-infrared wavelengths (Fig. 8), appear to be an adaptation to ensure adequate heating of the lichen thallus under stressful environmental conditions of rapid sensible heat loss associated with persistent, strong winds and low temperature.

Conclusion

The reflectance spectra of lichens differ from that of vascular plants in the visible portion of the solar spectrum apparently as a result of their symbiotic character and resultant photosynthetic system. More research is needed to evaluate the nature and purpose of lichen fungal pigmentation in lichen photosynthesis and physiology. Lichens exhibit a stepped reflectance pattern similar to green vascular plants; but the depth of the visible-near-infrared step is characteristically smaller, and there is a greater contrast in visible and ultraviolet reflectances of the dominant lichens.

These differences between lichens and vascular plants will affect spectral vegetation indices, such as the normalized difference vegetation index (NDVI), which contrasts near infrared and visible spectral reflectances (Goward et al. 1985; Norman, 1986). For example, the increasing significance of lichens in vegetation communities north of 50° latitude may in

part explain the steep gradient of decreasing spectral vegetation index values observed at high latitudes on the North American continent (Goward et al., 1985). That is, a completely lichen-covered surface may produce NDVI values which could be interpreted as a sparse cover of green vascular plants. The shortest band-pass wavelengths of the Landsat TM (0.45–0.52 μm) do not adequately capture the contrasts between lichen and green vascular plants to remedy this confusion between complete lichen ground cover and partial vascular plant ground cover. This points to the need to deploy new terrestrial sensor systems through which such contrasts may be observed.

The value of such observations may be appreciated in the context of current forecasts for global climate warming (Hansen et al., 1981). In addition to their relative abundance (and in some regions, dominance) in northern ecosystems, it appears that boreal and low arctic lichens, particularly of the genus *Cladina*, may be sensitive indicators of climate change of the regional scale or larger. While well adapted to moderately dry, cool, low light climatic conditions of woodlands (Carstairs and Oechel, 1978), *C. stellaris* and other *Cladinae* would not be able to tolerate warm, moist and/or high light conditions, caused by large-scale, long-term climatic change. Their death or deterioration would result from change toward warmer, wetter conditions since fungal hyphae live off sugars produced by the associated algal cells, and, in a continually moist environment, the fungi become too active and eventually kill off the algae through parasitism (Hale, 1985, personal communication). It appears that the perfect environment for lichen

domination of the boreal woodlands is one which is cool and mesic to allow a balanced metabolism by the fungal component. A marked trend toward regional warming and increased summer rainfall should cause a rapid degradation of the lichen understory of the boreal woodland and an apparent retreat northward of the boundary of the lichen understory with replacement by herbaceous species currently found southward of 52°N in central Quebec-Labrador. If climate warming is to occur, the greatest temperature increases are predicted to occur at high latitudes (Hansen et al., 1981). Some of the earliest ecological evidence of climatic change should be apparent in changes in the vigor and distribution of lichens in subarctic regions. Current knowledge of the functioning and distribution of arctic and subarctic ecosystems is limited. Remotely sensed observations in the appropriate spectral wavelengths should greatly improve this knowledge.

The unusual spectra of lichens offer the possibility of using multispectral observations to conduct detailed studies of subarctic and arctic ecosystems. In particular, the unique absorption pattern observed in the ultraviolet and blue wavelengths for the dominant *Cladinae*, in contrast to their visible wavelength reflectance, should provide sufficient information to identify the substantial presence of lichens in vegetation communities with spectral measurements. Together with their pervasive growth in open boreal woodlands today, the spectral reflectance patterns of these lichens will enable accurate monitoring of the boreal forest-tundra vegetation gradient and detection of its vigor and movement in the future. However, most current satellite observing

systems are not suited for such research because the spectral bands observed do not include the near ultraviolet and blue spectral regions necessary to identify the dominant *Cladinae*. Future sensors, such as the HIRIS and MODIS instruments proposed for the EOS (Earth Observing System), may remove this limitation if the appropriate spectral and radiometric configuration is implemented (NASA, 1986).

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Habitat Exposure and Predominance of Natural Vegetation
Along an Elevational Gradient in the
Boreal Forest - Tundra Ecotone of Central Quebec-Labrador

by

T. Milharn & D.E. Petzold¹

Department of Geography
University of Maryland
College Park, MD 20742, USA

¹Present address: Department of Geography,
University of Wisconsin-River Falls
River Falls, WI 52044, USA

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ABSTRACT

Detailed vegetation surveys of two slopes of opposing aspect across the boreal forest-tundra ecotone of central Quebec-Labrador revealed the existence of four distinct exposure habitats which affect lichen distributions. However, lichen growth was not related to edaphic factors, such as soil pH, moisture, and organic content on these slopes. *Cetraria nivalis*, *Alectoria ochroleuca* and *Cetraria nigricans* reached their maximum density in the most exposed habitat of minimal shrub growth, while *Cladina rangiferina* was more abundant in the more protected environs of the woodland. *Cladina stellaris* was ubiquitous and a generalist in habitat preference. The moderately exposed lichen shrub - lichen woodland exhibited the greatest species diversity. The data further indicate that slope aspect is a significant factor in determining vegetation growth patterns. Compression of habitats was observed upon contrasting a NNE-facing slope with a SW-facing slope.

Nomenclature follows R.S. Egan 1987. A fifth checklist of the lichen forming, lichenicolous, and allied fungi of the continental United States and Canada. *Bryologist* 90: 77-173, for lichens; H.A. Crum, W.C. Steere & L.E. Anderson 1973. A new list of mosses of North America north of Mexico. *Bryologist* 76: 85-130, for mosses. The herbarium of the McGill University Subarctic Research Station, Schefferville, Quebec, Canada was consulted for vascular plant identification.

INTRODUCTION

The preeminent role of climate in the natural distribution of vegetation is a fundamental principle of phytogeography. This principle has served as the basis for the development of climatic-vegetation classifications such as those of Köppen, Thornthwaite, and Holdridge (Tuhkanen 1980). Köppen (1900) suggested that plants may serve as meteorological instruments, representing an integration of several climatic elements. Due to the regularity of the ridge and valley topography of the Labrador Trough, a topographically induced vegetation gradient characterizes most of the slopes of the region. Vegetation-climate interactions at this latitude result in the development of arctic tundra at its southernmost extent in the northern hemisphere (Ahti 1977; Aleksandrova 1980).

The significance of such a topographically induced vegetation gradient must not be underestimated. Indeed, the extreme change in vegetation, from flora typical of boreal forest to that of the tundra, along a relatively small ground distance, such as 400-600 m transect, may be regarded as analogous to a much longer, latitudinal vegetation gradient. This altitudinal change corresponds to the change in vegetation which occurs between 51° N and 64° N: spruce forest typical of the southern boreal forest near Sept-Îles, Quebec, grades into vegetation typical of the middle belt of the subarctic tundra, as found on South Baffin Island (Aleksandrova, 1980). The existence of the small scale latitudinal vegetation gradient is well-documented (e.g., Köppen 1900, 1936; Thornthwaite 1931, 1948; Holdridge 1947, 1966; and for Quebec-Labrador, Hare 1950; Hustich 1939, 1979; Payette 1983; Rousseau, 1968). In contrast, detailed study of topographically-

induced, large scale vegetation gradients in the eastern Canadian subarctic is lacking, although such study would enable close scrutiny of the interaction between the biotic and abiotic realms.

A transect from valley bottom to adjacent ridgetop allows one to observe the diminished stature and presence of boreal floristic elements until only relict islands of spruce woodland or prostrate branches of krummholz birch remain in scattered pockets, sheltered by micro-relief from harsh climatic conditions. Concurrently, and in contrast, the presence and prevalence of the non-vascular plant form, lichen, increases from valley bottom to ridgetop. The dominance of lichens is notable in that, to the human eye, the most predominant species, *Cladina stellaris* (which has habitat affinities ranging from open woods to tundra), appears very bright, and may be mistaken for summertime snow in the subarctic landscape (for example, Figure 1). Although *C. stellaris* is the most prevalent lichen in northern Quebec-Labrador, its photographic brightness (Figure 1) conceals the presence of a variety of other lichens such as the gray *Stereocaulon paschale* (arctic-boreal affinities); the dull gray *Cladina rangiferina* (arctic-temperate affinities); the powdery straw-yellow *Cetraria nivalis* (arctic-alpine and boreal affinities); the yellow-green *Alectoria ochroleuca* (arctic-alpine affinities); and the black lichen, *Cetraria nigricans* (low arctic affinity). Although other regions of the boreal forest-tundra ecotone may be characterized by other plant associations (e.g., moss, larch, willow), the greatest interest here is in the unique domination of the light colored, terricolous lichens. Support for such focus may be found in Aleksandrova (1980), as she noted the prevalence of a well developed ground cover of lichen in the Labrador province of the subarctic tundra.

To understand the change in vegetation-type predominance from boreal to mesothermic species, an energy balance perspective may provide unique and useful insights into the definition of distinct exposure habitats. Such an approach would entail consideration of habitat preferences of dominant lichens by considering their tolerance of exposure to or protection from solar irradiance. Therefore, the objective of this paper is to define exposure habitats which will provide greater understanding of the transition between vascular and non-vascular (lichen) plant domination along the vegetation gradient in the boreal forest-tundra ecotone.

STUDY AREA AND RESEARCH METHODS

The setting for the research is a geologically young and climatically rigorous landscape near Schefferville, Quebec (54° 48' N, 66° 49' W). The region is situated in the Labrador Trough of the Canadian Shield. The landscape is characteristic of former glaciation, with gently rolling ridge and valley topography, oriented northwest to southeast, and a predominance of glacial lakes. Deglaciation occurred about 6,000 years BP, and therefore young, acidic and nutrient poor soils prevail. The regional climate is characterized by low monthly mean temperatures (-22.2° C in January, and 12.5° C in July), a three month growing season, and a mean annual precipitation of 785 mm, of which almost half falls as snow (Petzold 1982). Winds are strong and persistent, averaging between 3.5 and 6.0 m sec⁻¹ throughout the year, flowing predominantly from the NW in every season; there is no calm season. Ridgetops above 700 m in elevation are typically underlain by discontinuous permafrost. Lichen-heath tundra is associated

with cold, exposed ridgetops while lichen woodland dominates valley bottoms (Petzold & Mulhern 1987).

Upon completion of a thorough investigation of potential study sites, two transects were identified which represented a transition from a wooded valley bottom to an adjacent lichen-heath tundra ridgetop. These research areas, studied during July of 1986 and 1987, were: Transect I, a 400 m long, SW-facing slope along Boundary Ridge in Labrador; and Transect II, a 600 m long, NNE-facing slope along Boundary Ridge in Quebec. The transects were approximately 30 km WNW of the town of Schefferville, Quebec, in a natural setting, undisturbed by fire and devoid of anthropogenic impacts. The transects complement each other as they represent opposing aspects of the same ridge and have mean slope inclinations of 12.1° and 12.4° , respectively.

The methods employed for site selection along the transects and in vegetation analysis are detailed by Petzold & Mulhern (1987). Simple survey techniques identified data sample levels at every 5.0 m decrease in elevation from the ridge crest such that there were 15 sample levels along the SW transect and 21 along the NNE transect. Five throws of a wooden 1 x 1 m quadrat, along the elevational contour, were used to define individual data sites at each sample level. Using a quartered quadrat for scale, ground cover percentages were estimated, and the presence, height and type of shrub/tree shelter were noted.

Other vegetation data collected at the sites included mean podetial diameters of *Cladina stellaris* (at the widest point of the podetium for 30 replicates per sample level); scar lengths on spruce tree trunks and the average heights of birch (*Betula glandulosa*) and alder (*Alnus crispa*) shrubs,

which were used to as surrogate data to determine mean winter snow depths (Scott et al. 1987; Chernov 1985).

Wind and solar irradiance data were collected at one representative site in each habitat. Casella anemometers with 12.7 cm cups were placed at heights of 50, 100 and 175 cm above the surface of the lichen, moss and/or herb layer. Wind speed data were collected at half hour intervals for four to five days in each habitat. From these data, representative surface roughness lengths, Z_0 , could be calculated following a procedure discussed by Sellers (1965). The value, Z_0 , is the level above the surface where the wind speed is theoretically reduced to zero by the roughness or structure of the surface. Solar irradiance was measured in an open, unobstructed location near the study site (K_+) and simultaneously at the level of the surface vegetation (K_f) to determine depletion by the shrub and tree canopy ($1-K_f/K_+$). Two recently calibrated Lintronic Dome Solarimeters, sensitive to solar irradiance in the wavelength range, 0.3 to 3.5 μm , were used to collect these data at half-hourly intervals over a four to five day period in each habitat type.

At each site a soil sample was extracted and placed in a sealed plastic bag (15 x 20 cm). Soil depths rarely exceeded 3 cm before rock was encountered; however, deeper soils were encountered in the valley woodlands. In the laboratory, fresh weight, oven-dried weight (oven temperature, 105°C) and baked weight (oven temperature, 500°C) of the soil samples were determined, in accordance with procedures outlined in Hesse (1971), so that soil moisture and organic content could be calculated.

Live lichen samples were collected from each site for the analysis of relative water content. The lichens were weighed three times to determine

their fresh, turgid, and oven-dried weights. Relative water content was then calculated as discussed by Slatyer (1967).

To study community diversity along the transects, diversity indices or weighted measures of species proportions were employed. Pielou (1975) observed that community diversity is dependent upon both the number of species present and the relative proportions of those species. Thus, two ratio techniques were employed to derive types of phytospectra which would reflect both of these considerations. These ratios were:

$$RSC = Sx_i / \sum Sx_{\Sigma i} \times 100\%$$

where RSC = relative surface cover of one surface cover type

Sx_i = percent of surface cover "x" in habitat i

$Sx_{\Sigma i}$ = percent of surface cover "x" in all habitats;

and $PSC = Sx_i / \sum Sx_i \times 100\%$

where PSC = proportional surface cover

$\sum Sx_i$ = the sum of all surface covers in habitat i.

These ratios represent the proportions of species present at each sample level belonging to each habitat as they were computed from mean values of percent surface cover for each sample level for both traverses. Classifying the results of equations (1) and (2) in conjunction with other vegetation characteristics enabled the definition of distinct vegetation habitats along these slopes.

VEGETATION HABITAT DEFINITION

BACKGROUND

Traditionally, vegetation habitats have been defined by the natural

environment which supports a certain association of flora. From the time of Humboldt (1807), climatic conditions have been considered in the development of habitat types. However, it is usually a predefined vegetation unit or community which is linked to certain general growth conditions that are able to support the vegetation (e.g., Hasse 1986; Table 1). While the establishment of such links are not inaccurate or inappropriate, we believe that a consideration of surface vegetation's exposure to prevailing winds and solar irradiance, the ultimate supplier of energy to the earth-atmosphere system, may determine a priori the development of certain vegetation types and tendencies of species to form associations. It is evident that surface utilization of available solar irradiance and exposure to wind will also influence, either directly or indirectly, the following: sensible heat flux to the air (thus air temperature); evapotranspiration (thus moisture content of the vegetation and air above it); soil moisture; organic decomposition rate; soil temperature (thus soil microfaunal activity); etc. These conditions together may determine the environment in which certain species grow. However, such a simplistic view of the importance of exposure neglects the influence of other preexisting conditions such as the underlying geology, soil type and chemistry, and surface/subsurface drainage. Such edaphic factors may be important locally. For example, a flat slope terrace will capture sufficient soil moisture to allow the dense, luxuriant growth of a birch thicket amongst low shrub tundra on adjacent steeper slopes. Though the growth of such a thicket is not induced by climate, its presence will affect the distribution of solar irradiance at and the wind exposure of the ground surface beneath. There, diminished fluxes of available solar

irradiance will influence the vegetation species capable of developing at the ground level.

Along these slopes, lichens dominate the surface cover (54%) while vascular plants comprise 27% of the surface and mosses, 15%. Exposed soil and rock account for the remaining 4% of the surface cover; however, they occur most frequently at the highest elevations due to the development of stoney earth circles associated with underlying permafrost (Annersten 1964). Furthermore, lichen cover decreases downslope as vascular plant (particularly birch shrub) and moss growth increases (Petzold & Mulhern 1987). The definition of vegetation habitats along these transects which cross the boreal forest-tundra ecotone will focus on the prevalence of terricolous lichens¹ in relationship to surface exposure to wind and to solar irradiance. Details of the vegetation distributions along these transects is provided by Petzold & Mulhern (1987). The purpose here is to delimit habitats by analyzing vegetation characteristics at each of the sample levels along the two slope transects.

The abundance and size of birch shrubs were the primary diagnostic elements for the development of habitat definition. These characteristics of birch shrubs were chosen because (1) they grow at all elevations along these slopes and become more abundant downslope; (2) their proportion of the surface cover is inversely related to that of lichens (Petzold & Mulhern, 1987); and (3) birch shrub heights reflect maximum wintertime snowcover and

¹Crustose saxicolous lichens are not reported. Exposed rock surfaces comprise about 2% of the ground cover along these slopes and not all rocks are lichen covered. Thus, saxicolous lichens constitute an insignificant proportion of the vegetation in the region.

thus indicate relative exposure to abrasive, dessicating, and cooling winds (Chernov 1985). The relationship between birch heights and elevation along the opposing slopes is shown in Figure 2. Although scatter is caused by the microrelief of a terraced landscape, the downslope increase in birch heights is consistent along both slopes. The calculated regression lines are plotted to help visualize the individual relationships; however, corresponding equations and other statistics are meaningless, so they are not given. Not only do birch heights increase downslope, but the girth, leaf density and number of plants are also noticeably greater. This is the result of decreased wind, greater protective snow depths, and warmer effective temperatures at lower elevations.

HABITAT CATEGORIES

Four exposure habitats were observed along these slopes. The criteria used for their definition are presented in Table 1. The most exposed habitats were found at the highest elevations of the ridge, including the crest; however, they were not limited to those elevations. Habitats which afforded least protection for the surface vegetation had such sparse shrub growth that it was not evident on the landscape as shown in Figure 3. The few shrubs here were very low growing or prostrate and had relatively few leaves. Such conditions are typical of the circumpolar low arctic. The correspondence of the exposed habitats with the ridgetop is the direct result of strong, prevailing NW winds blowing the crests free of a protective snowcover. Shrubs protruding above the scant upland snowcover would be exposed to cold, drying air and would have their growth buds pruned by wind abrasion, thus producing the observed birch growth characteristics. The

pattern of snow cover also determines the distribution of plant communities through its effects on soil moisture and the disposition of solar irradiance (Webber 1974). Ridgetops in this region with no or minimal snowcover and elevations above 700 m are usually underlain by permafrost, thus assuring cold soil temperatures throughout the year. It appears then, that exposed habitats will be cooler, drier, windier and will have greater solar receipts year round. This is corroborated by the low surface roughness length and lack of irradiance depletion associated with this habitat (see Table 2, data columns 4 and 5). These data indicate that the total flux of solar radiation is available to the surface vegetation, and turbulent eddies, which are responsible for sensible heat, water vapor and momentum exchanges between the surface and overlying atmosphere, come closer to approaching the surface vegetation than in any other habitat. On the north-northeast-facing slope, the exposed habitat may be found farther downslope (as noted by the larger sample level numbers) than on the southwest-facing slope.

A short distance downslope, moderately exposed habitats were observed. Noticeably denser, taller birch growth characterized this habitat, although pale colored lichens common to the exposed tundra continue to dominate the surface vegetation. The surface is still exposed, but the birch shrub cover increases from 5 to 15 percent with an average height of about 0.5 m (see Figure 4). In response, the calculated surface roughness length increases and 12 percent of incident solar irradiance was attenuated by the birch shrubs as noted in Table 2. The vegetation typical of these moderately exposed conditions is described by Bliss (1981) as low shrub tundra of the low arctic.

In moderately protected habitats, the introduction of trees to the landscape indicates a noticeable visual change in the vegetation (Figure 5) as well as a substantial increase in surface protection. In addition to sparse tree growth, birch shrubs continued to increase in size and density, approaching 1 m in height and 20% surface cover. The increased density of the tree and shrub canopy produced a dramatic, almost threefold increase in both the surface roughness and irradiance depletion (Table 2). With turbulent eddies unable to approach the surface, evaporation from the surface vegetation is reduced, so the vegetation (and the soil beneath) remains moist and shaded. These conditions provide moderate protection for the low growing surface vegetation (see Table 1). Pale colored reindeer lichens still comprise a substantial portion of the surface (30-45%) and remain visually distinct. Total lichen cover, however, decreased substantially from that of either of the exposed habitats. This habitat is associated with the northern boundary of the boreal forest, approaching the tree line, and is often termed open lichen woodland or forest tundra (Bliss 1981; Payette 1983).

The most protected habitats (Figure 6) consist of dense shrub growth which may or may not be associated with spruce woodland. There were relatively few occurrences of this habitat along the transects, where they were found on flat terraces along the lower levels of the slopes. The terraces interrupted surface and subsurface drainage which produced increased soil moisture and dense vascular plant growth. The synergistic effect of such verdant plant growth also helps maintain high levels of soil moisture. This results from the 150% increase in surface roughness produced along the gradient between the moderately protected and protected habitats. Such

conditions are detrimental to the growth of many lichens, since abundant moisture may cause rapid food consumption by the fungal component with cannibalization of the algal component (Hale 1985). In this habitat, lichen growth is minimal. Low surface light levels (solar irradiance depletion approaches 50 percent at ground level) also may prohibit lichen growth (see Table 2). Only *Nephroma arcticum*, a hygrophilous, foliose lichen, grows well over moist hummocks and moss, beneath trees and dense shrubs. The step-like topography of the terraces also induces snow drifting (in late June, 1986 and early July, 1987 several deep, extensive snow patches were present on the terraces of the NNE-facing slope). Such deep snow would protect the shrubs from bud abrasion, allowing them to attain dense growth in excess of 1 m in height.

SURFACE COVER PREDOMINANCE IN DIFFERENT EXPOSURE HABITATS

GENERAL TRENDS

The proportional surface cover data (Tables 3 and 4) for the four general surface cover types (lichen, moss, vascular plants, soil/rock), reveal distinct variations in surface cover predominance based on habitat exposure. Along the southwest-facing slope, lichens dominate in exposed and moderately exposed habitats, moss cover peaks in the moderately protected habitat, vascular plants prevail in the protected habitat, while exposed soil and rock are common only in the exposed and moderately exposed habitats. The north-northeast-facing slope exhibits similar habitat exposure related predominances; however, the trends are more pronounced among the surface covers, with the exception of moss cover. For example, there is a

steeper gradient in total lichen cover from the moderately exposed to the moderately protected habitats. Further example of the more pronounced gradation in surface cover is evinced by vascular plant and exposed soil/rock cover. Vascular plant cover increases substantially in the protected habitat (e.g., as demonstrated by the relative surface cover of *B. glandulosa* in Figure 7f), while exposed soil/rock cover decreases rapidly from the exposed to the moderately exposed habitats. Although moss is prevalent in the moderately protected and protected habitats on the north-northeasterly transect, this exposure preference is much more apparent on the southwest-facing slope.

TRENDS OF SELECTED SPECIES

The most habitat specific lichens (*A. ochroleuca*, *C. nigricans*, and *C. nivalis*) are most abundant in the most exposed conditions, as illustrated in the plots of relative surface cover in Figure 7 a, b, c. The less common *N. arcticum* is also habitat specific to protected habitats along these slopes. Members of the first three species are a major component of surface vegetation and form an integrated lichen mat together with *C. stellaris* on the open tundra. The development of such a homogeneous mat leads to the appearance of uniform brightness, as seen in Figure 3. In this habitat, the most notable deviation in surface brightness occurs as a result of the sporadic presence of stoney circles which are often bordered by the black lichen, *C. nigricans*, and scattered vascular plants.

Several vascular plants grow in or next to the lichen mat, but their occurrence is scattered. They include prostrate branches of *B. glandulosa*, as well as low-growing heaths such as *Empetrum nigrum* (black crowberry),

Arctostaphylos alpina (alpine bearberry), *Phyllodoce caerulea* (mountain heath), and *Vaccinium vitis-idaea* var. *minus* (mountain cranberry). Occasionally small tufts of *Diapensia lapponica* and individual plants of *Rubus chamaemorus* (cloudberry) may be found. *Lycopodium annotinum* var. *pungens* (bristly clubmoss) is scattered amongst lichens or under birch shrubs. Bryophytes are uncommon in this habitat due to the low availability of moisture; however, *Racomitrium lanuginosum* may grow near stoney earth circles or rock outcrops. Krummholz spruce were virtually absent from this habitat.

A similar mixed lichen mat dominates the moderately exposed habitat, but with the noted absence of *C. nigricans*, which is able to grow only in the most exposed environments at this latitude. Vascular species were also the same as those found in the exposed habitat, with increased growth of *B. glandulosa*. The other noticeable characteristic of this habitat is the development of moss hummocks within the lichen-heath. These so-called "dry hummocks" are comprised primarily of *Dicranum elongatum* and infrequently *Polytrichum juniperinum* (Dunnett 1969), and are responsible for the increase in moss cover in this habitat.

Although the proportional surface cover of lichens decreases considerably from that of the exposed habitat categories, the moderately protected woodland habitat exhibits the greatest diversity of both lichen and vascular plant species. This is due to the existence of exposed, lichen-dominated patches between spruce trees, at one extreme, while the trees provide a protected environment for the vegetation growing beneath them, at the other extreme. Thus, a wide range of microenvironments comprise this habitat.

The habitat specific arctic lichens cannot compete successfully in the shaded environment provided by the spruce woodland and increased birch growth, thus they are absent from the moderately protected habitat. The lichen ground cover of the woodland floor is comprised of large areas of a single species, usually *C. stellaris* (e.g., see Figure 7d) and less frequently, *C. mitis*, *C. rangiferina*, and *S. paschale*. The latter is most common in microdepressions, small drainage gullies, and on slopes covered by late-melting snowpacks. It is our impression that the distribution of *S. paschale* in the region is underrepresented in the data of Tables 3 and 4; it is more plentiful in areas adjacent to our transects. *C. rangiferina* reaches its greatest relative surface cover in this habitat, as shown in Figure 7e. It is most plentiful near the edge of spruce tree and birch shrub branches such that it receives moderate fluxes of solar radiation. Exposure to extremes of solar irradiance limits its growth.

Surface shading provided by the trees and denser birch growth allows mosses common to moist surfaces to grow in the protected habitats; *Sphagnum* species and *P. juniperinum* are the most prevalent.

In the most protected habitat, birch and alder thickets growing among scattered spruce trees dominated the surface vegetation. Fewer lichen species are able to grow well on the typically moist surface beneath such dense vegetation. This habitat exhibits the smallest diversity of vegetation. The dominant bryophytes are the same as those first detected in the moderately protected habitat.

MICROENVIRONMENTAL RELATIONSHIPS

To elucidate the significance of exposure, several soil and vegetation characteristics were also analyzed, including *C. stellaris* podetial diameters, *B. glandulosa* heights, *C. stellaris* relative water content, and soil moisture, organic content, and pH. These data were utilized to determine the microenvironment within the defined exposure habitats. The edaphic data (Table 5) indicate no apparent trend in comparison of habitat exposure extremes: pH is generally consistent, but shows a slight decrease with surface protection, downslope (a similar weak trend was also found by Moore (1987, personal communication), who suggested that it was due possibly to lower productivity of the tundra), while soil organic content and moisture fluctuate without indication of any pattern. These results counter evidence provided by Rouse & Kershaw (1973) that soil moisture and organic content contribute to the formation of a vegetation gradient. In contrast, our results further support the idea that exposure of surface vegetation to climatic elements is most important for understanding the transition between boreal forest and tundra plant communities in the eastern Canadian subarctic.

The habitat characteristics of Table 2 are related to the microclimate and growth characteristics of surface vegetation. *C. stellaris* podetial diameters increase as surface protection increases, and are generally larger on the southwest-facing slope. Birch heights also indicate similar tendencies, in that they grow to greater heights on the southwesterly transect and their heights increase from the exposed to the protected habitats. Notably, the podetial size of *C. stellaris* is directly related to the height and protection afforded by *B. glandulosa*, as illustrated in

Figure 8. As the height of *B. glandulosa* increases, protection of surface lichens from rapid thallus dehydration increases through diminished wind speed (as evidenced by the greater roughness lengths shown in Table 2) and less exposure to solar irradiance. Under more exposed upslope conditions lichens minimize their evaporative surface area, so podetial diameters decrease and individual podetia protrude less above the lichen mat. Thus, it appears that *C. stellaris* demonstrates phenotypic plasticity in different microenvironments. These results agree with those of Kershaw & Rouse (1971), in that podetial diameters were smaller when *C. stellaris* grew in xeric, exposed habitats.

The relative water content of *C. stellaris* also reflects the influence of protection from desiccation which a shrub layer provides. On both slopes the relative water content of *C. stellaris* is lowest in the exposed habitat of the ridgetop. In the more protected habitats downslope, relative water contents are consistently higher, although there is no trend toward the most protected environment. These results contrast Kershaw's (1975) conclusion that *C. stellaris* on ridgetops held more water than the valley bottom phenotype. Lower relative water contents on the southwest-facing slope indicate the existence of higher evaporative stress due to greater intensity of solar radiation and receipt of the prevailing northwesterly winds.

CONCLUSIONS

Habitat exposure induces significant microenvironmental variations with which the vegetation must interact. The vegetation patterns along these slopes indicate that hekistothermic species dominate the exposed habitats,

while boreal species are limited to the protected habitats. On these slopes, the equivalent of the latitudinal boreal forest-tundra ecotone is apparent, as a substantial change in lichen dominance occurs between the moderately exposed and moderately protected habitats.

The protection provided by winter snow (as represented by birch shrub heights) further ameliorates the subarctic winter climate in the protected habitats. Larson & Kershaw (1975) have noted that snow depths greater than 20 cm effectively diminish snow-air interface temperatures. For those species capable of tolerating the desiccating winds and cold temperatures of an exposed environment, such as lichens and heaths, ridge crests blown free of snow would provide a longer effective growing season.

By studying the microenvironment within these habitats, one begins to understand the significant role which energy exchange between biotic and abiotic realms plays in the development of the natural distribution and morphology of vegetation. This is corroborated by the variations of both surface roughness and solar irradiance depletion by habitat. Larson and Kershaw (1976) have called attention to the significance of energy exchange at the plant level by studying surface area to weight ratios, thallus shape, and degree of clumping of thalli for *Alectoria nitidula*, *A. ochroleuca*, *Cetraria nivalis*, and *Cladina stellaris*. They found that *A. nitidula*, *A. ochroleuca*, and *C. nivalis* had relatively lower resistances to evaporation, in contrast to that of *C. stellaris*. Species with low resistances were those which are known to thrive in xeric environments. This corroborates our results which show their prevalence in sun and wind exposed habitats which are generally snow-free. Larson & Kershaw (1976) also noted that single thallus occurrences of *C. stellaris* are found where the lower branches

of adjacent spruce trees provide an additional boundary layer. We also observed single thallus forms of *C. stellaris* in protected habitats, where their podetial surface cover is least. Furthermore, the podetial diameters of the single thallus forms of *C. stellaris* were largest in the protected habitats. This increases surface roughness which lowers resistance to evaporation (Larson & Kershaw 1976). Generally in exposed habitats, lichens with smoother surfaces exhibit greater resistance to the diffusion of water vapor into the atmosphere and have adapted to the desiccating environment in which they dominate. Thus, morphological variation of *C. stellaris*, reflected in its podetial size and surface roughness, illustrates the importance of studying the environmental biophysics of plant species and communities to understand the natural distribution of vegetation.

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Table 1. Criteria for Defining Habitat Categories

<u>Exposure Habitat</u>	<u>General Vegetation Type</u>	<u>Transsect Sample Levels</u>	<u>Criteria-Description</u>
Exposed	Lichen-heath tundra	I: 1,2,4, II: 1,2,3,4,9,14	No birch or minimal protection from sparse, low growing birch (<30 cm tall); birch < 5% of ground cover; occasionally rocky due to presence of stoney earth circles (periglacial patterns); lichens dominate; xeric, well drained soils.
Moderately Exposed	Low shrub tundra ²	I: 3,5,7,8 II: 7,8,10,12,15	Birch and/or krummholz spruce are evident on the landscape, but surface is exposed; lichens dominate; taller, more dense birch (20-60 cm); mesic, well drained soils.
Moderately Protected	Open woodland/forest tundra ²	I: 6,9,12,13,14,15 II: 5,6,11,13,18,20,21	Tall birch (60-100 cm) and/or sparse, mature spruce trees dominate the landscape; spruce tree density, 10-20% same exposed lichens between stands; mosses common beneath trees/shrubs.
Protected	Tall shrub tundra ² /wood- land with dense shrub understory	I: 10,11 II: 16,17,19	Scattered, mature spruce; dense shrub thicket (> 100 cm tall); birch > 25% of ground cover; maximum protection of surface; few to no lichens present; mosses common beneath trees/shrubs; poorly drained soils.

1. sample level 1 indicates the ridge crest; elevation decreases at 5 m intervals with increasing sample level number; Transect I faces SW, and Transect II faces NNE.
2. described by Bliss (1981).

Table 2. Vegetation and microenvironmental characteristics (mean values per habitat)

HABITAT	C. stellaris diameter (mm)	C. stellaris relative water content (%)	Birch shrub heights (cm)	Surface Roughness (cm)	Irradiance Depletion by Canopy (1-K+f/K+)
<u>SW Slope</u>					
Exposed	15.1	27	32.0	--	--
Mod. Exposed	19.2	34	61.5	--	--
Mod. Protected	25.1	33	97.7	--	--
Protected	25.4	34	113.5	--	--
<u>NNE Slope</u>					
Exposed	13.8	58	12.8	1.2	0
Mod. Exposed	19.3	67	23.8	7.3	12
Mod. Protected	22.5	64	61.5	20.3	32
Protected	24.5	68	97.7	50.2	47

Table 3. Proportional surface cover (%) by habitat - SW-facing slope transect.

<u>Surface Cover</u>	<u>Exposed Habitat</u>	<u>Moderately Exposed Habitat</u>	<u>Moderately Protected Habitat</u>	<u>Protected Habitat</u>
1. Lichens				
Alectoria ochroleuca	5	1	—	—
Cetraria nigricans	1	—	—	—
Cetraria nivalis	8	1	—	—
Cladonia amaurocraea	+	1	1	—
Cladonia cristatella	1	1	1	—
Cladonia uncialis	—	3	1	—
Cladonia sp.	1	4	+	1
Cladina mitis	—	+	10	1
Cladina rangiferina	1	6	7	20
Cladina stellaris	53	58	38	27
Nephroma arcticum	—	—	+	+
Stereocaulon paschale	—	—	2	—
TOTAL* LICHEN COVER	71	75	59	48
2. Vascular Plants				
Alnus crispa	—	—	+	1
Betula glandulosa	3	6	9	27
Carex sp.	1	+	3	2
Empetrum nigrum	8	3	1	2
Ledum groenlandicum	—	1	—	—
Picea mariana ^a .	5	3	2	—
Vascular sp., other	1 ^b .	1 ^b .	2 ^c .	1 ^c .
TOTAL* VASCULAR COVER	17	13	16	32
3. Mosses	1 ^d .	6 ^e .	24 ^f .	19 ^f .
4. Exposed soil/rock	11	6	1	1

- NOTES: + trace occurrence; less than 0.5% average surface cover.
 * subtotals may not equal the sum of components due to round-off error.
- Only includes branch tips within study quadrats; tree densities were 10-18% based on 900 m² surveys.
 - primarily *Arctostaphylos alpina*, *Salix uva-ursi*, *Vaccinium vitis-idaea* var. *minus*, and *hyco podium annotinum* var. *pungens*.
 - primarily of the family *Poaceae*, *Cornus canadensis*, *V. uliginosum* var. *alpinum*, and *L. annotinum*.
 - primarily *Racomitrium lanuginosum*.
 - primarily *R. lanuginosum*, *Dicranum elongatum*, *Ptilidium ciliare*.
 - primarily *Sphagnum* spp., *Polytrichum juniperinum*.

Table 4. Proportional surface cover (%) by habitat - NNE-facing slope transect.

<u>Surface Cover</u>	<u>Exposed Habitat</u>	<u>Moderately Exposed Habitat</u>	<u>Moderately Protected Habitat</u>	<u>Protected Habitat</u>
1. <u>Lichens</u>				
Alectoria ochroleuca	18	10	--	--
Cetraria nigricans	4	--	--	--
Cetraria nivalis	7	2	+	--
Cladonia amaurocraea	+	1	+	--
Cladonia cristatella	--	+	+	--
Cladonia uncialis	--	--	+	--
Cladonia sp.	--	+	1	--
Cladina mitis	--	+	1	+
Cladina rangiferina	3	9	13	4
Cladina stellaris	34	43	17	1
Nephroma arcticum	--	--	+	+
Stereocaulon paschale	+	1	3	1
TOTAL* LICHEN COVER	65	66	35	7
2. <u>Vascular plants</u>				
Alnus crispa	--	--	2	+
Betula glandulosa	3	13	17	57
Carex sp.	1	2	3	2
Empetrum nigrum	4	4	9	11
Ledum groenlandicum	1	+	4	--
Picea mariana ^{a.}	--	--	+	1 ^{c.}
Vascular sp., other	5 ^{b.}	2 ^{b.}	1 ^{c.}	1 ^{c.}
TOTAL* VASCULAR COVER	14	21	38	72
3. <u>Mosses</u>				
	10 ^{d.}	12 ^{e.}	26 ^{f.}	22 ^{f.}
4. <u>Exposed soil/rock</u>				
	11	1	+	--

- NOTES: + trace occurrences; less than 0.5% average surface cover.
 * subtotals may not equal the sum of components due to round-off error.
- Only includes branch tips within study quadrats; tree densities were 10-18% based on 900 m² surveys.
 - primarily *Arctostaphylos alpina*, *Salix uva-ursi*, *Vaccinium vitis-idaea* var. *minus* and *Lycopodium annotinum* var. *pungens*..
 - primarily of the family *Poaceae*, *Cornus canadensis*, *V. uliginosum* var. *alpinum*, and *L. annotinum*.
 - primarily *Racomitrium lanuginosum*.
 - primarily *R. lanuginosum*, *Dicranum elongatum*, *Ptilidium ciliare*
 - primarily *Sphagnum* spp., *Polytrichum juniperinum*.

Table 5. Edaphic characteristics (mean values per habitat)

HABITAT	Number of Sites Sampled*	pH	Organic Content (%)	Soil Moisture (%)
<u>SW Slope</u>				
Exposed	3	4.3	47	240
Mod. Exposed	4	4.2	23	158
Mod. Protected	6	4.2	14	120
Protected	2	3.9	20	244
<u>NNE Slope</u>				
Exposed	6	4.3	32	131
Mod. Exposed	5	4.2	29	108
Mod. Protected	7	4.2	35	149
Protected	3	4.2	27	115

*Five replicates were taken at each sample site.

LIST OF FIGURES

- Figure 1. Aerial photo of open lichen woodland in southwestern Labrador, taken at a height of approximately 1630 m above ground level. The dark vegetation is spruce trees (typically *Picea mariana*) and the light colored surface is lichen, predominantly *Cladina stellaris*.
- Figure 2. The relationship between birch shrub heights and elevation along opposing slopes of the same ridge.
- Figure 3. Vegetation cover of the exposed habitat at the ridgetop. The typical surface cover is comprised of lichen-heath tundra and exposed soils of stoney earth circles.
- Figure 4. Low shrub tundra of the moderately exposed habitat. Note the appearance of sparse birch shrub growth.
- Figure 5. Open lichen woodland of the moderately protected habitats. Widely spaced black spruce and birch shrubs provide a range of exposures to wind and solar irradiance for the surface vegetation of lichens and mosses.
- Figure 6. Dense birch and alder shrub growth of the most protected habitat. The leaf canopy intercepts a large enough proportion of solar irradiance; few lichens are able to grow on the ground.
- Figure 7. Mean relative surface coverage (calculated by Equation 5) of a. *Alectoria ochroleuca*, b. *Cetraria nigricans*, c. *Cetraria nivalis*, d. *Cladina stellaris*, e. *Cladina rangiferina*, and f. *Betula glandulosa* in each habitat.
- Figure 8. The relationship between mean birch shrub heights and *C. stellaris* podetial diameters for all vegetation habitats and slope aspects.

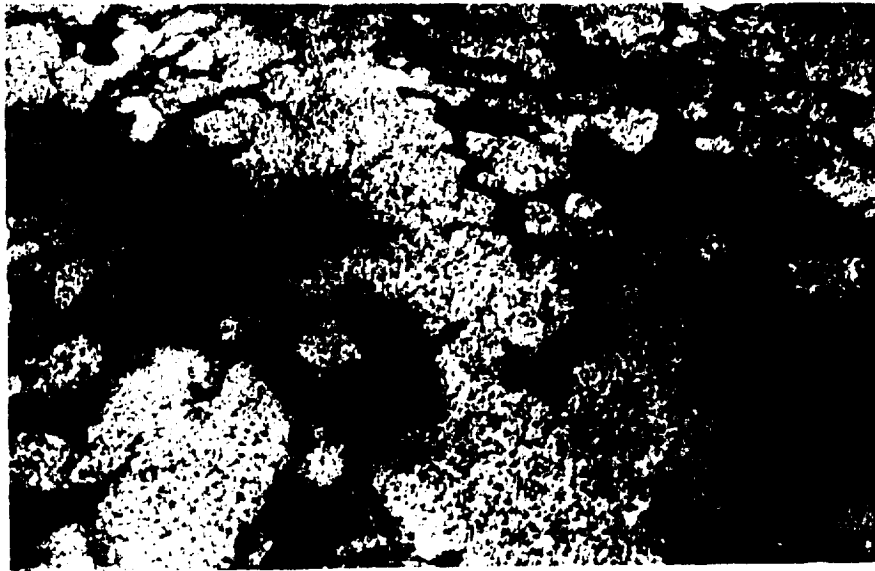


Figure 1.

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OF POOR QUALITY

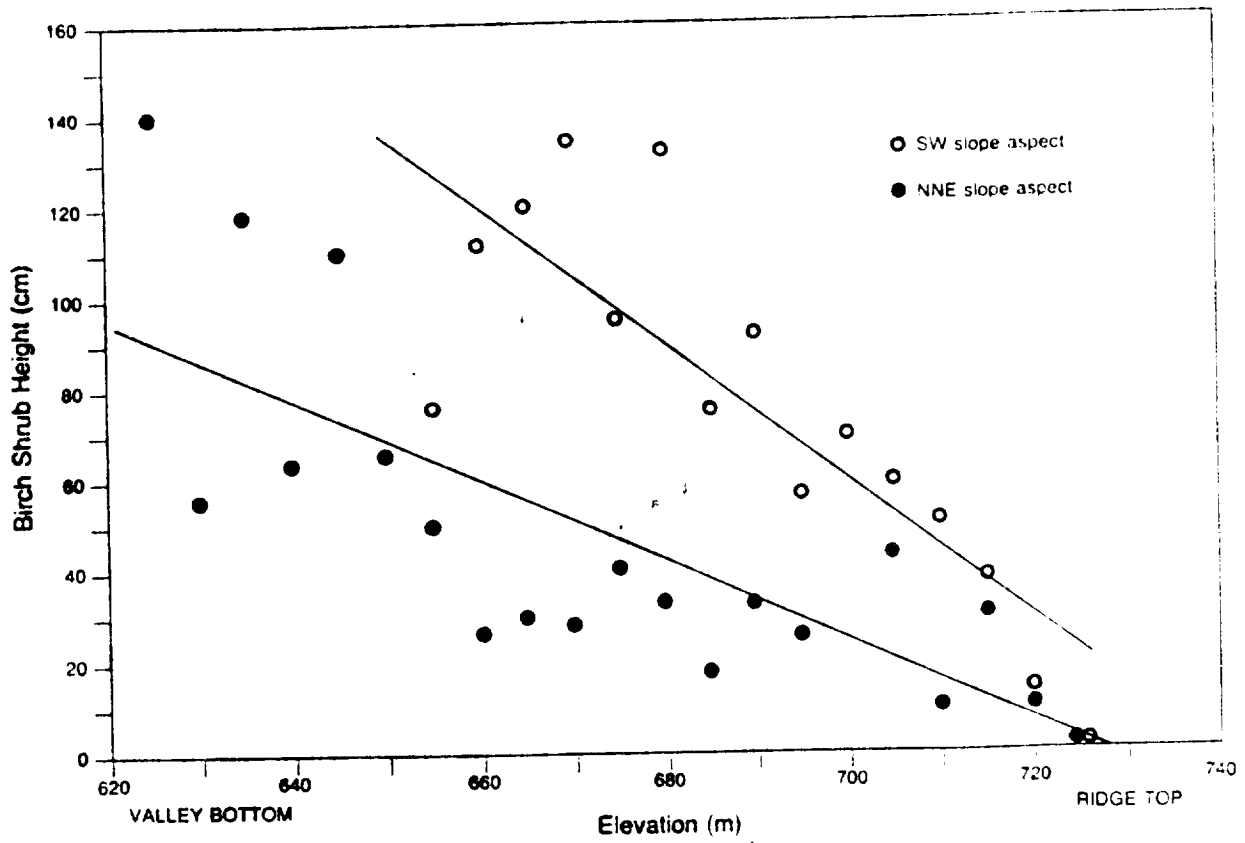


Figure 2.



Figure 3.



Figure 4.



Figure 5.

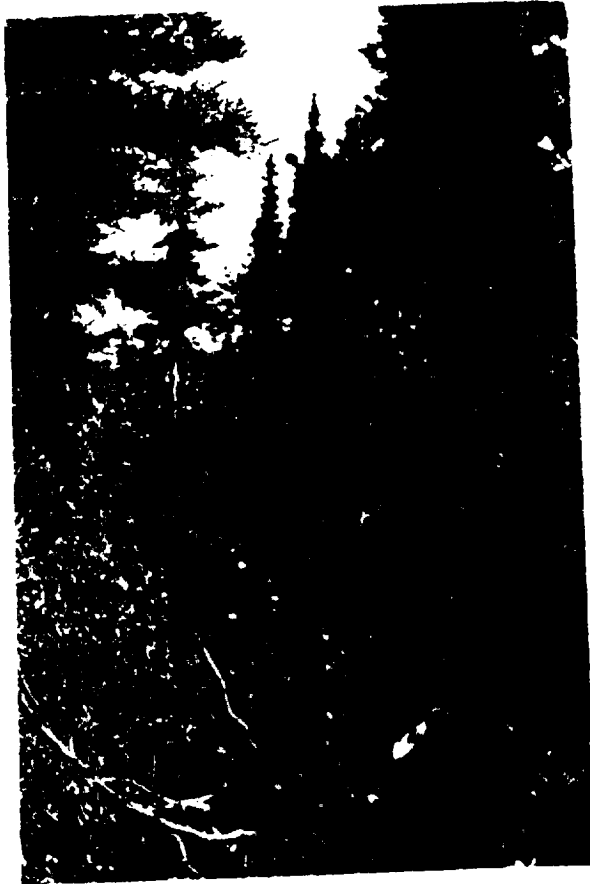


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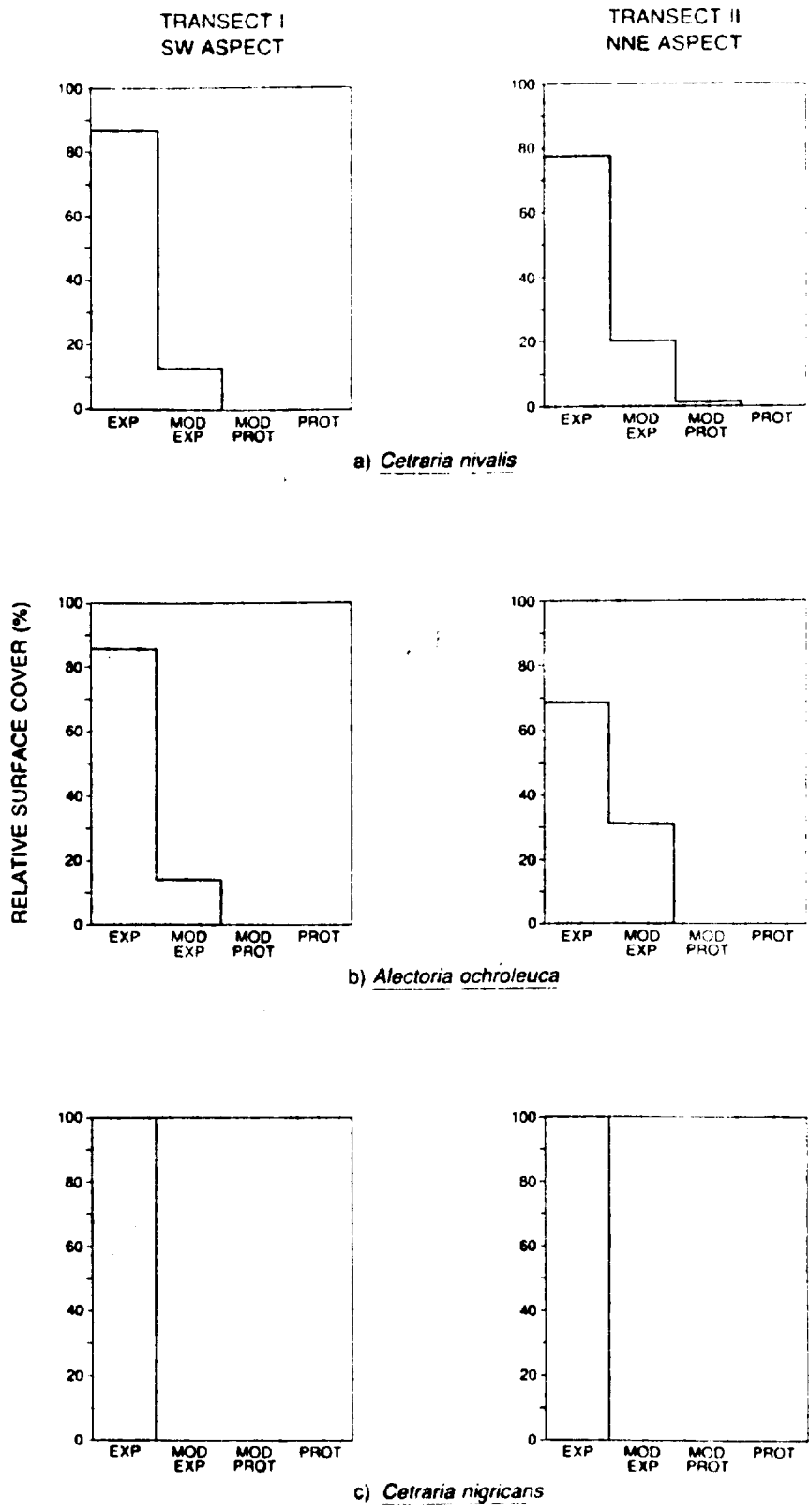
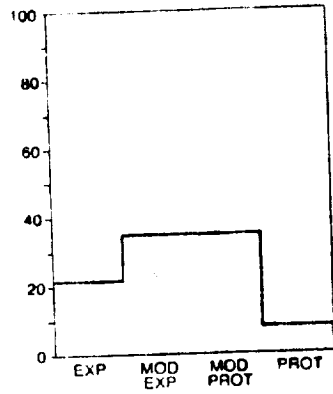
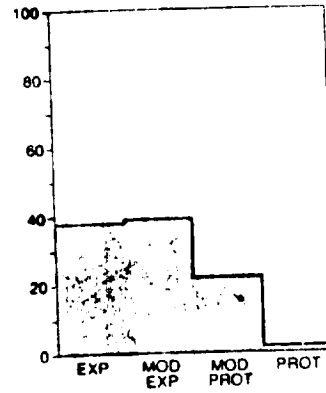


Figure 7 (a-c).

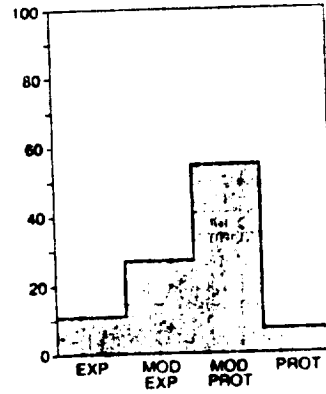
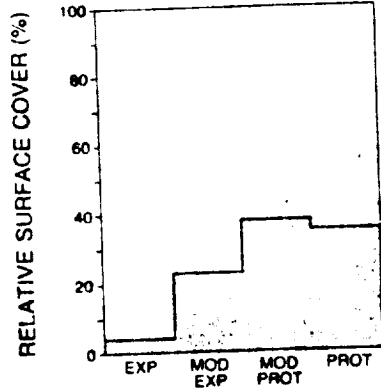
TRANSECT I
SW ASPECT



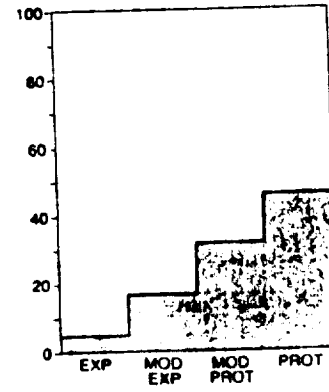
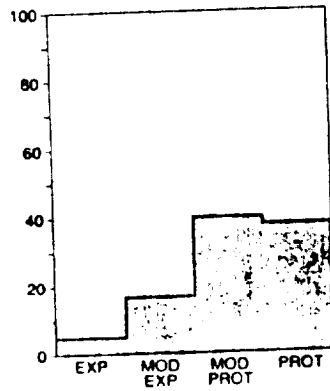
TRANSECT II
NNE ASPECT



d) *Cladina stellaris*



e) *Cladina rangiferina*



f) *Betula glandulosa*

Figure 7 (d-f).

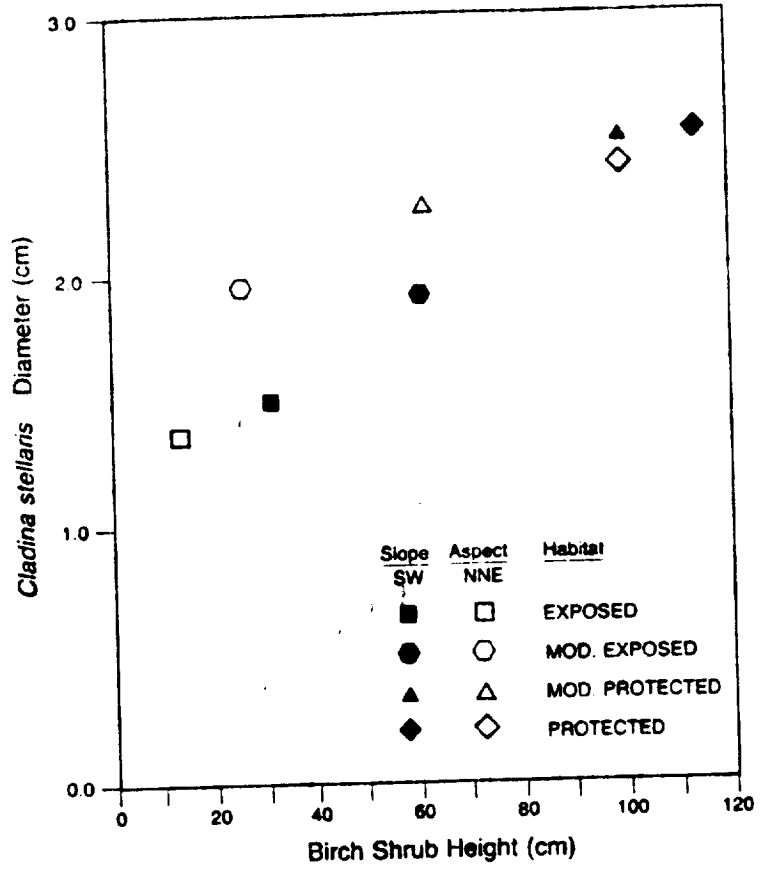


Figure 8.