

## Microclimate differences above ground-layer vegetation in lichen-dominated pine forests of north-central British Columbia

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### ABSTRACT

Lodgepole pine forests of north-central British Columbia have patchy ground-layer vegetation, typically dominated by either fruticose lichens, feathermosses, or ericaceous vascular plants; this patchy structure has been shown to correspond with environmental variables that likely moderate the ground-layer microclimate. To investigate the potential role of microclimate on patterns of dominance of ground-layer functional groups, we recorded temperature and relative humidity above the ground-layer vegetation during 25 summer days over patches dominated by mat-forming lichens, feathermosses, or vascular plants. Data were summarized for raw microclimate attributes and daily water potential of the air, and in terms of modelled equilibrium water content of moss or lichen thalli. Analysis of variance revealed significant differences in the water potential of air above the three patch types under sunny conditions, but not under overcast conditions. Differences in vegetation cover were only associated with differences in atmospheric moisture when using data from sunny periods during the daytime. These data confirm that lichens occupy microclimatic niches that are distinctly drier than those of feathermosses or vascular plants, and corroborate the suggested mechanism by which canopy or soil properties influence these types of ground-layer vegetation.

### 1. Introduction

Many studies have described the influence of humidity, water potential, and other measures of atmospheric moisture on physiological activity in bryophytes and lichens under controlled conditions (Longton, 1988; Proctor, 2000). Because the greatest diversity of lichens and mosses occurs in locations with exceptionally high rainfall, the greater importance of precipitation compared to other types of atmospheric water is clear (Goward and Spribille, 2005; Hauck and Spribille, 2005; Radies et al., 2009; Turner et al., 2006). Nevertheless, when precipitation is limited, water supplied as condensate or vapour (e.g., dew or fog) may be an important mechanism of hydration, leading to rich and diverse communities on its own (Kidron et al., 2002; Lange et al., 1991). Studies that investigate the relationship between water availability and cryptogam dominance or distribution, should therefore incorporate both precipitation events and the various forms of water vapour.

The frequency or duration of water supply can be affected by small-scale variation in vegetation cover or topography, particularly when this variation affects whether or not a given patch receives direct irradiance from the sun (Chen et al., 1993; Jones, 1983; Kidron, 2005).

Such processes are thought to be responsible for much of the patchiness in understory (including field and ground-layer) vegetation of boreal regions (Kembel and Dale, 2006; Kuuluvainen and Hokkanen, 1993). For example, differing irradiance may be responsible for the differentiation of epixylic bryophyte communities on fallen logs between eastward-facing and westward-facing aspects (Jansová and Soldán, 2006), and the combination of differing irradiance and precipitation interception appear to be important controls on the small-scale patchiness of lichen and feathermoss-dominated ground layers of lodgepole pine (*Pinus contorta* var. *latifolia*) forests (Haughian and Burton, 2015; Sulyma and Coxson, 2001).

The associations between ground cover vegetation and microclimate in lichen-dominated ecosystems have been studied intensively in parts of central Canada, but studies elsewhere have tended to consider the role of microclimate only indirectly, via the assumed effects of other habitat variables. For example, soil moisture conditions have been shown to coincide with both the growth rate and size of lichen thalli (Kershaw and Rouse, 1971), and with the overall community composition of ground layer vegetation over space and time (Kershaw, 1977; Rouse and Kershaw, 1973). Scientists in western Canada have also suggested that niche differentiation among ground-layer functional

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groups is driven by moisture availability and evaporative stress, with mat-forming *Cladonia* species preferring more xeric sites and feathermosses or low vascular plants preferring more mesic sites (Ahti and Hepburn, 1967; Brown et al., 2000; Carroll and Bliss, 1982; Cichowski and Williston, 2008; Haughian and Burton, 2015; Sulyma and Coxson, 2001), but their evidence was correlational, and limited to the likely moderators of these microclimatic properties, including soil texture, organic layer depth, and canopy cover.

The objectives of this study were to determine whether the three dominant ground-layer functional groups (namely reindeer lichens, feathermosses, and low-vascular plants) in boreal lodgepole pine forests are associated with distinct microclimatic niches. We predicted that lichen patches would have the least, and feathermoss patches would have the greatest moisture availability.

## 2. Methods

### 2.1. Study area

The study area spanned 125° 00′–126° 30′ W longitude and 55° 30′–57° 00′ N latitude, in the Omineca Mountains of northern British Columbia. All sites are located in the Stikine variant of the dry-cool Boreal White and Black Spruce biogeoclimatic subzone (BWBSdk1, DeLong, 2004), range from approximately 800–1000 m in elevation, have a mean annual precipitation of 511–622 mm, and have a mean annual temperature of  $-0.1$  to  $1.3^{\circ}$  C (values from Climate BC v 3.21, Wang et al., 2006). Pine-dominated sites in the BWBSdk1 are generally nutrient-poor, xeric or subxeric in moisture regime, and of glacial-fluvial or colluvial origins that are extremely coarse-textured (DeLong, 2004; Plouffe, 1997a, 1997b), but surficial geology data specific to the sites were not available in site selection. Where the stoniness is low enough, soils are Dystric Brunisols under the Canadian System of Soil Classification (Soil Classification Working Group, 1998), but are merely skeletal amid large concentrations of cobbles and boulders in some locations.

Forest fires occur frequently in the study area, contributing to canopies dominated by lodgepole pine with occasional subdominant hybrid white spruce (*Picea engelmannii* x *glauca*), black spruce (*Picea mariana*), subalpine fir (*Abies lasiocarpa*), or trembling aspen (*Populus tremuloides*). The forest understory is sparsely dominated by *Shepherdia canadensis* in the shrub layer, and by *Vaccinium* spp., *Arctostaphylos uva-ursi*, *Pleurozium schreberi* or *Cladonia* (subgenus *Cladina*) and *Stereocaulon* species in the ground layer (DeLong, 2004). Commercial logging has been operating in the area for several decades, but tends to favour the more productive mesic sites for harvesting. It is unlikely that the stands examined have been logged in the recent past, as no cut stumps were encountered.

### 2.2. Plot layout and sampling procedures

We selected twenty-four forest inventory polygons, each at least 400 ha in size, that were dominated by lodgepole pine (B.C. MoFR 2007), documented as caribou winter range from radio telemetry data (McNay et al., 2009), and within 1 km of access roads. These selection criteria ensured that sites were of a ‘lichen-dominated pine forest’ type.

The centroid of each polygon served as a starting point from which three systematically arranged circular plots were surveyed for vegetation and soil characteristics. Using a handheld global positioning system receiver, we established the first of three sample plots on the polygon centroid itself. The second and third plots formed the other corners of a 50 m equilateral triangle, with the first axis sequentially alternating clockwise through the four subcardinal directions among sites. Each group of three plots within a forest polygon is collectively referred to as a ‘site’.

Three small vegetation quadrats were located within each plot; quadrats were  $0.25\text{ m}^2$  squares with the sides facing cardinal directions.

This size of quadrat is small enough that functional group dominance and species percent-cover estimates are easy to assess, and coincide with what are considered genetically uniform patches of feathermoss or lichen (Ahti, 1961; Cronberg et al., 2006). Each of these quadrats was placed on the most completely dominated patches of mat-forming lichen, feathermoss, and vascular plants within the plot. Where possible, functional group patches that appeared to be in a state of persistent dominance were selected over those that appeared transitional. These quadrats are henceforth referred to as lichen, feathermoss, and vascular plant for their respective dominant ground cover functional groups. Additional information on study site, plot, and quadrat placement, and the species composition of the quadrats can be found in (Haughian and Burton, 2015).

### 2.3. Data logger deployment

Temperature and relative humidity (RH) data loggers (Hobo® U23-001, Onset Computer Corporation) were placed at one quadrat in the centre plot of all sites. Among sites, logger placement alternated from lichen to feathermoss to vascular quadrats, so that each functional group (FG) received approximately equal representation (Table 1). Data loggers were secured to the north-facing side of a wooden stake, at a height of approximately 2 cm above the vegetation. To minimize the difference between temperatures at the top and bottom of the unit, loggers were oriented horizontally, and shielded from the sun by a  $10 \times 12$  cm foil pan, approximately 5 cm above the top of the logger. Relative humidity and temperature were recorded once every five minutes for six weeks, between July 15th and September 15th, 2008. To reduce the potentially inflated variability associated with having non-synchronous time periods over which data were collected (added influence from time of year, or seasonality), the recording window used in analyses was narrowed to a 25-day period from the 5th to the 30th of August 2008. These dates corresponded with the last deployment and first retrieval of the data loggers, ensuring that they experienced the same overall weather patterns during the same time-span.

### 2.4. Water potential

Using the altitude-adjusted equation in Nobel (1999), we calculated the water potential of air ( $\Psi_{air}$ ) from temperature and RH measurements for each five-minute recording period ( $n = 7201$  at each site). The water potential of air is a more direct indicator of the desiccating power of the air than either temperature or RH is alone (cf. Jones, 1983; Nobel, 1999). Because mosses and lichens are poikilohydric and can absorb water in either liquid or vapour form, water potential additionally represents the potential for air to supply moisture to plant tissue, and can be used to calculate the equilibrium water content of plants and lichens (Heatwole, 1966; Bayfield, 1973; Proctor, 2000; Jonsson et al., 2008).

For each site, we took the average of daily minimum, mean, and maximum water potentials under either ‘sunny’ or ‘overcast’ conditions, yielding six summaries of  $\Psi_{air}$  for each site. Next, we tested these  $\Psi_{air}$  summary statistics to see if any differences occurred among functional groups (lichen, feathermoss, or vascular plant), using factorial ANOVA followed by Tukey-Kramer multiple comparison tests; a large critical alpha value was used to allow for the small sample sizes ( $\alpha = 0.10$ ). Tests were conducted using SAS v. 9.2.1 (SAS Institute, 2010), with the GLM procedure.

### 2.5. Water content thresholds

Jonsson et al. (2008) used a similar derivation of water potential to determine its relationship with the equilibrium water content ( $WC_{eq}$ ) of *Cladonia rangiferina* (L.) Weber ex F.H. Wigg. After testing thalli across a range of ambient humidity levels, they determined that the two measures showed an exponential relationship, which can be represented by

**Table 1**  
Distribution of temperature and RH data loggers throughout study area.

Site	Dominant vegetation	Date and time of Deployment	Time (days)	Latitude (Dec. °)	Longitude (Dec. °)	Elevation (m)	Canopy closure (%)
7	lichen	08/04/2008 08:00	49	56.034	−125.238	935	39
13	lichen	07/19/2008 12:10	46	55.832	−125.216	985	56
18	lichen	07/31/2008 15:05	46	56.377	−125.469	932	49
28	lichen	07/28/2008 14:30	46	55.653	−124.682	1091	49
43	lichen	07/30/2008 09:40	46	56.411	−125.671	951	59
48	lichen	07/16/2008 12:15	46	56.037	−125.428	983	50
51	lichen	07/17/2008 16:15	46	56.081	−125.573	1043	45
100	lichen	08/03/2008 09:45	44	56.311	−125.320	965	41
1	moss	07/29/2008 09:00	33	55.806	−125.305	1005	53
6	moss	08/04/2008 13:35	44	56.020	−125.275	993	46
9	moss	08/03/2008 15:45	44	56.146	−125.152	868	55
12	moss	07/18/2008 15:35	46	55.831	−125.207	978	53
17	moss	08/01/2008 09:15	45	56.370	−125.440	911	49
29	moss	07/26/2008 13:55	57	55.658	−124.682	1108	48
41	moss	07/30/2008 15:30	46	56.404	−125.623	977	49
46	moss	07/15/2008 17:15	46	56.041	−125.390	1009	54
49	moss	07/17/2008 10:00	46	56.078	−125.598	1013	42
19	vascular	08/01/2008 15:20	45	56.373	−125.423	983	51
27	vascular	07/20/2008 09:45	45	56.016	−125.229	969	52
33	vascular	08/05/2008 09:10	39	55.927	−125.189	993	46
34	vascular	07/18/2008 10:00	46	55.952	−125.197	1017	47
42	vascular	07/31/2008 09:00	53	56.407	−125.601	1027	55
44	vascular	07/15/2008 10:45	46	56.037	−125.396	946	49
45	vascular	07/16/2008 16:35	46	56.036	−125.411	958	50

the equation:

$$WC_{eq} = WC_{sat} \cdot e^{(W_{eq} \cdot \Psi_{air})}$$

where  $WC_{sat}$  is the water content at full saturation (cell turgidity) in the lichen thallus, and  $W_{eq}$  is a species-specific constant, related to the tissue structure of the species and how readily it absorbs and holds water (Jonsson et al., 2008). Since the authors expressed water content as the observed weight of water divided by the weight of water at saturation,  $WC_{eq}$  is expressed as a percentage between zero and 100, while  $WC_{sat}$  is constant at 100 (Jonsson et al., 2008). Jonsson et al. (2008) calibrated their models using the full range of  $WC_{eq}$  (0–100%). This measure of water content is commonly described as the relative water content (RWC), or percent saturation, and is more useful than other measures when comparing across taxa. Indeed, the minimum RWC of mosses at turgidity seems to be remarkably similar among species, and because full turgidity coincides with maximum photosynthetic rate ( $P_{max}$ ), RWC is an appropriate indicator of potential physiological status (Proctor 2000).

Using Jonsson et al.'s (2008) formula, water content at equilibrium for *Cladonia rangiferina* was calculated for each five-minute measurement interval in all quadrats. These data were then summarized for each site as the frequency (proportion of total measurements) for which one of four  $WC_{eq}$  thresholds exceeded. The thresholds used were 10%, 20%, 40%, and 70% saturation, corresponding to  $\Psi_{air}$  values of −19.19, −13.41, −7.64 and −2.97 MPa, respectively; they are subsequently referred to as low, medium, high, and highest  $WC_{eq}$  thresholds, and coincide with published data on  $P_{min}$ , water compensation points, and  $P_{max}$  for various species of lichen (including *C. rangiferina*) or moss (Heatwole, 1966; Kershaw, 1977; Bayfield, 1973; Jones, 1983; Alpert and Oechel, 1985; Longton, 1988; Williams and Flanagan, 1996; Csintalan et al., 2000; Proctor, 2000; Uchida et al., 2002; Coxson and Wilson, 2004). The frequencies of threshold exceedance were tested for linear relationships with understory functional group cover using Pearson's correlation tests. Analyses were conducted using SAS v. 9.2.1 (SAS Institute, 2010), with the CORR procedure ( $\alpha = 0.10$ ).

## 2.6. Ambient weather conditions

Because no weather stations were within the study area, and observers were not present to document weather conditions between

August 5th and August 30th, it was necessary to infer whether skies were overcast or sunny using (1) the relative differences in temperature variability from the Hobo® data loggers during installation periods (when cloud cover was directly documented), and (2) observations of temperature and precipitation at the nearest weather stations (within a 150 km radius) of the area, from July 18th to August 5th. Data loggers showed a consistently wider range in temperature on sunny days than overcast ones, and estimates of cloud cover using these data were invariably corroborated by local weather station records of cloud cover. Ambient conditions data were obtained from the four nearest weather stations within a 200 km radius (from the centre of the study area) that had daily records during the summer of 2008, via the National Climate Data and Information Archive (Environment Canada, 2010).

## 3. Results

### 3.1. Ambient weather conditions

Although the time spent in the field was not constant from July 18th until August 5th, both sunny and overcast conditions were recorded for at least several days in succession. The single sunny stretch of four days coincided well with a period of increasing daily temperature range for both regional weather stations and study area data loggers, as well as with decreasing daily minimum RH from data loggers and zero precipitation for weather stations (Fig. 1). The overcast periods showed the opposite pattern: decreasing or low daily temperature ranges, high relative humidity, and measurable precipitation (Fig. 1). These observations agree with the prediction that patterns in the average daily temperature range and minimum RH of data loggers could be used to determine whether days were sunny or overcast in the absence of observers. Specifically, the days estimated to be sunny were August 5–9, 11, 14–17, and 28–29, while days estimated to be overcast were August 10, 12–13, and 18–27.

### 3.2. Water potential

The average daily maximum water potential was not significantly influenced by quadrat (vegetation patch) type, regardless of weather conditions. Only above feathermoss did the mean  $\Psi_{air}$  reach a peak of −3.0 MPa for several hours of any day; vascular quadrats did so for

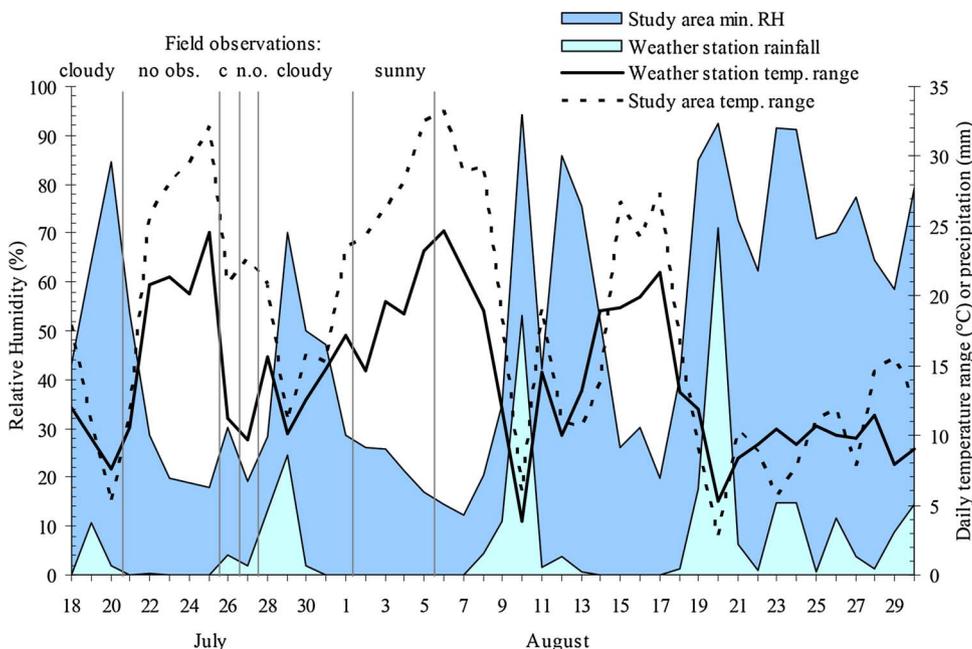


Fig. 1. Daily temperature range, relative humidity, and precipitation as recorded at ground level in the study area and as ambient conditions at regional weather station. Conditions labelled as “study area” are the mean of all data loggers, whereas those labelled as “weather station” are from Environment Canada (2010). Overlaid vertical bars and text at the top-left indicate observations of general weather conditions for periods when observers were in the study area (no obs. and n.o. indicate that the observers were not present to observe or record ambient conditions at these times).

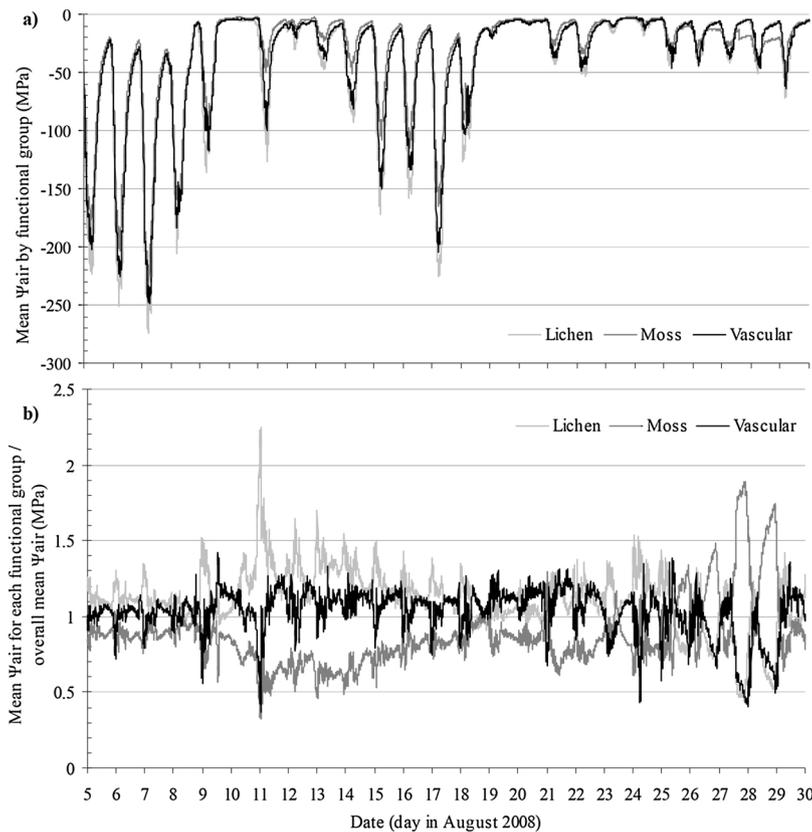


Fig. 2. (a) Raw mean water potential of air, and (b) corrected (functional group mean/overall mean) mean water potential of air over three types of ground-layer vegetation, measured 2 cm above the vegetation in three functional groups of ground-layer vegetation over 25 days in August 2008. Note: in panel a, higher values on the Y-axis equate to greater moisture availability, whereas the opposite is true in panel b; the pattern from panel a appears inverted in panel b because both the overall mean and the functional group means are negative integers.

only a few minutes per day, while lichen quadrats did not exceed this threshold at all (Fig. 2). The mean daily minimum  $\Psi_{air}$  differed significantly among functional groups under all weather conditions ( $F_{(2,21)} = 6.19, p = 0.008, \eta^2 = 0.37$  for sunny and  $F_{(2,21)} = 3.07, p = 0.068, \eta^2 = 0.23$  overcast conditions), though differences were minimal under overcast conditions (Fig. 2). The mean daily mean  $\Psi_{air}$  differed significantly among functional groups under sunny conditions only ( $F_{(2,21)} = 3.58, p = 0.046, \eta^2 = 0.25$ ).

Multiple comparison testing confirmed that the air above feathermoss patches had more water than that above other functional

groups. The mean daily minimum  $\Psi_{air}$  above feathermoss ( $-135.81 \pm 7.77$  S.E. MPa) was significantly greater than that above lichens ( $-180.75 \pm 9.22$  MPa) or vascular plants ( $-169.76 \pm 12.78$  MPa) under sunny conditions (Fig. 3). Under overcast conditions, the average daily min.  $\Psi_{air}$  was also significantly greater above feathermoss ( $-32.72 \pm 3.99$  MPa) than above lichens ( $-48.24 \pm 4.45$  MPa), while daily min.  $\Psi_{air}$  above vascular plants was intermediate and not significantly different from either group (Fig. 3). Similar trends were observed for daily mean  $\Psi_{air}$  during sunny conditions. On average, daily mean  $\Psi_{air}$  was significantly greater

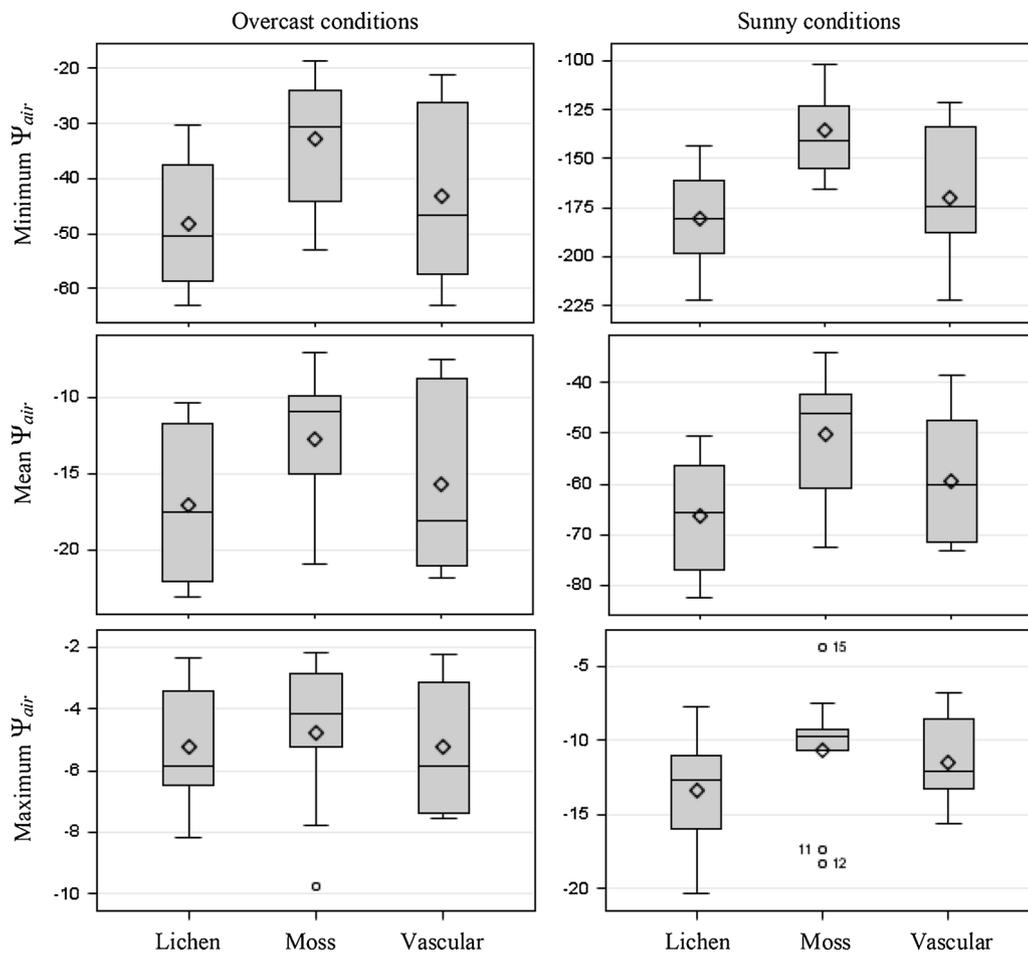


Fig. 3. Daily minimum, mean, and maximum water potential of air ( $\Psi_{air}$ , in MPa), calculated from measurements of temperature and relative humidity taken 2 cm above ground-layer vegetation in lichen, feathermoss, and vascular plant patches. Diamonds represent the mean, boxes show the median and 25–75 interquartile range, and whiskers represent the bounded maximum and minimum values.

over feathermosses ( $-50.32 \pm 1.45$  MPa) than lichens ( $-66.31 \pm 1.97$  MPa), with vascular plants being intermediate and not significantly different from either (Fig. 3).

Estimates of  $WC_{eq}$  (derived from  $\Psi_{air}$ ) ranged from 0.0–73.6% for lichen ( $23.7 \pm 0.3$ ), 0.0–83.8% for feathermoss ( $31.4 \pm 0.3$ ), and 0.0–75.8% for vascular plants ( $25.7 \pm 0.3$ ), although we stress these  $WC_{eq}$  estimates were, in this study, used for comparative purposes, rather than as accurate predictions of hydration status.

### 3.3. Water content thresholds

Throughout this section, whenever multiple  $r$  and  $p$ -values are presented, they are in order from the lowest (10%) to the highest (40%)  $WC_{eq}$  thresholds; due to a high number of zero values (i.e., 29% of quadrats did not attain a water potential of more than  $-2.97$  MPa), the highest (70%)  $WC_{eq}$  threshold (as originally defined) was excluded from the analysis. Correlation analyses revealed some marginally significant associations ( $0.05 < p < 0.10$ ) between the frequency at which  $WC_{eq}$  thresholds were exceeded in given quadrats and lichen cover (Table 2). Significant associations with time above  $WC_{eq}$  thresholds were detected only when conditions were sunny. Lichen cover was negatively correlated with the low (10%) and medium (20%)  $WC_{eq}$  thresholds under sunny conditions.

## 4. Discussion

Previous studies in lodgepole pine forests of B.C. have clearly demonstrated that the dominance of different ground-layer functional groups is related to microsite conditions in the understory, including the amount and configuration of canopy cover and several soil edaphic

properties (Cichowski and Williston, 2008; Haughian and Burton, 2015; Sulyma and Coxson, 2001). These and other authors (e.g., Lechowicz and Adams, 1973; Busby et al., 1978; Dynesius et al., 2008) have suggested that many of these apparent relationships are mediated through the influence that canopy and soil properties have on patch microclimate. Our study is the first to demonstrate that the patch-scale microclimate itself is related to functional group dominance, thereby adding support to the hypothesis that small-scale differences in canopy and soil variables can influence patch-dominance through their influence on microclimate.

The feathermoss quadrats clearly showed greater minimum and mean daily water potential than lichens (Fig. 3), thereby corroborating our predictions that lichens and feathermosses would occupy relatively dry and moist microhabitats, respectively. It is somewhat surprising that maximum water potential was not more strongly associated with feathermoss dominance, especially considering the relative infrequency of water potentials in this study that correspond with photosynthetic optima from the literature (Proctor, 2000). One explanation for this lack of association may be that the maximum water potentials observed were simply not long enough in duration to be of biological relevance. True equilibrium between plant or lichen water content and atmospheric water potential is rarely achieved under natural settings. More often, changes in tissue water content will lag behind changes in atmospheric water potential, though this lag time tends to be greater for lichens than for mosses (Heatwole, 1966; Hernández-García et al., 1999; Jonsson et al., 2008; Kershaw, 1985).

Daily maximum water potentials (and the highest frequency of water content thresholds) were generally reached in the early morning hours, coinciding approximately with sunrise, and lasted for approximately 1 h thereafter, while daily minimum water potentials were

**Table 2**  
Correlation coefficients (Pearson's  $r$ ) and  $p$ -values for ground-layer functional group cover and time spent above the water content thresholds.

Variable	Statistic	Sunny conditions			Overcast conditions		
		Low (10%)	Medium (20%)	High (40%)	Low (10%)	Medium (20%)	High (40%)
Vascular Plant Cover	$r$	0.230	0.187	0.131	0.231	0.163	0.118
	$p$	0.280	0.381	0.542	0.277	0.448	0.582
Lichen Cover	$r$	<b>-0.398</b>	<b>-0.357</b>	-0.308	-0.341	-0.325	-0.316
	$p$	<b>0.0540</b>	<b>0.087</b>	0.143	0.103	0.121	0.132
Moss Cover	$r$	0.319	0.301	0.308	0.255	0.266	0.291
	$p$	0.129	0.153	0.143	0.229	0.209	0.167

Bold font indicates a significant correlation at  $\alpha = 0.10$ .

generally reached in the afternoon; this agrees well with others' observations of diurnal fluctuation in photosynthesis and moisture levels (Moser and Nash, 1978; Lechowicz and Adams, 1973). Although water potential dropped steeply after 09:00 each day, the 3–4 h window of high water potential ( $> -10$  MPa) during daylight hours is probably sufficient to achieve net carbon assimilation. Moreover, while dark respiration rates also positively associate with hydration (Lechowicz and Adams, 1973), recent research suggests that lichen wetness during dark periods facilitates improved growth, perhaps by enhancing carbohydrate conversion into biomass (Bidussi et al., 2013). Yet, the lower overnight temperatures likely reduce metabolic demand while moisture levels increase throughout the night, and photosynthetic activity is surely prolonged in both lichens and mosses past the times of peak ambient humidity, particularly when dew is deposited (Carleton and Dunham, 2003; Gauslaa, 2014). The fact that maximum ambient moisture differed little among patches suggests either that these functional groups do not differ in their ability to equilibrate with higher ambient humidity overnight, or that the consistent, uniform distribution of heavy dewfall overnight has a homogenizing effect on microhabitat-caused differences, thereby preventing our detection of such differences during mornings and overnight. In contrast, the minimum daily water potentials represent the combination of evaporative stress and resistance to moisture depletion for a given functional group. The differences observed in functional group relationships to these summary variables suggest that the functional groups differ primarily in their tolerance of desiccation stress, rather than their preference for maximum moisture availability.

Differentiation among functional groups was unlikely during overcast days, because the foremost contributor to differences in evaporative stresses among microhabitats was likely the different levels of shading from the forest canopy or local topographic masking. On these days, minimum water potentials and the frequency of exceedance for thresholds in water content is likely a much more direct indicator of potential photosynthetic rates in terrestrial lichens and mosses of boreal and sub-boreal regions, which have been shown to be limited by water availability (Busby et al., 1978; Moser and Nash, 1978; Palmqvist and Sundberg, 2000; Uchida et al., 2002; Williams and Flanagan, 1996). The water potential of air is less ecologically relevant if rain and dew are periodically allowing lichens and mosses to become fully saturated, because the vegetation will be operating at  $P_{\max}$  for some time after such periods under even sunny conditions, due to an accretion of external capillary space water (Moser and Nash, 1978; Kershaw, 1985; Proctor, 2000; Jonsson et al., 2008). Indeed, if the nearest weather stations were an appropriate indication of days with precipitation (and it is likely that they were, given their close relationships with temperature and RH measurements from the study area), it would indicate that a large proportion of the time over which these data loggers were operating was not moisture limited, and therefore the relationships detected during these times were not particularly sensitive for detecting differences in microclimate among functional groups.

Only the lichen functional group showed a significant correlation with time spent above  $WC_{eq}$  thresholds, and only for the low and

medium thresholds. This suggests both that lichens may be more sensitive to microclimate than the other ground-layer functional groups, and that excessive humidity may negatively impact these lichens. Indeed, research has shown that  $CO_2$  exchange may be limited by prolonged thallus saturation in lichens (Lange and Tenhunen, 1981); however, the coarse-textured soils and continental climate of the study area make such explanations unlikely for the present study. Rather, we suggest that the negative correlation between lichen abundance and time spent above 10% and 40%  $WC_{eq}$  thresholds results from lichens being outcompeted by feathermosses and vascular plants in wetter microhabitats.

It is uncertain whether the associations we detected in this study were the result of vegetation responding to environment, or vegetation changing the environment. We speculate that all three functional groups likely exhibit some form of positive feedback for microhabitat moisture levels, as compared to bare ground, and that this would be most prevalent in feathermosses, less so in reindeer lichens, and least in vascular plants. The reasons for this putative ranking are that (1) the vascular plants (and especially those in the Ericaceae) are better adapted to conserve water than the other groups (which are poikilohydric), and will therefore lose relatively little moisture to surrounding air, and (2) feathermosses have a much denser, more horizontally-layered colony structure than reindeer lichens, which have a relatively upright, porous structure. Both mat-forming lichens (Rouse and Kershaw, 1971; Kershaw and Field, 1975; Kershaw, 1985), and feathermosses (Busby et al., 1978; Hylander, 2005; Williams and Flanagan, 1996) have been shown to increase moisture and decrease temperatures near the ground as compared with open habitats in boreal and subarctic regions. Unfortunately, there were no unoccupied (bare ground) control quadrats for comparison, and quadrat selection was purposely directed towards well-vegetated patches, making discernment between habitat and vegetation-caused patterns impossible. Nevertheless, we believe that the microhabitat probably exerted more control than the ground cover, because diurnal trends showed clear peaks in humidity at night, and troughs during the day; a daytime peak would instead have indicated a dominant transpirational effect. Clarification of true cause and effect relationships will require additional study.

#### 4.1. Summary and conclusions

The water potential of air above patches dominated by different ground-layer functional groups differs with patch type: feathermosses patches tend to exhibit the highest (least negative)  $\Psi_{air}$ , while lichens have the lowest, and vascular plants are intermediate. This is most apparent when using minimum daily  $\Psi_{air}$  as the metric (rather than maximum or mean), and during sunny conditions, when precipitation is unavailable and evaporative stresses are greater. The time spent above estimated (lichen thallus) water content thresholds of 10% and 20% was negatively related to lichen cover during sunny periods. Although it is clear that patch occupancy of different functional groups is responding to microsite- and forest canopy-mediated environmental conditions, it is also possible that the vegetation influences

microclimate to some extent. Further study of microclimatic conditions should include control (unvegetated) patches for comparison, and should more directly examine the role of vegetation in regulating microclimatic conditions by use of reciprocal transplants, vegetation removal, and direct measurement of water content or water stress. In addition, microclimatic measurements should include measures of local precipitation, to further elucidate the relative biological importance of atmospheric moisture and precipitation.

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