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## Microsite Displacement of Terrestrial Lichens by Feather Moss Mats in Late Seral Pine-Lichen Woodlands of North-central British Columbia

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Abstract. *Pine-lichen woodlands in north-central British Columbia show a long period of successional development where reindeer lichens (*Cladina *spp.) dominate plant cover at the forest floor surface. However, in mid- to late-successional stands lichen cover is replaced in a mosaic of surface microsites by feather moss mats (largely* Pleurozium schreberi*), with moss mats often burying lichen mats that previously had occupied these microsites. We have compared moss and lichen dominated microsites at this stage of stand development, looking at the influence of canopy structural variables and development of forest floor plant communities on microsite expression. Microsites with high feather moss mat cover had greater canopy leaf area index values, compared to microsites where lichen cover predominated. Leaf area index values were highly correlated with stand level structural variables, including basal area, total volume, and biomass of the dominant canopy tree species* Pinus contorta. *Changes in stand architecture were further associated with the accumulation of litter and organic matter at the forest floor surface. These factors suggest that the manipulation of stand structure in managed forests, for instance through partial-cut harvesting, may delay successional changes and promote continued lichen growth in these forest types. This is an important consideration in the management of pine-stands in northern B.C., where lichen mats provide significant forage values for caribou populations.*

Lichen woodlands dominate coniferous forests across large areas of northern Canada (Kershaw 1978). These woodlands are typically characterized by a post-fire seral sequence where mat-forming lichen communities at the forest floor surface are replaced by feather moss mat dominated communities late in stand life. Within pine-lichen forests of western Canada reindeer lichens (*Cladina* spp.) are most prolific in 80 to 100 yr old *Pinus contorta* stands (Johnson 1981; Rowe 1984; Stevenson 1991). This stage, in absence of stand destroying fires, is followed by a feather moss dominated stage, which occurs approximately 150 yr after stand initiation (Carroll & Bliss 1982; Maikawa & Kershaw 1976; Payette et al. 2000).

The shift between a lichen dominated mid-seral stage and a moss dominated late-seral stage is often

associated with stand characteristics at a site (Brulisauer et al. 1996; Johnson 1981; Lesica et al. 1991; Maikawa & Kershaw 1976). Among factors that have been postulated as important in this respect are increased levels of shading and resultant changes in moisture availability that result from reduced incident solar radiation at the forest floor surface (Johnson 1981; Lesica et al. 1991). This has been expressed in general terms as a reference to crown closure increasing as a stand ages, which creates shaded conditions more suitable for feather moss to become established (Carroll & Bliss 1982; Maikawa & Kershaw 1976).

These same trends occur in pine-lichen woodlands of north-central British Columbia (Coxson & Marsh 2001; Coxson et al. 1998). However, the reference to crown closure does not appear to adequately describe the functional components that influence the transition from lichen- to moss-domi-
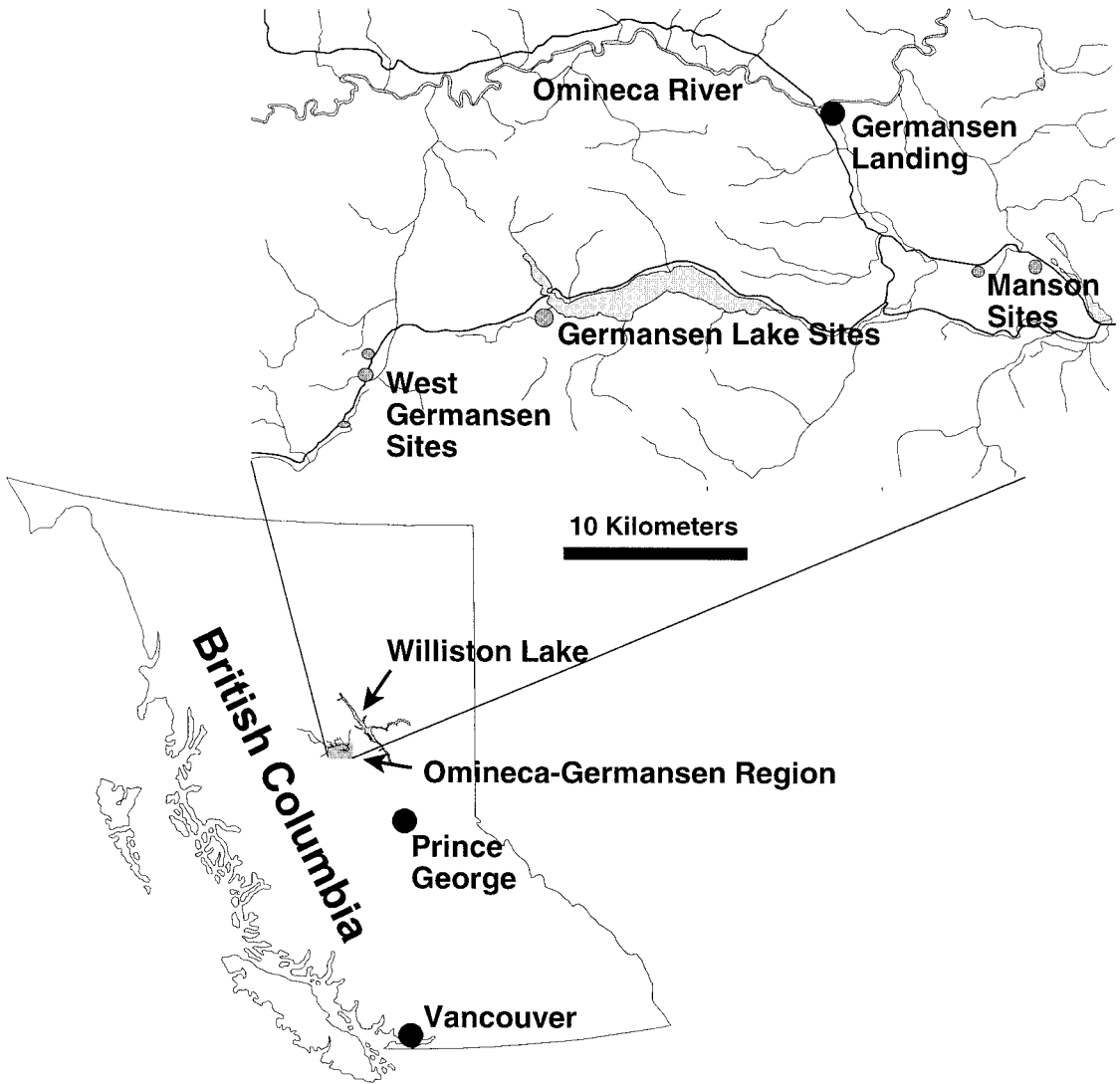
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FIGURE 1. Stand sampling areas in Omineca-Germansen area.

nated ground cover in these sites. This is primarily based on the reasoning that crown closure of pine stands occurs long before forest floor lichen communities shift to a feather moss dominated stage (Farnden 1996). The processes involved appear to be complex, involving overall stand development, particularly changes in total tree biomass. Recent findings of Pharo and Vitt (2000) further point to the role of stochastic events in determining the development of bryophyte and macro-lichen cover in local microsites.

We have now characterized spatial distribution of reindeer lichens (*Cladina* spp.) and feather moss mats (comprised predominately of *Hylocomium splendens*) within canopy gaps in late-succesional pine-lichen woodlands from the Omineca region of north-central British Columbia, correlating changes in the relative cover of lichens and mosses with changes in overstorey forest canopy structure and biomass. These factors have recently assumed greater significance to forestry managers, as attempts are made to extend the duration of lichen dominated successional phases within managed pine forests as a means of providing forage for caribou populations (Harris 1996; Racey et al. 1996; Rosso & Rosentreter 1999).

## STUDY AREA

Pine-lichen woodlands were located in an area 300 km northwest of Prince George, BC, in the vicinity of Germansen Lake (Fig. 1). This area falls within the Omineca River watershed and is in the boreal white and black spruce (BWBS) biogeoclimatic zone. The chosen sites fall under a dry cool variant of the BWBS biogeoclimatic zone identified as the dk1 (Meidinger & Pojar 1991).
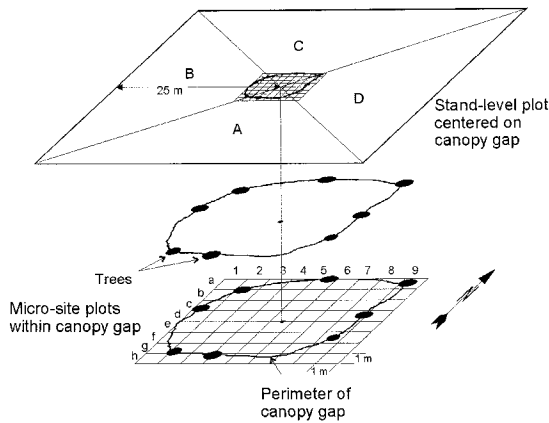
FIGURE 2. Layout of stand sampling protocol. Top: stand sampling area centred on canopy gap; Bottom: detailed location of sample plots within canopy gap.

In the Omineca region the BWBS zone is found from valley bottoms up to 1,100 m elevation in an area roughly north of 54°N latitude (Meidinger & Pojar 1991). Characterized by a northern continental climate, the zone has long cold winters and a short growing season. Average monthly temperatures remain below 0°C for 5–7 months of the year and rise above 10°C for only two to four months of the year. July is the warmest month with a mean summer temperature of 13.0°C (Anonymous 1993). Between 330 and 570 mm of precipitation falls annually, 35 to 55 percent of this falling as snow.

Study sites in pine-lichen woodlands were chosen so as to represent stands at a similar stage of late successional development, from 100 to 130 yr in age, where the forest floor surface was dominated by terrestrial lichen mats, predominantly *Cladina mitis* and *C. rangiferina*. Stands were labelled as West Germansen, Germansen Lake, and Manson. Terrain at the West Germansen and Manson sites was flat-uniform, while terrain at the Germansen Lake site was slightly more variable ranging from flat-uniform to slightly rolling.

## METHODS

Measurements within pine-lichen woodlands were taken at two different scales of study. Stand-level plot measurements were conducted within 625 m² plots, these centered on a candidate canopy gap within the stand as outlined in Figure 2. Within this canopy gap detailed microsite plot measurements were taken, using one m² quadrats located within the perimeter of a canopy gap (Fig. 2).

A total of thirty stand-level plots were established in natural gaps within the pine-lichen woodland, ten at each study site (Table 1). These gaps result from self-thinning during the first century of stand development. Five of the stand-level plots at each site were selected based on the dominant expression of reindeer lichens at the forest floor surface and five were selected based on the dominant expression of feather moss mats. A quick assessment was conducted to determine if moss dominated microsites had the potential to support lichens. This was done by looking for remnant or buried lichen mats within or under existing moss mats.

Microsite plots were implemented within each canopy gap, these centered within the stand-level plots as outlined in Figure 2. This allowed for the detailed characterization of forest floor plant communities within canopy gaps and of surrounding canopy structure within the stand. A systematic format of data collection was employed. The stages involved were: 1) laying out the nested design within the stand-level plots; 2) obtaining percent cover measurements within all microsite plots based on estimation within the following categories: *Cladina* spp. i.e., reindeer lichens; foliose lichens e.g., *Peltigera* spp.; other lichens; feather moss mats, predominately *Pleurozium schreberi*; other mosses; mineral soil; rock; coarse woody debris; litter; and forbs. Although these categories for the estimation of non-vascular plant cover are based on morphology, in many ways these groups, particularly the differentiation between ''reindeer lichens'' and feather-moss mats, act as functional groups in that they delineate mid- and late-seral successional stages within these stands (Coxson & Marsh 2001); 3) measuring the presence or absence of all vascular and selected non-vascular (macrolichens, mosses and liverworts only) plant species within randomly selected microsite plots; 4) measuring tree density in all four quarters of the stand-level plots and obtaining detailed measurements of other tree parameters (basal area, tree volume, tree biomass, crown biomass, and crown area) within the south quarter of stand-level plots (the south side of each plot location having the greatest influence on direct light interception within the canopy gap); 5) sampling randomly chosen microsite plots for organic matter accumulation, separated by aboveground components (the cumulative biomass of lichens, acrocarpous moss and litter) and below-ground components (humus accumulation) including all litter, above the mineral soil horizon; and 6) measuring leaf area index in all microsite plots.

This sampling protocol insured that vegetation cover estimates were obtained prior to other stand-level measures being taken, thereby minimizing disturbance effects on surface vegetation.

Detailed assessments in the stand-level plots were conducted using standard forest mensuration techniques to collect tree data (Husch et al. 1993). Qualitative assess-

TABLE 1. Plot locations in the Germansen-Omineca region of north-central British Columbia.

| Site | Longitude | Latitude | Elevation | Plot type | Stand ages | | | |
| | | | | | Oldest tree | Mean age | S.E. | n |
|---|---|---|---|---|---|---|---|---|
| West Germansen Sites | 125°06′50″ | 55°38′55″ | 1,120 m | Lichen | 153 | 119 | 10 | 100 |
| | | | | Moss | 147 | 121 | 6 | 100 |
| Manson Sites | 124°34′00″ | 55°42′05″ | 955 m | Lichen | 150 | 117 | 3 | 100 |
| | | | | Moss | 154 | 114 | 4 | 100 |
| Germansen Lake Site | 124°56′53″ | 55°40′50″ | 1,045 m | Lichen | 160 | 113 | 2 | 100 |
| | | | | Moss | 146 | 114 | 12 | 100 |

ments on tree form and overall health were also recorded. A subset of 20 stems, based on the 10 largest and another 10 chosen from a range of diameter classes, was selected to determine the age of each stand plot. Core samples were taken at stump height (0.30 m) and rings were counted in the field. A correction factor of seven years was applied to determine total age, based on comparisons with trees destructively sampled at the forest floor surface. Tree volumes were subsequently calculated using the volume equations in the Forestry Handbook (Watts 1983). Biomass figures were determined using equations derived by Standish et al. (1985) and crown area was determined using equations from Cade (1997).

The composition of forest floor plant communities and organic matter accumulation was assessed in a minimum of 10 randomly chosen quadrats for each microsite plot series. Species composition within microsite plots was determined using visual estimates taken within $0.71 \times 0.71$ m quadrats nested in the southwest corner of the larger one $m^2$ quadrat. Nomenclature of lichens, mosses, liverworts and vascular plants follows Esslinger and Egan (1995), Lawton (1971), Stotler and Crandall-Stotler (1977), and Hitchcock and Cronquist (1973), respectively. Voucher specimens for lichens and bryophytes are in the University of Northern British Columbia herbarium (UNBC).

Leaf area index (LAI) was measured in microsite plots using the remote mode procedure of the LI-COR LAI-2000 plant canopy analyser. LAI data was collected during time periods when there was no direct radiation on the foliage, under conditions of diffuse overcast sky.

*Data analysis.*—Measured values are reported as the mean plus or minus one standard deviation. Treatment effects (moss versus lichen dominated microsites) were examined by analysis of variance at each stand location. The statistical significance of treatment effects in microsite plots (leaf area index and soil litter/organic matter content) at each stand was examined using paired *t*-tests. These comparisons are denoted as significant in the text when probability values in any of the stand locations do not exceed 0.05. To determine if differences existed with stand characterization variables (which could be correlated to the microsite level) the significance level was set at 0.1. This reduced the probability of a Type II error resulting from extraneous data in the sample. *T*-tests were also used to evaluate the significance of correlation coefficients (Fisher 1990).

Leaf area index values were compared between quadrats with less than a one percent cover of feather moss versus those with one percent or greater. This threshold represents the percent cover that can be clearly expressed through ocular evaluation of quadrats. An index value of moss was derived for each plot based on the coding of moss presence for each quadrat. This code was compared to the average LAI value for each plot. The correlation between the two variables, moss presence code and LAI, indicates the relationship between them.

Not all quadrats within the chosen openings were used in the analysis of leaf area index. Assessment of the raw data indicated that most outlier data points occurred in quadrats that were adjacent to a tree or that had a tree within the quadrat. Tree stems within one meter of the sensor blocked out a large portion of the visible sky but did not accurately represent foliage interceptance cover. In turn, all quadrats around the perimeters of the gaps were dropped. Though the relationship was consistent between the raw data and the data not containing quadrats on the perimeter, the effect is greater where outliers were dropped.

RESULTS

The species composition of vascular plants within moss or lichen dominated microsites showed little variation between plot types (Table 2). Likewise, this consistency was maintained between the three sites supporting the classification of all three sites into the same plant association. The two exceptions are the presence of *Vaccinium membranaceum* at the West Germansen site and not at the other two and the absence of *Arctostaphylos uva-ursi* from the West Germansen, though it was present at both the other sites. Regarding relationships between moss and lichen dominated microsites, *Empetrum nigrum* is the only vascular plant that expressed a week trend of higher cover on moss dominated microsites.

The cover of non-vascular plants and cryptogams also expressed limited variation at the species level when assessed both between different types of microsites and between sites. *Pleurozium schreberi* is the only species to express a significant difference in the percent cover between microsite types. Another weak trend that is expressed is the relationship of a higher cover of *Cladonia* spp. at lichen microsites compared to moss microsites. This trend concurs with the successional development of lichen woodlands in the Omineca (Coxson & Marsh 2001).

Table 3 lists percent cover estimates by evaluation category. Lichen and litter cover related categories expressed consistent trends of higher values at the lichen dominated microsites. Only moss related estimates showed trends of higher values in moss dominated microsites. The Feather Moss group was the sole category to express significant differences between moss and lichen dominated microsites.

At all three sites consistent relationships were found between stand structure and the presence of moss or lichen dominated microsites (Table 4). Analysis of variance indicates a significant "treatment" effect between moss or lichen dominated microsites and canopy structural variables within each stand. At each site, plots with dominant moss cover had significantly higher values for total plot tree basal area, total plot tree volume, total plot tree biomass, and total plot crown biomass compared to lichen dominated plots. An additional variable that supports this trend is crown area, however, it was found to be significantly different at only two of the three sites. Consistent trends were observed between stand structural variables and the presence or absence of moss within each of the sampling locations. However, structural variables for both plot types (moss and lichen) were lower at the West Germansen Site.

TABLE 2. Percent frequency occurrence and mean percent cover by species ($\pm$ 1 standard deviation) in moss-and lichen-dominated microsites plots at West Germansen, Manson, and Germansen Lake Sites. Total $n$ for lichen- and moss-dominated microsite plots was 36 and 112, respectively.

| Species | Micro-plot type | West Germansen sites | | | Germansen Lake sites | | | Manson sites | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Percent frequency | Mean percent cover | S.E. of cover | Percent frequency | Mean percent cover | S.E. of cover | Percent frequency | Mean percent cover | S.E. of cover |
| **Vascular Plants** | | | | | | | | | | |
| *Arctostaphylos uva-ursi* | lichen | 0 | 0 | — | 28.6 | 0.21 | 0.15 | 33.3 | 0.54 | 0.33 |
| | moss | 0 | 0 | — | 27.9 | 0.32 | 0.14 | 56.8 | 0.49 | 0.11 |
| *Arnica cordifolia* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 3.1 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| *Calamagrostis canadensis* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 0 | 0 | — | 0 | 0 | — | 2.7 | 0.00 | 0.00 |
| *Calamagrostis purpurascens* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 0 | 0 | — | 2.3 | 0.01 | 0.01 | 0 | 0 | — |
| *Cornus canadensis* | lichen | 76.5 | 0.41 | 0.12 | 85.7 | 0.47 | 0.27 | 0 | 0 | — |
| | moss | 87.5 | 0.86 | 0.12 | 65.1 | 0.37 | 0.08 | 13.5 | 0.07 | 0.03 |
| *Empetrum nigrum* | lichen | 11.8 | 0.09 | 0.06 | 0 | 0 | — | 0 | 0 | — |
| | moss | 46.9 | 1.02 | 0.30 | 2.3 | 0.02 | 0.02 | 8.1 | 0.23 | 0.19 |
| *Epilobium angustifolium* | lichen | 0 | 0 | — | 14.3 | 0.01 | 0.01 | 0 | 0 | — |
| | moss | 0 | 0 | — | 18.6 | 0.02 | 0.01 | 0 | 0 | — |
| *Geocaulon lividum* | lichen | 0 | 0 | — | 0 | 0 | — | 16.7 | 0.04 | 0.04 |
| | moss | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| *Linnaea borealis* | lichen | 23.5 | 0.09 | 0.05 | 71.4 | 0.44 | 0.17 | 58.3 | 0.58 | 0.24 |
| | moss | 43.7 | 0.20 | 0.05 | 72.1 | 0.91 | 0.23 | 83.8 | 0.57 | 0.12 |
| *Lycopodium complanatum* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 34.4 | 0.40 | 0.15 | 0 | 0 | — | 0 | 0 | — |
| *Oryzopsis asperifolia* | lichen | 5.9 | 0.01 | 0.01 | 14.3 | 0.07 | 0.07 | 16.7 | 0.05 | 0.04 |
| | moss | 18.8 | 0.04 | 0.02 | 11.6 | 0.04 | 0.02 | 21.6 | 0.11 | 0.04 |
| *Oryzopsis punjens* | lichen | 5.9 | 0.03 | 0.03 | 42.9 | 0.16 | 0.10 | 16.7 | 0.13 | 0.09 |
| | moss | 3.1 | 0.02 | 0.02 | 25.6 | 0.07 | 0.02 | 16.2 | 0.04 | 0.02 |
| *Pyrola asarifolia* | lichen | 5.9 | 0.06 | 0.06 | 0 | 0 | — | 0 | 0 | — |
| | moss | 3.1 | 0.02 | 0.02 | 2.3 | 0.01 | 0.01 | 0 | 0 | — |
| *Pyrola secunda* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 3.1 | 0.00 | 0.00 | 0 | 0 | — | 0 | 0 | — |
| *Rosa acicularis* | lichen | 0 | 0 | — | 28.6 | 0.16 | 0.14 | 8.3 | 0.01 | 0.01 |
| | moss | 9.4 | 0.07 | 0.06 | 27.9 | 0.15 | 0.10 | 8.1 | 0.01 | 0.00 |
| *Vaccinium caespitosum* | lichen | 88.2 | 0.65 | 0.16 | 0 | 0 | — | 16.7 | 0.08 | 0.06 |
| | moss | 84.4 | 1.66 | 0.45 | 9.3 | 0.06 | 0.05 | 2.7 | 0.01 | 0.01 |
| *Vaccinium membranaceum* | lichen | 41.2 | 0.28 | 0.13 | 0 | 0 | — | 0 | 0 | — |
| | moss | 59.4 | 0.45 | 0.10 | 0 | 0 | — | 0 | 0 | — |
| *Vaccinium vitis-idea* | lichen | 0 | 0 | — | 100 | 0.39 | 0.07 | 66.7 | 1.71 | 0.97 |
| | moss | 0 | 0 | — | 90.7 | 0.93 | 0.13 | 78.4 | 1.03 | 0.23 |
| **Non-vascular Plants** | | | | | | | | | | |
| *Barbilophozia lycopodioides* | lichen | 52.9 | 0.19 | 0.06 | 100 | 0.34 | 0.13 | 83.3 | 1.25 | 0.43 |
| | moss | 56.3 | 5.82 | 2.82 | 53.5 | 0.17 | 0.04 | 64.9 | 0.45 | 0.09 |
| *Cetraria cucullata* | lichen | 0 | 0 | — | 0 | 0 | — | 8.3 | 0.01 | 0.01 |
| | moss | 0 | 0 | — | 4.7 | 0.00 | 0.00 | 13.5 | 0.04 | 0.02 |
| *Cetraria ericetorum* | lichen | 94.1 | 0.42 | 0.04 | 85.7 | 0.20 | 0.08 | 91.7 | 0.46 | 0.04 |
| | moss | 40.6 | 0.14 | 0.04 | 27.9 | 0.17 | 0.12 | 86.5 | 0.41 | 0.04 |
| *Cetraria nivalis* | lichen | 0 | 0 | — | 0 | 0 | — | 8.3 | 0.01 | 0.01 |
| | moss | 6.3 | 0.03 | 0.02 | 2.3 | 0.00 | 0.00 | 2.7 | 0.00 | 0.00 |
| *Cladina mitis* | lichen | 100.0 | 21.94 | 3.98 | 100.0 | 9.71 | 2.13 | 91.7 | 6.08 | 0.79 |
| | moss | 68.8 | 3.23 | 0.96 | 97.7 | 8.24 | 1.48 | 100.0 | 5.87 | 1.03 |
| *Cladina rangiferina* | lichen | 70.6 | 2.04 | 0.55 | 85.7 | 1.09 | 0.41 | 91.7 | 2.92 | 0.90 |
| | moss | 81.3 | 4.33 | 0.88 | 83.7 | 2.50 | 0.70 | 100 | 2.46 | 0.44 |
| *Cladina stellaris* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 9.4 | 0.23 | 0.17 | 2.3 | 0.05 | 0.05 | 0 | 0 | — |
| *Cladonia bellidiflora* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 18.8 | 0.08 | 0.03 | 0 | 0 | — | 0 | 0 | — |
| *Cladonia borealis* | lichen | 5.9 | 0.03 | 0.03 | 0 | 0 | — | 0 | 0 | — |
| | moss | 9.4 | 0.02 | 0.02 | 0 | 0 | — | 0 | 0 | — |
| *Cladonia carneola* | lichen | 41.2 | 0.11 | 0.05 | 14.3 | 0.01 | 0.01 | 8.3 | 0.04 | 0.04 |
| | moss | 18.8 | 0.05 | 0.03 | 4.7 | 0.00 | 0.00 | 5.4 | 0.02 | 0.01 |
| *Cladonia cenotea* | lichen | 5.9 | 0.01 | 0.01 | 0 | 0 | — | 16.7 | 0.05 | 0.04 |
| | moss | 6.3 | 0.01 | 0.00 | 2.3 | 0.00 | 0.00 | 8.1 | 0.02 | 0.01 |

TABLE 2. Continued.

| Species | Micro-plot type | West Germansen sites | | | Germansen Lake sites | | | Manson sites | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Percent frequency | Mean percent cover | S.E. of cover | Percent frequency | Mean percent cover | S.E. of cover | Percent frequency | Mean percent cover | S.E. of cover |
| *Cladonia cervicornis* | lichen | 29.4 | 0.08 | 0.04 | 14.3 | 0.01 | 0.01 | 33.3 | 0.10 | 0.06 |
| | moss | 12.5 | 0.04 | 0.02 | 7 | 0.01 | 0.00 | 13.5 | 0.04 | 0.02 |
| *Cladonia chlorophaea* | lichen | 35.3 | 0.11 | 0.05 | 28.6 | 0.03 | 0.02 | 33.3 | 0.17 | 0.07 |
| | moss | 31.3 | 0.09 | 0.03 | 18.6 | 0.02 | 0.01 | 40.5 | 0.13 | 0.03 |
| *Cladonia cornuta* | lichen | 76.5 | 0.29 | 0.06 | 71.4 | 0.24 | 0.09 | 91.7 | 0.43 | 0.05 |
| | moss | 53.1 | 0.18 | 0.04 | 62.8 | 0.18 | 0.03 | 86.5 | 0.36 | 0.03 |
| *Cladonia crispata* | lichen | 47.1 | 0.19 | 0.07 | 71.4 | 0.31 | 0.14 | 58.3 | 0.27 | 0.09 |
| | moss | 46.9 | 0.55 | 0.23 | 37.2 | 0.12 | 0.03 | 56.8 | 0.23 | 0.04 |
| *Cladonia deformis* | lichen | 58.8 | 0.18 | 0.05 | 0 | 0 | — | 25.0 | 0.09 | 0.06 |
| | moss | 25.0 | 0.08 | 0.03 | 18.6 | 0.03 | 0.01 | 27.0 | 0.09 | 0.03 |
| *Cladonia ecmocyna* | lichen | 100 | 1.29 | 0.37 | 85.7 | 0.33 | 0.14 | 83.3 | 0.75 | 0.31 |
| | moss | 78.1 | 0.46 | 0.07 | 62.8 | 0.22 | 0.04 | 83.8 | 0.37 | 0.04 |
| *Cladonia fimbriata* | lichen | 41.2 | 0.14 | 0.05 | 14.3 | 0.01 | 0.01 | 41.7 | 0.14 | 0.06 |
| | moss | 21.9 | 0.06 | 0.03 | 0 | 0 | — | 40.5 | 0.13 | 0.03 |
| *Cladonia gracilis* | lichen | 0 | 0 | 0 | 28.6 | 0.09 | 0.07 | 16.7 | 0.05 | 0.04 |
| | moss | 31.3 | 0.23 | 0.08 | 4.7 | 0.00 | 0.00 | 29.7 | 0.06 | 0.02 |
| *Cladonia multiformis* | lichen | 5.9 | 0.01 | 0.01 | 0 | 0 | — | 0 | 0 | — |
| | moss | 21.9 | 0.10 | 0.04 | 0 | 0 | — | 5.4 | 0.01 | 0.00 |
| *Cladonia phyllophora* | lichen | 70.6 | 0.21 | 0.05 | 85.7 | 0.31 | 0.09 | 58.3 | 0.29 | 0.07 |
| | moss | 25.0 | 0.09 | 0.03 | 32.6 | 0.11 | 0.03 | 51.4 | 0.19 | 0.04 |
| *Cladonia pleurota* | lichen | 0 | 0 | — | 28.6 | 0.03 | 0.02 | 8.3 | 0.01 | 0.01 |
| | moss | 21.9 | 0.08 | 0.03 | 7.0 | 0.02 | 0.01 | 16.2 | 0.02 | 0.01 |
| *Cladonia pyxidata* | lichen | 47.1 | 0.19 | 0.06 | 14.3 | 0.01 | 0.01 | 0 | 0 | — |
| | moss | 12.5 | 0.03 | 0.02 | 0 | 0 | — | 10.8 | 0.01 | 0.01 |
| *Cladonia sulphurina* | lichen | 64.7 | 0.21 | 0.06 | 28.6 | 0.14 | 0.09 | 25.0 | 0.03 | 0.01 |
| | moss | 34.4 | 0.25 | 0.16 | 18.6 | 0.02 | 0.01 | 32.4 | 0.11 | 0.03 |
| *Cladonia uncialis* | lichen | 47.1 | 1.58 | 0.70 | 85.7 | 1.09 | 0.67 | 91.7 | 0.85 | 0.39 |
| | moss | 34.4 | 0.28 | 0.13 | 55.8 | 0.26 | 0.07 | 78.4 | 0.87 | 0.24 |
| *Dicranum* spp. | lichen | 82.4 | 0.69 | 0.24 | 85.7 | 0.51 | 0.15 | 75.0 | 0.77 | 0.24 |
| | moss | 84.4 | 4.87 | 2.16 | 76.7 | 0.44 | 0.07 | 97.3 | 1.33 | 0.27 |
| *Nephroma* spp. | lichen | 5.9 | 0.01 | 0.01 | 14.3 | 0.43 | 0.43 | 0 | 0 | 0 |
| | moss | 0 | 0 | 0 | 7.0 | 0.12 | 0.10 | 0 | 0 | 0 |
| *Pannaria pezizoides* | lichen | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | moss | 0 | 0 | 0 | 2.3 | 0.00 | 0.00 | 0 | 0 | 0 |
| *Peltigera aphthosa* | lichen | 35.3 | 0.60 | 0.47 | 57.1 | 1.94 | 1.68 | 83.3 | 1.84 | 0.74 |
| | moss | 46.9 | 0.19 | 0.05 | 83.7 | 1.21 | 0.33 | 94.6 | 1.53 | 0.29 |
| *Peltigera malacea* | lichen | 17.6 | 0.09 | 0.06 | 71.4 | 1.61 | 1.26 | 58.3 | 1.55 | 0.84 |
| | moss | 28.1 | 0.22 | 0.11 | 55.8 | 0.45 | 0.12 | 45.9 | 0.84 | 0.30 |
| *Pleurozium schreberi* | lichen | 76.5 | 0.44 | 0.13 | 85.7 | 0.44 | 0.12 | 66.7 | 0.38 | 0.11 |
| | moss | 90.6 | 17.46 | 4.30 | 100 | 22.68 | 3.64 | 100 | 16.82 | 3.32 |
| *Pohlia* spp. | lichen | 58.8 | 0.29 | 0.12 | 14.3 | 0.01 | 0.01 | 16.7 | 0.08 | 0.06 |
| | moss | 50.0 | 0.28 | 0.07 | 30.2 | 0.03 | 0.01 | 40.5 | 0.19 | 0.04 |
| *Polytrichum juniperinum* | lichen | 52.9 | 0.31 | 0.12 | 85.7 | 0.33 | 0.14 | 50.0 | 1.04 | 0.56 |
| | moss | 56.3 | 0.45 | 0.19 | 39.5 | 0.24 | 0.08 | 54.1 | 0.87 | 0.31 |
| *Ptilidium pulcherrimum* | lichen | 0 | 0 | — | 0 | 0 | — | 0 | 0 | — |
| | moss | 0 | 0 | 0 | 2.3 | 0.00 | 0.00 | 0 | 0 | 0 |
| *Ptilium crista-castrensis* | lichen | 5.9 | 0.03 | 0.03 | 57.1 | 0.06 | 0.02 | 8.3 | 0.04 | 0.04 |
| | moss | 40.6 | 0.21 | 0.07 | 30.2 | 0.10 | 0.05 | 18.9 | 0.11 | 0.04 |
| *Stereocaulon alpinum* | lichen | 52.9 | 0.39 | 0.13 | 71.4 | 0.26 | 0.14 | 41.7 | 0.18 | 0.09 |
| | moss | 43.8 | 0.18 | 0.04 | 39.5 | 0.18 | 0.10 | 54.1 | 0.36 | 0.15 |

Leaf area index values (direct measurements) showed the same trends as crown area estimates (derived from stand structural values), with higher values in both cases for moss plots (Tables 4 and 5). Significant relationships were also found between LAI and each of the three stand characterization variables. Pearson correlation coefficients (r) between LAI and the variables were: basal area $r = 0.738$; tree volume $r = 0.686$, and total tree biomass, $r = 0.735$. *T*-tests supported the significance of all three correlation coefficients. A significant relationship between the presence of moss and leaf area index values was also found, as represented by the Pearson Coefficient of 0.511.

Isopleth plots provide a visual representation of these trends towards higher leaf area index values

TABLE 3. Mean percent cover estimates by category ($\pm$ 1 standard deviation) for moss-dominated and lichen-dominated microsite plots at West Germansen, Manson, and Germansen Lake Sites.

| Site | No. of plots | Reindeer lichens | Leafy lichens | Other lichens | Feather moss | Other moss | Mineral soil | Rock | Coarse woody debris | Litter | Forbs |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **West Germansen** | | | | | | | | | | | |
| Lichen Dominated Microsites | 88 | 24.8 ±17.9 | 0.1 ±0.4 | 4.6 ±4.3 | 0 | 3.0 ±2.9 | 0.1 ±0.3 | 1.2 ±0.3 | 3.5 ±5.5 | 6.8 ±6.9 | 4.6 ±5.4 |
| Moss Dominated Microsites | 167 | 11.8 ±12.0 | 0.4 ±1.0 | 2.7 ±2.6 | 16.5 ±20.9 | 3.1 ±3.3 | 0 | 0.5 ±0.2 | 5.06 ±11.2 | 4.2 ±2.9 | 8.1 ±6.5 |
| **Manson Sites** | | | | | | | | | | | |
| Lichen Dominated Microsites | 90 | 12.1 ±5.7 | 1.4 ±2.2 | 1.0 ±0.9 | 0.2 ±0.2 | 1.5 ±2.2 | 0 | 0.2 ±0.5 | 1.7 ±3.0 | 9.1 ±5.8 | 4.8 ±2.7 |
| Moss Dominated Microsites | 94 | 9.6 ±6.9 | 2.3 ±2.6 | 1.6 ±1.5 | 9.3 ±11.3 | 2.6 ±1.6 | 0.1 ±0.4 | 0.1 ±0.4 | 2.1 ±3.7 | 6.5 ±2.6 | 4.6 ±2.4 |
| **Germansen Lake Site** | | | | | | | | | | | |
| Lichen Dominated Microsites | 92 | 12.9 ±5.3 | 2.5 ±3.5 | 0.9 ±0.6 | 0.1 ±0.2 | 1.0 ±1.2 | 0 | 0.6 ±1.0 | 0.3 ±0.8 | 7.8 ±5.8 | 5.6 ±2.6 |
| Moss Dominated Microsites | 22 | 11.5 ±9.0 | 2.5 ±2.9 | 0.7 ±1.3 | 21.8 ±19.8 | 2.1 ±3.4 | 0 | 1.1 ±2.2 | 0.3 ±1.3 | 6.6 ±7.3 | 4.2 ±2.6 |

in moss dominated quadrats (Fig. 3). Feather moss quadrats were most abundant in portions of the plot openings protected from solar exposure. In this example the south portion of the plot was provided greater cover by the adjacent stand than the north half of the plot. This pattern is supported by the LAI contour plot. In general, the location of the feather moss morphological group was found in microsite plots with greatest LAI values.

The assessment of the biomass on a subset of intensively sampled quadrats revealed similar trends as the percent cover data (Table 5). The only statistically significant finding was noted when comparing cover groups that form unfavorable substrates for feather moss establishment, such as rock as coarse woody debris. The biomass of lichens, acrocarpous mosses and litter was found to be significantly greater for lichen quadrats compared to moss quadrats at all three sites. Organic matter content of surface soil horizons indicated an opposite trend to the assessment of unfavorable moss substrates. While it is not statistically significant, there was a trend towards greater organic matter content at quadrats with a moss component versus those without it at all three sites (Table 5).

## DISCUSSION

The distribution of bryophytes and lichens at any given site reflects the combined interactions of past and present propagule availability and site charac-teristics, both of which interact to determine subsequent establishment and growth of plant communities. In general, for lichens to be successful, these factors must interact to create environments that preclude competitive displacement by other plants, due to the more ''stress-tolerant'' life history strategy adopted by many lichens (Grime 1977).

When considering site characteristics, features of the mineral soil are typically among the most influential in changing the nature and distribution of the overstorey plant canopy in lichen woodlands. Of particular importance is the role of edaphic factors on growth rates and live biomass of the dominant trees species on a site. On lichen sites that succeed to a moss woodland state, succession is considered to be a function of the forest overstorey development (Carroll & Bliss 1982; Maikawa & Kershaw 1976). These factors interact through time, with periodic stand destroying fires ''resetting'' both edaphic and successional factors.

The influence of the forest canopy on non-vascular plant communities at the forest floor surface may be expressed through several mechanisms. The more well-developed the canopy structure is, the greater will be the direct interception of precipitation, reducing available water at the forest floor surface (Rutter 1975). Although this factor is important at a watershed level in changing patterns of runoff and total streamflow, the impact on moss and lichen communities may be small, expressed main-

TABLE 4. Mean stand-level plot values (± 1 standard deviation) for basal area, tree volume, tree biomass, crown biomass, and crown area from stand plots centered on gap openings (see Fig. 2 for layout), these respectively selected for moss presence, denoted as 'Moss' Stand Plots, or for moss absence, denoted as 'Lichen' Stand plots. *T* values and significance values are shown for *t*-test comparisons between 'Moss' and 'Lichen' plots; values in parenthesis are *n*-1 for each stand plot combination.

| Plot variable | Site | 'Moss' stand plots | 'Lichen' stand plots | Significance values |
|---|---|---|---|---|
| Tree Basal Area (m²/m²) | | | | |
| | West Germansen | 0.0026 ± 0.00022 | 0.0020 ± 0.00035 | $t(9) = 3.24$ $p = 0.018$ |
| | Germansen Lake | 0.0032 ± 0.00028 | 0.0026 ± 0.00056 | $t(9) = 2.01$ $p = 0.100$ |
| | Manson | 0.0032 ± 0.00023 | 0.0029 ± 0.00041 | $t(9) = 1.96$ $p = 0.098$ |
| Tree Volume (m³/m²) | | | | |
| | West Germansen | 0.016 ± 0.0015 | 0.013 ± 0.0023 | $t(9) = 2.77$ $p = 0.028$ |
| | Germansen Lake | 0.025 ± 0.0015 | 0.021 ± 0.0028 | $t(9) = 3.48$ $p = 0.013$ |
| | Manson | 0.024 ± 0.0033 | 0.021 ± 0.0026 | $t(9) = 1.91$ $p = 0.097$ |
| Tree Biomass (kg/m²) | | | | |
| | West Germansen | 11.94 ± 0.69 | 9.15 ± 1.45 | $t(9) = 3.87$ $p = 0.012$ |
| | Germansen Lake | 16.10 ± 8.27 | 12.96 ± 2.11 | $t(9) = 3.10$ $p = 0.027$ |
| | Manson | 1.58 ± 1.53 | 13.66 ± 1.56 | $t(9) = 2.22$ $p = 0.062$ |
| Crown Biomass (kg/m²) | | | | |
| | West Germansen | 2.55 ± 0.07 | 1.89 ± 0.27 | $t(9) = 5.32$ $p = 0.027$ |
| | Germansen Lake | 2.71 ± 0.17 | 2.19 ± 0.49 | $t(9) = 2.24$ $p = 0.089$ |
| | Manson | 2.79 ± 0.14 | 2.50 ± 0.26 | $t(9) = 2.16$ $p = 0.074$ |
| Crown Area (m²/m²) | | | | |
| | West Germansen | 1.21 ± 0.11 | 0.9 ± 0.13 | $t(9) = 2.78$ $p = 0.027$ |
| | Germansen Lake | 1.46 ± 0.22 | 1.30 ± 0.41 | $t(9) = 0.81$ $p = 0.46$ |
| | Manson | 1.69 ± 0.16 | 1.38 ± 0.26 | $t(9) = 2.21$ $p = 0.069$ |

ly in a reduced magnitude of wetting during small precipitation events, when the canopy intercepts most of the throughflow precipitation. More importantly, exposure to direct solar radiation after precipitation events can result in transient high rates of photosynthetic uptake, but will lead to rapid dessication of non-vascular cryptogams at the forest floor surface in pine stands (Coxson 1987).

In pine lichen woodlands, the nature of stand initiation can also play an important part in contributing towards the legacy of residual canopy structure and the early initiation of more shaded conditions at the forest floor surface. On sites where stand destroying fires are less severe in nature, the greater retention of organic soils and seed/propagule pools may result in a community structure that contains more elements from previous seral stages. This was evident while selecting sites for study under this project. In pine stands that had many fire scarred trees (evidence of canopy retention after the last major fire), there tended to be a greater abundance of moss in the understorey, compared to stands that did not contain trees with fire scars (and presumably had a total loss of canopy structure during the last fire).

Overstorey canopy development can also influence surface cryptogams through the deposition of litter on potentially slow growing lichen mats and through the buildup of surface organic horizons. A trend of greater soil organic matter development on microsites dominated by moss was evident in the present study area, although it cannot be stated

TABLE 5. Mean microplot values (± 1 Standard Deviation) for leaf area index and organic matter accumulation, the later separated be above-ground components (the cumulative biomass of lichens, acrocarpous moss and litter) and below-ground components (humus accumulation). Significance values are shown for *t*-test comparisons between 'Moss' and 'Lichen' plots; numbers in parenthesis are *n*-1 values for indicated microplot conditions.

| Plot variable | Site | Moss plots | Lichen plots | Significance values |
|---|---|---|---|---|
| Leaf Area Index $(m^2/m^2)$ | | | | |
| | West Germansen | $1.617 \pm 0.267$ | $1.551 \pm 0.235$ | $t(254) = 4.62$ $p < 0.0001$ |
| | Germansen Lake | $1.700 \pm 0.259$ | $1.637 \pm 0.136$ | $t(113) = 3.75$ $p = 0.0004$ |
| | Manson | $1.961 \pm 0.418$ | $1.787 \pm 0.281$ | $t(183) = 3.67$ $p = 0.0003$ |
| Sum of lichens, acrocarpous moss, and litter $(kg/m^2)$ | | | | |
| | West Germansen | $0.84 \pm 0.40$ | $1.26 \pm 0.26$ | $t(48) = 4.36$ $p = 0.0001$ |
| | Germansen Lake | $0.95 \pm 0.37$ | $1.18 \pm 0.30$ | $t(49) = 2.29$ $p = 0.03$ |
| | Manson | $1.09 \pm 0.25$ | $1.27 \pm 0.29$ | $t(48) = 2.28$ $p = 0.28$ |
| Humus $(kg/m^2)$ | | | | |
| | West Germansen | $0.91 \pm 0.48$ | $0.77 \pm 0.36$ | $t(48) = 1.17$ $p = 0.25$ |
| | Germansen Lake | $1.11 \pm 0.82$ | $0.85 \pm 0.67$ | $t(49) = 0.98$ $p = 0.34$ |
| | Manson | $1.00 \pm 0.42$ | $0.83 \pm 0.40$ | $t(48) = 1.34$ $p = 0.19$ |

whether this is a causal factor or merely the result of greater litter accumulation after moss establishment. This effect is consistent with the findings of Steijlen et al. (1994), who found that microsites dominated by moss had significantly higher organic biomass compared to sites with just lichen.

The overall success of feather moss mats at the forest floor surface, however, may be determined most by changes in overstorey architecture. On all sites studied, the biomass of the forest overstorey was greater where feather moss was present. One method used to assess this was by evaluating leaf area index. In the Omineca site, LAI in pine-lichen woodlands was highly correlated with stand overstorey variables. In stands that have both a greater biomass of trees, and large tree sizes, LAI was higher. Larger trees, and thus higher leaf area index values, corroborate with lower levels of available solar radiation and the greater likelihood of microsites having feather moss present.

Although changes in canopy structure are covariate with time since stand initiation, recent findings of Coxson and Marsh (2001) indicate that low-impact (winter-harvest) removal of overstory canopy can result in the short-term return (at 30 yr after harvest) of sites to a moss-dominated status. This supports arguments that the development of moss- or lichen-dominated microsites within a stand reflects small-scale differences in the immediately subtending canopy structure. The development of these small-scale variations in canopy structure is time-dependant, reflecting previous stages of stand development and disturbance history.

Stochiastic events early in stand development will also play a role in determining the nature of initial propagule establishment. Pharo and Vitt (2000), for instance, did not find a strong correlation between canopy density and local variations in moss and lichen cover in montane forests from Alberta and speculate that early establishment events may be more important than we have previously thought. The burial of existing lichen mats through infilling by feather moss mats on our sites strongly suggests that the balance of competitive interactions between these species changes in localized microsites late in stand development. It is interesting in this regard that we have observed small stems of *P. schreberi* widely co-existent within terrestrial lichen mats in younger pine-lichen woodland stands near our sites (Coxson & Marsh 2001), suggesting a common point of initiation early in stand life for both functional groups. However, as in the case of epiphytic lichen communities (McCune & Antos 1982), competitive interactions are ultimately linked to environmental gradients involving both stand age, and available light and moisture at specific microsites. What is uncertain is
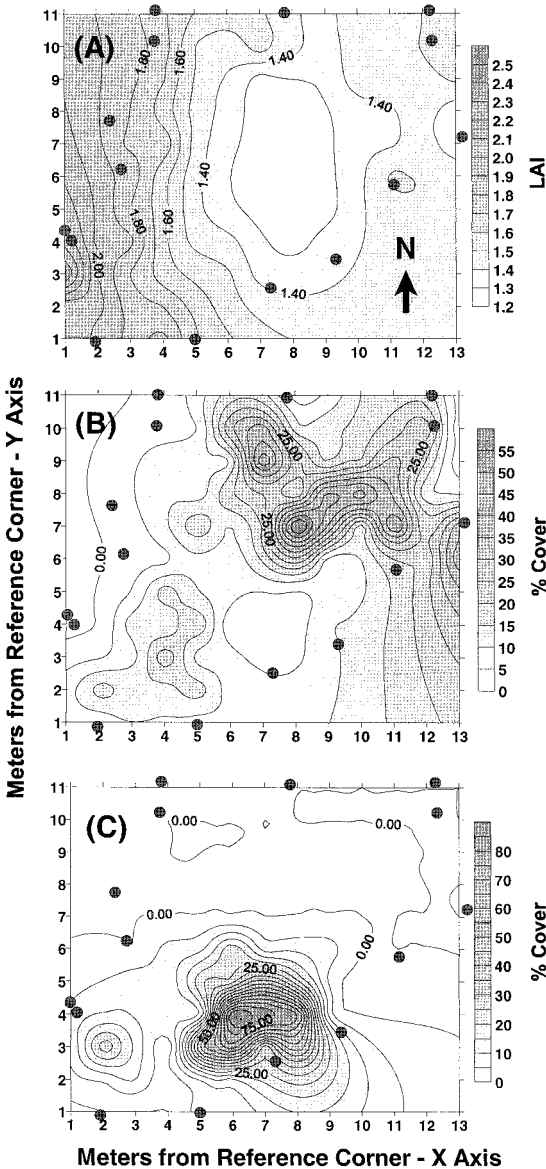
FIGURE 3.   Isopleth plot of forest floor in representative canopy gap in pine-lichen woodlands. From top: A) Leaf Area Index, B) percent cover of *Cladina* spp., and C) percent cover of feather moss mats.

whether the nature of these interactions may change within managed stands (Esseen et al. 1996).

The data set developed for this project does not provide critical thresholds for stand characterisation variables that can be used to differentiate moss versus lichen areas. Stand characterisation data express variation between the three sites. In particular, lower values for all characterisation variables were found at the West Germansen site, which is the highest elevation of all three in this study. Based on elevation alone, the West Germansen site could be classed as being in the Engelmann Spruce-Sub-

alpine Fir (ESSF) biogeoclimatic zone and have a slightly different microclimate. Because, the vegetation community and soils were not different from the other two sites, it was considered to be within the BWBS. The notion of microclimatic variation is supported by anecdotal information from residents in the study area. They indicated the snow depths in the vicinity of the West Germansen site can be deeper than those found at the other two sites. It is probable the West Germansen site is transitional to the higher elevation sites in the ESSF and could be considered a slightly different phase from the other two sites that are truly in the BWBS. The interaction of stand structure and surface microsite development, however, was similar in all three sites, despite these elevational differences.

The values determined for LAI within this study represent two dimensional relative measures from microsite sampling plots, each representing the portion of the sky that is blocked out of view by foliage (Welles & Norman 1991). High LAI measures therefore correspond to high foliage biomass of trees and attendant greater interception of solar radiation (Cable 1958; Cade 1997). The structure of trees is also an important factor in determining light and wind penetration to the forest floor (Korzukhin & Ter-Mikaelian 1995). Taller trees with greater vertical structure of the crown expose more leaves to incoming radiation than do shorter trees. This results in an improved efficiency of the absorption of solar radiation. Using equations derived by Standish et al. (1985) the calculated biomass of the crowns at each site is greater at the plots selected for moss presence than those selected for its absence.

The other important factor associated with the presence of larger trees is a decrease in the ventilation through a stand. Ventilation is a critical factor impacting growth rates for many lichen species. Reducing the air flow through a stand reduces the amount of moisture drawn away from a microsite. This increases the availability of atmospheric moisture (humidity) to plants that is an important precondition for the establishment of feather moss mats (Tamm 1964). Although both lichens and moss, in general, respond favorably to longer hydration episodes, which increase the duration of physiological activity, in practice, many lichen species seem to be excluded from sites with prolonged duration of hydration (Goward 1998). This may reflect the sensitivity of lichen symbiosis to prolonged wetting (Tysiaczny & Kershaw 1979). Additionally, under conditions of slow drying respiratory carbon loss from fungal bionts may have an adverse effect on long-term growth of *Cladina* (Tegler & Kershaw 1980). This constraint is not as severe in feather mosses mosses such as *Hylocom-*

*ium splendens,* where respiratory carbon loss at low water contents does not represent as high a proportion of overall carbon budgets (Sonesson et al. 1992).

A final constraint on the future development of pine-lichen woodlands is the widespread adoption of fire-suppression as a management policy in the past several decades. Future development of managed stands may differ greatly from those of historically fire-origin stands (Coxson & Marsh 2001). Factors such as tree stocking, density at planting, stand tending, and rotation length to harvest will each influence the development of understory plant communities. Our research findings indicate that stand structure is an important variable in retaining or enhancing the growth of reindeer lichens. Once overstorey forest biomass and resultant LAI values exceed threshold values, the transition of forest floor cryptogamic communities to a feather-moss dominated stage may occur quite rapidly.

Understanding the relationship between stand structure and lichen presence will provide resource managers with greater ability to retain a diversity of lichen communities in managed forests. However, care must be taken that the effects of stand level manipulations are considered in context of landscape level trends in lichen diversity and abundance (Dettki & Esseen 1998). In the Omineca region of northern British Columbia integrating information on stand structure and lichen development provides additional means towards insuring future availability of terrestrial lichen mats and the maintenance of related habitat values, such as forage availability for northern caribou.

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