

On the Vertical Zonation of Hair Lichens (*Bryoria*) in the Canopies of High-elevation Oldgrowth Conifer Forests

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Goward, Trevor. 2003. On the vertical zonation of hair lichens (*Bryoria*) in the canopies of high-elevation oldgrowth conifer forests. *Canadian Field-Naturalist* 117(1): 39–43.

Three vertical zones of *Bryoria* abundance are recognized in the canopies of mid- and upper-elevation oldgrowth conifer forests in southern inland British Columbia. Zone A, with virtually no *Bryoria*, is restricted to the lower trunk and lowermost branches, where its upper boundary (the "A/B threshold") corresponds roughly to the maximum settled depth of the winter snowpack. Zone B is located directly above Zone A, and supports *Bryoria* in variable amounts ranging from negligible to heavy; its upper boundary is defined by an abrupt increase in *Bryoria* at the "B/C threshold". Above this is Zone C: a well-ventilated region supporting maximum *Bryoria* loadings consisting predominantly of the nonsorediate species *B. fremontii*, *B. pseudofuscescens*, and *Nodobryoria oregana*. *Bryoria* loadings in Zone B benefit from litterfall from Zone C, in the absence of which, Zone B would predominantly support only the sorediate species *B. fuscescens* and *B. glabra*. Winters of exceptionally deep snow cause marked upward shifts in the A/B threshold, presumably resulting in reductions in the early-winter availability of *Bryoria* to Mountain Caribou. This reduced forage is expected to prolong early-winter migrations to lower elevations, where Caribou depend on lichen-rich oldgrowth forests. The existence of such forests is hypothesized to be integral to the long-term maintenance of healthy caribou populations.

Key Words: *Bryoria fremontii*, *Bryoria pseudofuscescens*, *Nodobryoria oregana*, arboreal lichens, conifer forests, Woodland Caribou, *Rangifer tarandus*, mountain ecotype, Wells Gray Provincial Park, British Columbia.

The mid- and upper-elevation oldgrowth conifer forests of southern inland British Columbia provide winter habitat for the mountain ecotype of the Woodland Caribou (*Rangifer tarandus caribou*). Unlike the more northerly Barrenground Caribou, Mountain Caribou are behaviourally adapted to survival in regions of deep snow (Paquet 1997). In winter, when deepening snows render terrestrial forage unavailable, these animals subsist predominantly on a diet of arboreal hair lichens (Edwards and Ritcey 1960; Rominger and Oldemeyer 1990).

At least 13 species of arboreal hair lichens occur within the winter range of Mountain Caribou, i.e., ten species of *Bryoria*, two of *Nodobryoria*, and one of *Alectoria* (Goward, in preparation). The extent to which a given species is utilized depends not only on its overall availability at foraging heights, but also on the foraging behaviour of Caribou. For example, the green hair lichen *Alectoria sarmentosa*, though most abundant in the lower canopy (Campbell and Coxson 2001), tends to be avoided by Caribou (Rominger et al. 2000). Rominger et al. (1996) emphasize that wintering Caribou forage preferentially on *Bryoria*, which they seek out especially in sites supporting heavy loadings.

Little is known about the relative contributions of individual species of lichen to the winter diets of Mountain Caribou, most previous studies having focussed at the genus level. However, recent work by Goward and Campbell (in preparation) suggests that *B. fuscescens* and, to a lesser extent, *B. glabra*

are the most common *Bryoria* species at foraging heights, at least in mid-successional stands. Still, because neither of these species dominates in the high-biomass sites most attractive to Caribou (Goward and Wright, in preparation), their contribution to caribou winter forage is therefore probably less than would be predicted based on frequency alone.

Much more abundant in preferred Caribou foraging sites are *B. fremontii*, *B. pseudofuscescens*, and *Nodobryoria oregana* (Goward, in preparation). These are long, pendulous lichens that characteristically lack soredia and apothecia, and hence rely on thallus fragmentation as the primary mode of reproduction. Related to this, all of these species exhibit indeterminate growth, their thalli being capable of elongating indefinitely. In practice, however, these species seldom measure more than about 10 to 30 cm long (except to 90 cm long in *B. fremontii*: Brodo and Hawksworth 1977). Maximum thallus size is reached once branch growth rates come into equilibrium with branch loss through fragmentation. The best available information suggests that, depending on initial fragment size, this state of equilibrium can be attained in under 20 years (Esseen and Renhorn 1996; Goward, unpublished data).

Much remains to be learned about the distribution of hair lichens in oldgrowth forests. Given the reported preference of wintering Caribou for heavy *Bryoria* loadings, it would be useful to determine under what conditions such loadings develop in por-

tions of the canopy accessible to these animals. The main objective of this paper is to address this question with respect to mid- and upper-elevation oldgrowth Engelmann Spruce (*Picea engelmannii*) - Subalpine Fir (*Abies lasiocarpa*) (ESSF) forests in southern inland British Columbia. More specifically, it attempts to summarize the vertical apportioning of *Bryoria* in these forests. The observations reported here build on the earlier findings of Goward (1998), and are based on incidental field studies carried out over a period of ten years in southern inland British Columbia, especially in the Sicamous Creek Research Forest (50°49'N, 118°50'W) (Hollstedt and Vyse 1997), and in Wells Gray Provincial Park (51°51'N, 119°52'W) (Goward and Ahti 1992).

"Mid-elevation" refers to those portions of the ESSF between about 1400 and 1900 m, with a more or less continuous forest cover. "Upper-elevation" forests occur between about 1900 and 2100 m, and are transitional to the alpine tundra; they are much more open and, as a consequence, better ventilated. These elevational boundaries are representative of conditions at about 52°N; north of this, they gradually descend, whereas to the south they climb.

Vertical Patterns of *Bryoria* in the Forest Canopy

The vertical apportioning of *Bryoria* in the canopies of mid- and upper-elevation oldgrowth forests can be divided into three zones. For convenience, these zones will be referred to here as Zone A, Zone B, and Zone C (Figure 1). The boundaries separating these zones are termed "thresholds".

Zone A

Zone A is restricted to the lowermost trunk and branches, often extending upwards to 2-4 m above the ground. Here hair lichens are essentially absent. Goward (1998) has suggested that the inability of hair lichens to establish in this portion of the canopy reflects a pronounced physiological sensitivity to

prolonged wetting as a consequence of burial under the winter snowpack (see also Coxson and Curteanu 2002). The upper limits of Zone A (henceforth the "A/B threshold") correspond roughly to the upper surface of the late winter snowpack (Taylor 1922).

Winter snowpacks can vary markedly from year to year. Reflecting this, the A/B threshold is subject to periodic shifts in vertical position. The most dramatic upward shifts are initiated during winters of exceptionally deep snow, when the A/B threshold can be elevated by a metre or more (Goward, in preparation). Once established, an elevated A/B threshold might require several years to recolonize downward to its original "average" position (Goward, in preparation). The rate of recovery is presumably linked to the rate of thallus recruitment from higher in the canopy.

Determining the "average" vertical position of the A/B threshold can be difficult, owing to the uneven snow surface beneath the canopies of trees. For general purposes, the trunks of large leaning trees provide a convenient point of reference. Here the upper limits of Zone A are denoted by the lower trimline of *Alectoria* and *Bryoria*.

Zone B

Situated immediately above Zone A is Zone B. In general, the "A/B threshold" is defined by a sudden upward increase in hair lichen biomass. Notwithstanding this, *Bryoria* biomass in Zone B is also highly variable. Within a given site, thallus loadings appear to be controlled by two opposing factors, both pertaining primarily to the nonsorediate species. These are ongoing inoculation from Zone C (see below), and periodic die-backs. Die-backs occur as a result of prolonged wetting, and result in the presence of necrotic thalli: a characteristic feature of Zone B (Goward 1998; Campbell and Coxson 2001). Prolonged thallus wetting is most frequent toward the branch tips (Goward 1998), where it is mediated by several small-scale phenomena, including needle cast, increasing branch length higher in the canopy, the seasonal development of snow clumps ("qali"), crown breakage, and, at the stand level, the stochastic formation of canopy gaps. These and other factors — especially prolonged wet, cool weather — ensure that *Bryoria* biomass in Zone B is unstable, fluctuating both spatially and temporally.

Depending on ventilation, Zone B can vary considerably in vertical amplitude: in closed stands it occupies virtually the entire crown, while in open stands it can be limited to the lowermost branches. In highly exposed situations, this zone can be lacking altogether (see Zone C).

Zone C

The upper limit of Zone B is marked by a dramatic increase in *Bryoria* biomass, a trend most readily observed in the canopies of old trees. Above this is Zone C: the zone of optimum *Bryoria* development.

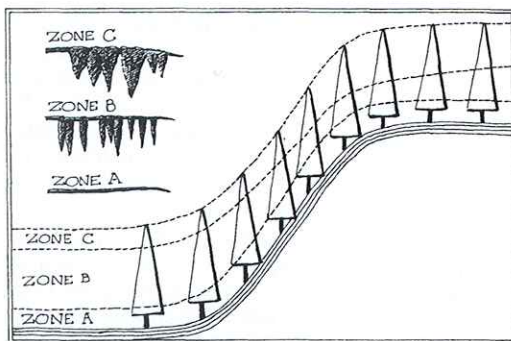


FIGURE 1. Vertical zonation of *Bryoria* in the canopies of high-elevation oldgrowth forests in southern British Columbia (see text).

The upward increase in *Bryoria* biomass is accompanied by subtle change in thallus morphology, at least among the nonsorediate species. In Zone B these species have long, narrow thalli that somewhat resemble the teeth of a comb. In Zone C, by contrast, they attach more broadly to the supporting branch, hence calling to mind triangular pennants or tattered curtains (Figure 1). This shift in thallus form presumably reflects a transition from suboptimal growing conditions in Zone B (where thalli are unable to develop laterally along the supporting branch) to optimal conditions in Zone C (where lateral growth is more pronounced).

Three additional B/C markers can be observed. The first of these involves the ability of healthy thalli to grow out towards the foliated branch tips in Zone C — a phenomenon not seen in Zone B, where healthy thalli are essentially restricted to the defoliated branch portions. The second marker is the general absence, in Zone C, of the necrotic thalli often so common in Zone B, especially toward the branch tips. And finally, the B/C threshold roughly corresponds to the upper limits of well-developed thalli of *Alectoria sarmentosa*. It should be noted, however, that this species is strongly dispersal-limited in the ESSF, and hence does not always occupy its full potential vertical range, even in oldgrowth stands; its upper trimline must therefore be interpreted with caution (Goward, in preparation).

The B/C threshold can be rather diffuse, sometimes spanning two metres or more. It also varies markedly in vertical position across short horizontal distances, often even within the canopy of a single tree. Such variations are correlated with ventilation. In forested sites, the B/C threshold occurs mostly in the middle or upper canopy, though in more exposed sites, it can descend virtually to the upper limits of Zone A. In the absence of a well-developed Zone B, the boundary between zones A and C can be referred to as the A/C threshold. A parallel trend is discernible also at the landscape level, with an elevated B/C threshold at the foot of hillslopes, and a much lower threshold on upper slopes and hillcrests (Figure 1).

Unlike Zone B, which in the ESSF is present in forests of all ages, a well-developed Zone C is usually restricted to oldgrowth forests; young stands support only meagre *Bryoria* loadings in Zone C (Goward and Campbell, in preparation). Zone C also differs from Zone B in supporting more consistently heavy *Bryoria* loadings. Presumably this reflects the uninterrupted accumulation of *Bryoria* biomass over extended periods; i.e., without the depleting influence of periodic die-backs, as in Zone B.

Zone C is invariably associated with exposure to high levels of ventilation, leading to significant loss of hair lichen biomass as a result of thallus fragmentation (Goward 2003). Presumably most thallus frag-

ments fall to the ground and are lost to decay (Coxson and Curteanu 2002). Some, however, are intercepted by branches lower in the canopy, over time accumulating to moderate or even heavy loadings. Litterfall from Zone C can thus provide a primary source of *Bryoria* biomass in Zone B — an observation consistent with the much greater incidence of nonsorediate *Bryoria* thalli in the lower canopies of forests with a well-developed Zone C (Goward, in preparation). In the absence of litterfall from Zone C, heavy *Bryoria* loadings are unlikely to develop in Zone B. The relationship between Zones C and B thus recalls the source-sink population model of Pulliam (1998), in which high quality source populations (as in Zone C) export propagules to low quality sink populations (as in Zone B). The latter populations are thus dependent for their long-term persistence upon the former.

Implications for Caribou Winter Ecology

This paper has presented four observations pertinent to the vertical zonation of *Bryoria* biomass in mid- and upper-elevation oldgrowth forests in British Columbia: (1) *Bryoria* loadings are consistently heavy in well-ventilated portions of the canopy (Zone C); (2) *Bryoria* loadings are more variable in poorly ventilated portions of the canopy (Zone B); (3) hair lichens (including *Bryoria*) are virtually absent from portions of the canopy buried by the winter snowpack (Zone A); and (4) winters of exceptionally deep snow induce marked upward shifts in the vertical extent of Zone A. It is emphasized that these findings are based on field observations, and must hence be considered preliminary until confirmed by careful quantitative studies. From a management perspective, however, it might be useful to draw attention to two potential implications arising from them, and pertaining to Mountain Caribou.

Bryoria availability

The widespread occurrence of a well-developed Zone C is pivotal to the winter ecology of Mountain Caribou. These animals benefit from Zone C both directly and indirectly. Direct benefits include access to heavy *Bryoria* loadings in a range of settings, including the upper canopies of downed trees, the lower canopies of standing trees, and, in the case of litterfall, the snow surface. A potentially important indirect benefit of Zone C is the continuous release of *Bryoria* fragments into Zone B. Here it can be noted that heavy *Bryoria* loadings are likely to occur in Zone B only in proximity to trees supporting a well-developed Zone C (Goward and Wright, in preparation).

The relative availability of Zone C to caribou varies markedly with elevation. Upper ESSF forests, for example, have an open, clumpy stand structure permitting the B/C threshold to descend, on average,

to the lower portions of the middle canopy. This results in a vertically broad Zone C that in turn contributes copious litterfall to Zone B. At lower ESSF elevations, stand structure is more closed. Here the B/C threshold occurs proportionately higher in the canopy, with the result that Zone C, being vertically reduced, contributes strikingly less *Bryoria* biomass to Zone B. Not surprisingly, heavy *Bryoria* loadings at foraging heights are much more localized in these lower ESSF forests. It must be stressed that the above comments pertain to oldgrowth stands; younger ESSF stands generally support only an incipient Zone C, with very low biomass (Goward and Campbell, in preparation).

Seasonal migrations

Beginning in late October or early November, many caribou herds move downwards into the valleys from their high-elevation summer ranges. Such early-winter migrations are well documented (Edwards 1954; Seip 1992), and have in the past usually been interpreted exclusively as a response to deep, unsettled snow (Edwards and Ritcey 1959; Antifeau 1987). However, another, probably complementary explanation is also possible: the migrations could be triggered by the temporary unavailability of *Bryoria* at upper elevations.

Caribou are capable of foraging to heights of only about 1.7 - 2 m (B. McLellan, personal communication). In forests with A/B (and A/C) thresholds higher than this, early winter is doubtless a difficult period for these animals. With terrestrial food sources rendered inaccessible by deepening snows, caribou must either subsist on lichen litter (mostly on downed trees), or else migrate to lower elevations where lesser snow packs permit access to arboreal lichens and terrestrial food sources (Rominger et al. 2000).

How long caribou remain at lower elevations during a given winter is probably a function of two variables pertaining to their upper ESSF habitats: (1) the vertical position of the A/B threshold; and (2) the rate of snow accumulation during a given winter. In principle, Caribou should return to their upper ESSF winter ranges only upon the development of a snow platform sufficiently elevated to support them at foraging heights. Winters of rapid snow accumulation would thus permit them to return earlier, while late winters could delay their return for weeks or possibly months.

It has already been observed that years of exceptionally heavy snows prompt upward shifts in the A/B threshold. In subsequent winters, especially if the snowpack is late in accumulating, caribou are probably obliged to remain at valley elevations much longer than normal. Such winters can be predicted to be highly stressful for these animals, first because they are at higher-than-average risk of encountering predators, and second, because as oldgrowth forests continue to be replaced by young plantation stands,

the likelihood of locating *Bryoria*-rich windthrown trees must also decline (Goward 2002). A similar situation might arise even in regions of lighter snowpacks, where typically non-migratory herds are from time to time forced to lower elevations. Such reflections, though admittedly speculative, emphasize the potentially crucial role played in Mountain Caribou winter ecology by lowland oldgrowth forests.

Acknowledgments

This study forms part of the Sicamous Creek Silvicultural Systems Project. Field studies were funded in part by the British Columbia Ministry of Forests. Additional funding was received through Susan Hall, of Parks Canada, as well as through Michael Burwash, of the British Columbia Ministry of Environment, Lands, and Parks. I thank Ian Eakins and Wes Bieber for transportation in the field, and André Arsenault, Wes Bieber, Jim Blueschke, Kristi Iverson, Ken MacKenzie, Bruce McLellan, John Surgenor, and especially Ken Wright for valuable assistance, as well as for stimulating discussion. Participants in the Second Annual *Bryoria* Workshop (Wells Gray Provincial Park, March 2000) also tested many of the ideas presented here. Susan Stevenson, Matthew Stewart, and Ken Wright kindly reviewed an earlier version of the manuscript.

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Received 1 November 2000

Accepted 5 May 2003