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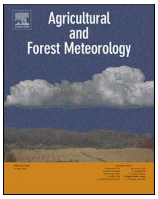

Microclimate differences above ground-layer vegetation in lichen-dominated pine forests of north-central British Columbia

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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° 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 engelmanii* 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 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 × 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 (Ψ_{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 equilibrial 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 Ψ_{air} for each site. Next, we tested these Ψ_{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