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Vegetation Distributions along Lichen-Dominated Slopes of Opposing Aspect in the Eastern Canadian Subarctic

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ABSTRACT. Detailed vegetation surveys along two opposing slopes in the boreal forest-tundra ecotone of Quebec-Labrador reveal distinct distributions and habitat preferences of prevalent lichen and shrub species. The presence or absence of a protective shrub layer was the main determinant of lichen distributions. Generally, there was an inverse relationship between the proportional surface coverages of vascular plants and lichens. At the most exposed site, nearest the ridge top, *Cetraria nivalis* (L.) Ach., *Alectoria ochroleuca* (Hoffm.) Massal. and *Cetraria nigricans* Nyl. were integrated well into the lichen mat and surrounded stoney earth circles. Increased shrub growth and protection quickly eliminated these lichens at lower elevations but allowed for more widespread growth of *Cladina rangiferina* (L.) Nyl. *Cladina stellaris* (Opiz) Brodo was the most pervasive lichen and appeared to be a generalist in habitat selection.

Slope aspect influenced the distributions of three lichens of limited habitat range. The northerly facing slope provides preferable conditions for their growth farther downslope, thus extending their suitable habitat range. These results suggest the possibility of defining distinct lichen habitats based on exposure or, conversely, on protection provided by the presence of a shrub-tree canopy.

Key words: lichens, vegetation gradient, subarctic, topography, tundra, eastern Canadian Subarctic

RÉSUMÉ. Des relevés détaillés de la végétation sur deux pentes opposées dans l'écotone de la toundra-forêt boréale du Québec-Labrador, ont révélé des distributions distinctes et des préférences d'habitat pour des espèces de lichens et d'arbustes prédominants. La présence ou l'absence d'une couche protectrice d'arbustes était le facteur principal qui déterminait la distribution des plantes vasculaires et des lichens. Il y avait en général une relation inverse entre les proportions des surfaces couvertes par les plantes vasculaires et de celles couvertes par les lichens. Au site le plus exposé, près de la crête, les espèces *Cetraria nivalis* (L.) Ach., *Alectoria ochroleuca* (Hoffm.) Massal. et *Cetraria Nigricans* Nyl. étaient intégrées profondément dans le tapis de lichens et entouraient des cercles de sol caillouteux. À des altitudes plus basses, la croissance et la protection accrues des arbustes éliminaient ces mêmes lichens tout en permettant une croissance plus répandue de *Cladina rangiferina* (L.) Nyl. L'espèce *Cladina stellaris* (Opiz) Brodo était le lichen le plus répandu et paraissait ne pas être spécifique dans le choix de son habitat.

L'aspect de la pente avait une influence sur la distribution de trois lichens ayant une gamme d'habitat limitée. Les pentes orientées face au nord offraient les conditions les plus favorables à leur croissance plus bas sur la pente, ce qui augmentait la gamme d'habitat qui leur convenait. Ces résultats semblent indiquer qu'il est possible de définir des habitats distincts pour les lichens à partir de l'exposition, ou, à l'inverse, de la protection fournie par une couverture d'arbustes.

Mots clés: lichens, gradient de végétation, zone subarctique, topographie, toundra, zone subarctique canadienne de l'est

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INTRODUCTION

The predominant land surface vegetative cover of the tundra biome and subarctic coniferous forest-tundra ecotone of central Quebec-Labrador is densely matted, pale-colored lichen. Lichens, although found in all terrestrial biomes, become a significant ground cover type in the northern boreal forest and tundra biomes. Ironically, there is a notable lack of understanding regarding the distributional tendencies of this prominent vegetative cover, particularly in the eastern Canadian Subarctic (Lechowicz *et al.*, 1984).

In studying the landscape in the forest-tundra ecotone, one can observe a vegetation gradient from a wooded valley bottom to a nearly barren adjacent ridge top, as shown in Figure 1. This gradient is induced by local climate variations related to altitude, aspect and exposure, as described in Granberg (1973) and Nicholson and Thom (1973). Exposed ridge tops above approximately 685 m in elevation in this region are often underlain by permafrost, which is indirectly related to the upslope development of stoney earth circles within a lichen-heath community (foreground, Fig. 1) (Annersten, 1964). Annersten (1964) further states that a zonal division of vegetation on these slopes is caused by exposure, with higher mean ground and air temperatures associated with greater vegetation development (background, Fig. 1).

The existence of a vegetative gradient along sloping terrain in the eastern Canadian Subarctic poses several interesting questions related to micro-climatic and micro-environmental interactions in lichen ecology. One concerns the role played by topographic factors in determining lichen species presence along a slope. Another concerns the ability to identify a simple environmental indicator that will enable generalization of lichen growth characteristics and micro-habitats along a slope. Studies of such interactions in a harsh subarctic environment are useful to the broader topic of general, global plant adaptations for three reasons: (1) the lichen life form is relatively simple, since they have no roots or stomates, yet they are photosynthetically active; (2) the density of trees and shrubs is low and the number of dominant species is few, so the establishment of vegetation relationships may be simplified; and (3) high latitude biomes are relatively more susceptible to climatic change. Thus the specific objective of this paper is to define the distribution of major lichen species in relation to vascular plant cover along slopes traversed by the altitudinal tree line. Additionally, we hope to determine the impact of slope aspect on vegetation relationships by choosing opposing flanks of one ridge for analysis. A more complete understanding of vegetation growth patterns in this ecotone may enable closer monitoring of lichen distributions as indicators of future large-scale climatic change.

STUDY SITE AND SAMPLING METHODS

Data collection was completed during a three-week period commencing in late June 1986, after deciduous shrub leaf-out

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FIG. 1. Vegetation distribution along a NE-facing slope in subarctic Quebec. The foreground (elevation 705 m a.s.l.) is composed of exposed lichen-heath tundra that grades downslope to open lichen woodland in the valley bottom (elevation approx. 490 m a.s.l.).

was complete. The study focused on two slopes of opposing aspects along a ridge that constitutes the boundary between Quebec and Newfoundland (Labrador), approximately 30 km northwest of the town of Schefferville, Quebec (54°48′N, 66°49′W). Transect 1, of southwesterly aspect, had an average slope of 11.0° and was 379 m long, with an elevational drop of 72 m. Transect 2, of north-northeasterly aspect, had an average slope of 11.8° and was 532 m long, with an elevational drop of 100 m. Each is characterized by a ridge top of incomplete vegetation cover that grades downslope to open lichen woodland at the valley bottom. Based on the transect lengths, a 5.0 m decrease in elevation was used to define data sampling levels along the slope. This elevation decrease provided an ample sample size for each transect so that anomalous situations might be averted without eliminating significant topographic variations. There were 15 sample levels for Transect 1 and 21 along Transect 2.

Once the sample levels were identified, the random throw of a wooden 1 m × 1 m quadrat along an elevational contour was used to delimit five study sites at each sample level (Larson and Kershaw, 1974). Using the quadrat to provide a sense of scale, gross ground cover percentages (lichen, vascular plant, moss, soil/rock) were estimated, and the presence of protective shrubs was noted at each site. Also, the presence, height and density of the dominant tree species, *Picea mariana* (Mill.) BSP (black spruce), both in the krummholz shrub form and in the tree form, were determined and noted. Close-up photographic slides of all sites, in which the quadrat filled the camera frame, were also taken to enable a more accurate estimation of particular plant species coverages at a later date. Upon completion of this analysis for all study sites, an average percent cover for the various ground cover species was calculated for each sample level along the transects.

VEGETATION DISTRIBUTIONS

Figures 2 and 3 depict the average surface coverage of lichen, vascular plants, moss and soil/rock at each sample level from the ridge top (sample level 1) to the adjacent valley bottom. Generally the proportional coverage of lichen appears to be inversely related to that of the vascular plants. Where lichens are least prevalent, vascular plant cover is dense and strongly established. Moss cover generally increases downslope, with peak values occurring at sample levels where both lichen and vascular plants are at their minimum. Along these slopes terraces provide a protected environment and moist, organic soils, which allow the dominance of birch and particularly mosses (e.g., Transect 1, level 12; Transect 2, level 6). Otherwise moss is a constant, but minor, component of the surface vegetation. Exposed soil and rock increase with the approach of the ridge crest. This is due primarily to the presence of periglacial phenomena known as stoney earth circles, which occur at the most exposed, high elevations in this environment and usually indicate underlying permafrost (Annersten, 1964). Glacially strewn boulders and cobbles are found scattered at all elevations along the slope.

The distributional tendencies of Figures 2 and 3 suggested further study of the component species of the ground vegetation. Figures 4 and 5 present lichen species coverage along each slope, while the shaded portions of Figures 2 and 3 represent the percentage of coverage of *Betula glandulosa* Michx., a dominant birch shrub. Only the most prevalent ground lichens are considered in this part of the analysis, including two pervasive "caribou lichens," *Cladina stellaris* (Opiz) Brodo and *Cladina rangiferina* (L.) Nyl., as well as *Cetraria nivalis* (L.) Ach., *Cetraria nigricans* (Nyl.) and *Alectoria ochroleuca* (Hoffm.) Massal.

Certain lichen species appear to be regionally specific in their distributions, while others are widely distributed along these slopes. *C. stellaris* and *C. rangiferina* tolerate a wide range of exposures and habitats, with *C. stellaris* being generally more abundant along each of the transects. Notably, *C. stellaris* is the largest constituent of all ground lichens, but its distribution also shows decreased growth at lower elevations on each slope. *C. rangiferina* does not grow in the most exposed habitats. This is noted by the inverse surface coverage relationship between *C. rangiferina* and *A. ochroleuca*. The latter is prolific around stoney earth circles in the most exposed, shrubless habitats of highest elevation.

C. nigricans, *A. ochroleuca* and *C. nivalis* are much smaller constituents of the lichen mat present on Transect 1, the SW-facing slope. Yet they are unique in that their distribution is limited to the highest elevations of Transect 1: *C. nigricans* is present only at the ridge top; *A. ochroleuca* and *C. nivalis* grow

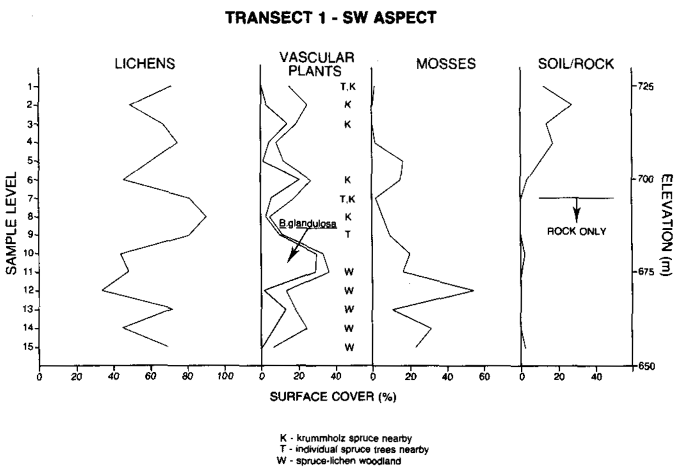

FIG. 2. Average surface cover on the SW-facing slope. The occurrence of spruce tree forms is noted in the plot of vascular plants.

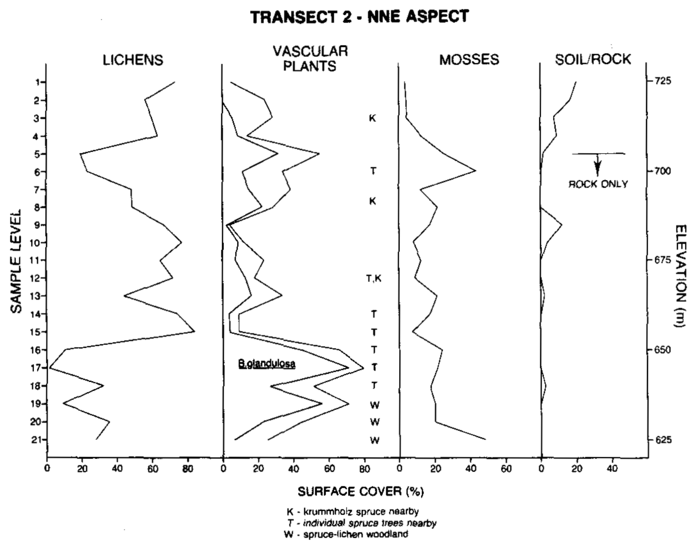

FIG. 3. Average surface cover on the NNE-facing slope. The occurrence of spruce tree forms is noted in the plot of vascular plants.

only in the upper 20 m of elevation along the slope. The distributions of the latter on the NNE-facing slope are similar; however, their distribution limits are expanded downslope to lower elevations. This appears to be the result of cooler, snowier conditions extending to a lower elevation along the NNE-facing slope. It is evident that less intense direct and global solar radiation would impinge on this northerly slope aspect. This was confirmed by the presence of several deep snow patches found along this transect during the period of field data collection (late June-July 1986), while the SW-facing transect was snow free at the same time. A corresponding ground and surface temperature difference between SW- and NE-facing slopes was also found by Annersten (1964), who further stated that permafrost in this area is almost always found beneath slopes of N-E aspects. *A. ochroleuca* and *C. nivalis* exhibit the same distributional trends, but with different proportional coverages; the peaks and dips in their distributions are almost always co-occurrent. Since both species occur in the most exposed environs and will not grow under the protection of even minimal shrub growth, one may hypothesize that upslope absences of these lichens are due to differing habitat conditions induced by differing degrees of shelter afforded by shrubs and trees present, as well as by microtopography.

P. mariana is the only tree species capable of attaining erect, mature growth on these slopes. (The occurrences of spruce are indicated at their appropriate elevations on the central plot of Figures 2 and 3.) Both krummholz spruce and individual trees are found at the highest elevation of the SW-facing slope. In contrast, there was relatively less spruce growth along the upper 50 m of elevation along the NNE-facing slope. There, krummholz spruce were more widely scattered and appeared less healthy (chlorotic needles) than those growing at corresponding elevations on the SW aspect. At higher elevations above the tree line individual trees are scattered across the slope. The open lichen woodland, defined where tree growth is consistent and more or less continuous, commenced at 675 m in elevation on the SW slope, while continuous tree growth was found at elevations less than 640 m on the NNE slope, as expected. At the elevational tree line, woodland density (expressed as the percentage of tree branch area to total surface area) was calculated to be 10.1% at sample level 11 on the SW aspect and 18.1% at sample level 19 on the NNE aspect.

DISCUSSION

The variations in lichen coverage, as well as in that of other cover types, appear to be related directly to topography. Rosenberg (1974) suggests that the low sun elevation and cloudiness of this region produce a solar flux rich in diffuse radiation, which reduces the importance of slope and aspect to the biological environment. However, evidence presented here suggests that slope aspect does influence the distributional tendencies of the more narrowly distributed lichen species, krummholz spruce and the elevational tree line. The NNE-facing slope provides preferable conditions for the growth of *C. nigricans*, *A. ochroleuca* and *C. nivalis* farther downslope, thus extending their suitable habitat range. In contrast, *C. stellaris* and *C. rangiferina* exhibit wide distributional preferences and appear to be generalists in habitat selection.

Previous research, however, found *C. stellaris* (on older, peat-rich ridges) and *A. ochroleuca* (on younger, inorganic ridges) commonly growing in sheltered areas on the Hudson Bay lowland of northern Ontario (Kershaw and Larson, 1974). A similar contrast occurs again, as Larson and Kershaw (1975) found *A. ochroleuca* preferred younger ridge crests while *C. nivalis* preferred lower slopes and ridge bottoms in a lichen-heath association (although the species were not found to be mutually exclusive). In Quebec-Labrador this trend was not apparent; *C. nivalis* and *A. ochroleuca* were always co-occurrent.

Perhaps these differences in research findings may be explained by differences in geology, soils and topography of the two regions. Grayson (1956) considered the vegetational formations of northern Quebec-Labrador to be primarily under the control of climate, due to the constancy of the bedrock foundation and soil development. The high relief and the thin, stoney, well-drained soil, generally lacking organics, are typical of the ridge-and-valley topography of the Labrador trough, in which our study sites were located. In contrast, the research sites on the Hudson Bay lowlands had a relief of only several meters, were very young geologically and were at a relatively much lower elevation. Kershaw and Larson (1974) also suggested the depth of peat to be another factor controlling the establishment of

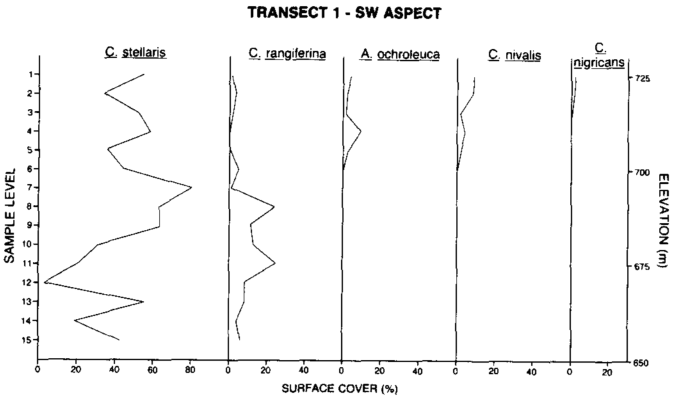

FIG. 4. Average percent cover of selected lichen species on the SW-facing slope.

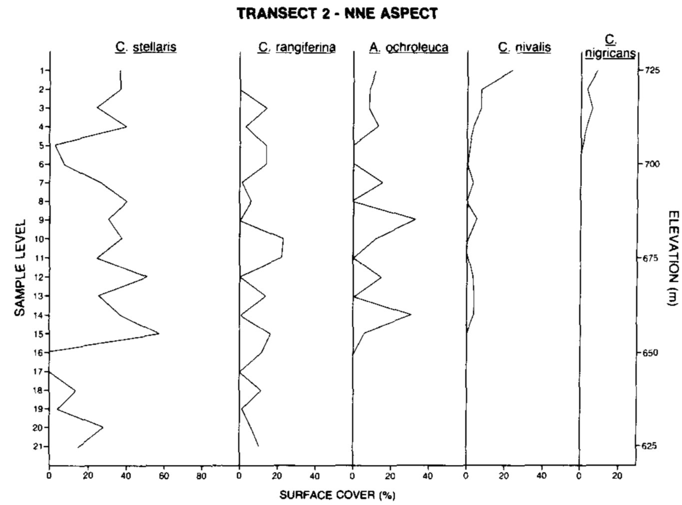

FIG. 5. Average percent cover of selected lichen species on the NNE-facing slope.

certain lichen colonies. Despite the varied growth of several lichens and vascular species, this seems to be relatively unimportant in the boreal forest-tundra ecotone of eastern Canada, since little or no peat was found along either of the transects, with the exception of sample levels dominated by mosses.

A further investigation of the constituents of the vascular plants present on the transects identifies *B. glandulosa* as the dominant species present. Yet the morphology of *Betula* varies along the slopes, with a trend toward greater abundance and taller growth with decreasing elevation. Of the remaining vascular species, *Empetrum nigrum* L., a very low-growing heath, is most prevalent, particularly at higher elevations along Transect 1. It thrives under conditions suitable for the growth of most lichens: acidic soils of varying moisture levels. Additionally, other heaths (*Vaccinium* ssp.), shrubs (*Ledum groenlandicum* Oeder [Labrador tea] and *Alnus* sp. [alder]) and sedges are scattered among the vascular species present and constitute less than 6% of the surface cover in any habitat. Of these only the birch and alder shrubs offer protection and shading of the surface, thus altering significantly the radiation and energy balances of the surface beneath. It appears that the dominant lichens of this ecotone are not capable of growth under low radiation conditions provided by a dense shrub layer. Individual spruce trees or krummholz spruce, due to their low density and scattered growth, have little effect on lichen distributions along these elevational vegetation gradients.

Future research should therefore focus on dividing the general environment along such vegetation gradients into distinct habitats based on variations in degree of exposure of the ground surface. Ultimately, such habitat designations should be made in conjunction with corresponding microclimatic and pedological variations that occur along the same slopes. Perhaps then better understanding of the habitat preferences and community structure of these lichens can be achieved.

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