

Review Article

The Manna Effect – a review of factors influencing hair lichen abundance for Canada’s endangered Deep-Snow Mountain Caribou (*Rangifer arcticus montanus*)

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Abstract

Canada’s endangered Deep-Snow Mountain Caribou (DSC) are endemic to mountainous southern inland British Columbia, where they subsist in winter on an almost exclusive diet of epiphytic hair lichens, especially *Bryoria fremontii* and *B. pseudofuscescens* (the high-biomass *Bryoria* spp.) and *Alectoria sarmentosa*. Importantly, stand-level hair lichen loadings adequate for the dietary needs of DSC rarely occur in forests younger than c. 120–150 years, an unusual form of old-growth dependence hypothetically linked to certain structural features of old forest ecosystems. Not only does this hypothesis accord well with recent insights into hair lichen ecophysiology, it also allows the formulation of a conceptual ‘hyperabundance’ model for the high-biomass *Bryoria* spp. and lays the foundation for a similar model for *A. sarmentosa*. In both cases the models point to a massive standing crop of hair lichens in the overstories of old-growth forests; it is this reservoir that, partly by releasing a constant manna-like rain of thallus fragments into the lower canopy, sustains DSC during the winter half year. The outcome is a sustained-yield system resistant to degradation from overbrowsing, yet vulnerable to fragmentation of old-growth forests by industrial forestry, a process of progressive forage reduction that must ultimately place DSC at risk of winter malnutrition. We conclude that stand-level hair lichen hyperabundance is necessarily an attribute of advanced forest age and, at least in the case of *Bryoria*, cannot be silviculturally induced in stands younger than c. 120–150 years.

Keywords: *Alectoria*; *Bryoria*; hair lichens; mountain caribou; old-growth forest

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Introduction

Canada’s Deep-Snow Mountain Caribou (DSC) are among the world’s most southerly *Rangifer*, the genus describing domestic and wild reindeer and caribou. Historically resident as far south as 42°N, this iconic ungulate (Seip & McLellan 2008) once roamed the mountains of northern Washington, Idaho and Montana (Environment Canada 2014), though today it is restricted to southern inland British Columbia (BC) (Robbins 2018). Even in Canada (Fig. 1), however, DSC have long been in decline (COSEWIC 2002) and were formally designated as endangered in 2014 (COSEWIC 2014). Industrial logging and the accompanying widespread loss and fragmentation of habitat is widely held to be the ultimate agent of their decline, although the proximal agent is predation due to changes in predator-prey relations brought about by these landscape changes (Environment Canada 2014).

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DSC have long been regarded as an ecotype of the widely distributed Woodland Caribou (*Rangifer tarandus caribou*) (Environment Canada 2014), although recent molecular findings argue for their recognition as a subspecies of barren-ground Caribou (*Rangifer arcticus montanus*) (Harding 2022). Varying from nearly all other *Rangifer*, DSC are behaviourally adapted for survival in mountainous regions of deep snow, where ground vegetation is out of reach for several months each year. Instead of pawing for food in winter, DSC walk on top of the snowpack in search of epiphytic hair lichens, their almost exclusive forage during this season (Antifeau 1987). DSC depend on hair lichens, mostly *Alectoria* in early winter (Rominger & Oldemeyer 1990) and *Bryoria* in late winter (Rominger *et al.* 1996), for c. 150–180 days each year (Antifeau 1987; Rominger & Oldemeyer 1990). Rominger *et al.* (1996) have shown that adult female caribou in winter must consume 2–3 kg of lichen dry mass daily to maintain body mass, a rate of intake achievable only in forests where hair lichens are widely available at above-average loadings, conditions previously documented by Rominger *et al.* (1996) in the south Selkirk and adjacent mountains of the Idaho interior wetbelt (Table 1).

Studies conducted in North America and Europe consistently show that such stand-level loadings, henceforth referred to as



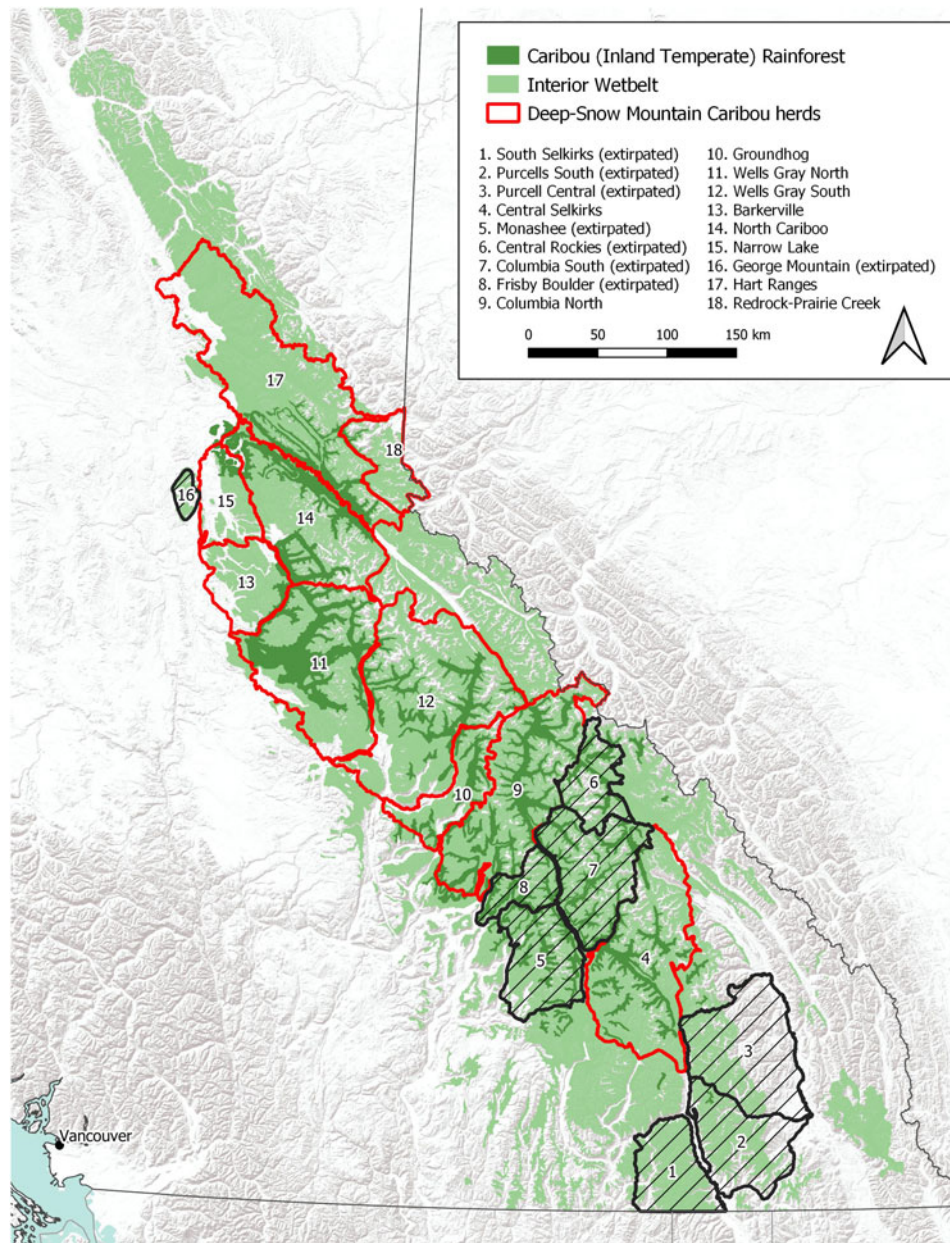


Figure 1. Geographical range of southern Deep-Snow Mountain Caribou in British Columbia showing the extent of the interior wetbelt and Caribou (Inland Temperate) Rainforest. Cross-hatched areas show extirpated herds. In colour online.

hair lichen hyperabundance, are disproportionately associated with forests of advanced age (Edwards *et al.* 1960; Esseen *et al.* 1996; Rominger *et al.* 1996; Price & Hochachka 2001; Bartels & Chen 2015; Boudreault *et al.* 2015). The early work of Edwards *et al.* (1960) was instrumental in calling attention to the potential for high hair lichen loading in old forest canopies, with stand-level lichen biomass estimates of up to 3300 kg ha⁻¹ documented, based on extrapolations from per-tree lichen loading to stand-level tree density (Table 1, Fig. 2). Stevenson (1979) subsequently documented lichen loading in the critical lower canopy zone (2–6 m above ground) where caribou typically forage on late winter snowpack, finding an average of 44 to 53 g combined *Alectoria* and *Bryoria* per branch (Table 1), values similar to those reported by McLellan & Terry (1998) (Table 1). Lewis (2004) also found canopy lichen loadings of combined *Alectoria* and *Bryoria* between 40

to 80 kg ha⁻¹ in intermediate aged forests (50–100 years in age). In one of the most detailed studies of canopy lichen loading, Campbell & Coxson (2001) used canopy climbing approaches to document gradients in canopy lichen loading in subalpine *Picea-Abies* forests, finding over 200 kg ha⁻¹ combined *Alectoria* and *Bryoria* at study sites in the north Cariboo Mountains (Table 1, Fig. 3). Stevenson (2001) likewise found over 400 kg ha⁻¹ canopy lichen loading (*Alectoria* and *Bryoria*) in the same area (Table 1). An important qualification to these estimates is provided by Antifeau (1987), who notes a ten-fold variability in canopy lichen loading between individual plots within the north Thompson region (Table 1). Factors contributing to within-stand variability are poorly known and are the focus of our discussion below.

Fortuitously, old-growth forest stands with high canopy lichen loading also buffer DSC against predation by wolves and cougars,

Table 1. Summary of past studies on arboreal caribou forage lichen loadings within the historic range of Deep-Snow Mountain Caribou in British Columbia and Idaho. Tree abbreviations follow BC Ministry of Forests (<https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/tree-seed/tree-seed-centre/seed-testing/codes>): Douglas fir (FDI), Engelmann spruce (SE), subalpine fir (BL), lodgepole pine – interior (LPI), trembling aspen (AT), western red cedar (CW). Stand ages are from forest age-class mapping unless otherwise indicated. Study site elevation above sea level (a.s.l.) is indicated where data is provided by original authors. The Caribou Rainforest area follows Coxson *et al.* (2020) (wet and very wet interior cedar-hemlock forests) but includes Engelmann spruce-subalpine fir (ESSF) forests where these are immediately adjacent in mountain valleys. The definition of interior wetbelt follows DellaSala *et al.* (2021).

Reference	Geographical location	Stand age - years (Tree species) Elevation	Lichen loading, mean values dry weight (DW)
Old forests			
Edwards <i>et al.</i> 1960	Wells Gray Park, BC. Interior Wetbelt.	Site 1: 80–130 y (FDI, SE, BL) 792 m a.s.l. Site 2: 50–60 y (LPI, FDI, AT, BL) 792 m a.s.l. Site 3: 150–180 y (SE, BL) 1127 m a.s.l. Site 4: 141–250 y (SE, BL) 1828 m a.s.l.	Site 1: 838 kg ha ⁻¹ Site 2: 283 kg ha ⁻¹ Site 3: 756 kg ha ⁻¹ Site 4: 3291 kg ha ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> – whole canopy estimates)
Stevenson 1979	Selkirk Mtns. Interior Wetbelt.	141–250 y (SE, BL) 1800 m a.s.l.	Plot 1: 67 kg ha ⁻¹ ; 44 g branch ⁻¹ Plot 2: 103 kg ha ⁻¹ ; 53 g branch ⁻¹ Plot 3: 105 kg ha ⁻¹ ; 49 g branch ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> within 2–6 m above ground)
Antifeau 1987	North Thompson. Caribou Rainforest.	ESSF-low (SE, BL, LPI, CW) 1506–1650 m a.s.l.	ESSF-low 9.5 kg ha ⁻¹ (range: 1.8–24.7 kg ha ⁻¹)
		ESSF-high (SE, BL) 1718–1800 m a.s.l.	ESSF-high 11.0 kg ha ⁻¹ (range: 5.3–17.5 kg ha ⁻¹)
		Parkland (SE, BL) 1800–1845 m a.s.l.	Parkland 22.2 kg ha ⁻¹ (range: 9.6–44.3 kg ha ⁻¹) (<i>Alectoria</i> and <i>Bryoria</i> within 0–6 m above ground)
Rominger <i>et al.</i> 1994	South Selkirk Mtns and adjacent Idaho. Interior Wetbelt.	141–250 y (SE, BL) Idaho: 1750 m a.s.l. BC: 1800 m a.s.l.	Idaho: 264 kg ha ⁻¹ ; 9 g branch ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> within 2–6 m above ground) South Selkirks (BC): 147 kg ha ⁻¹ ; 5.5 g branch ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> within 2–6 m above ground)
		Revelstoke (SE, BL) 1350–1800 m a.s.l. Prince George (Sugarbowl) (SE, BL) 1372–1677 m a.s.l.	Revelstoke: 40 kg ha ⁻¹ Prince George: 53 kg ha ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i>) (Extrapolation from per tree clump estimates based on stand density for lichens within reach of caribou)
Campbell & Coxson 2001	North Cariboo Mtns, BC. Caribou Rainforest.	141–250 y (SE, BL) (Individual trees up to 400 y) 1475 m a.s.l.	226 kg ha ⁻¹ ; 29.6 g branch ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> – whole canopy estimates)
Stevenson 2001	Lucille Mtn (upper Fraser River watershed). Caribou Rainforest.	141–250 y (SE, BL) 1340–1585 m a.s.l.	472, 583 and 500 kg ha ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> within 2–6 m of ground (from control and preharvest irregular shelterwood, and single-tree selection sites respectively))
Waterhouse <i>et al.</i> 2007	East-central BC (east of Likely). Caribou Rainforest.	Spruce: 297 y Fir: 426–446 y (SE, BL) (Individual tree ages) 1440–1690 m a.s.l.	BBS site: 14 kg ha ⁻¹ BBW site: 23 kg ha ⁻¹ LGC site: 19 kg ha ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i>) (Values measured in stands immediately after 30% partial-cut harvesting)

(Continued)

Table 1. (Continued)

Reference	Geographical location	Stand age - years (Tree species) Elevation	Lichen loading, mean values dry weight (DW)
Young to mature forests			
Antifeau 1987	North Thompson. Interior Wetbelt Caribou Rainforest.	ESSF-low (SE, BL, LPI, CW) 1615–1672 m a.s.l.	1.6 kg ha ⁻¹ (range: 0.6–2.4 kg ha ⁻¹) (<i>Alectoria</i> and <i>Bryoria</i>)
Goward & Campbell 2005	Trophy Mtn, near Well Gray Park, BC. Interior Wetbelt.	Open stand: 61–64 y Closed stand: 50–59 y (BL, SE, LPI, AT) 1325 m a.s.l.	Open stand: 0.597 g (total measured on 60 cm branch segments) Closed stand: 1.06 g (total measured on 60 cm branch segments) (<i>Alectoria</i> and <i>Bryoria</i>) (Values for lower canopy, under 3 m height)
Lewis 2004	Blue River, North Thompson, BC. Interior Wetbelt.	Intermediate age forests: 50–100 y (BL, SE)	40–80 kg ha ⁻¹ (<i>Alectoria</i> and <i>Bryoria</i> within 4.6 m of ground)

their primary predators, which typically avoid old-growth forests (Wittmer *et al.* 2005a). Apps *et al.* (2013) provide a review of this ‘apparent competition’ phenomenon for endangered DSC in British Columbia. For both reasons (winter forage and predator avoidance), the long-term persistence of these caribou depends on the availability of extensive tracts of old-growth forests (Environment Canada 2014).

While the crucial role played by old-growth conifer forests in providing DSC with winter forage is well established (Environment Canada 2014), the mechanisms involved in the stand-level acquisition of hair lichen hyperabundance remain obscure. At issue is a curious mismatch between, on the one hand, the effective dispersal (Goward 2003b) and early entry into regenerating forests by *Alectoria* and especially *Bryoria* (Goward & Campbell 2005; Goward *et al.* 2022) and, on the other hand, their much-delayed transition into hyperabundance at *c.* 120–150 years post disturbance (Stevenson *et al.* 2001; Boudreau *et al.* 2009) or even later (Esseen *et al.* 1996). Such a prolonged delay cannot be attributed to slow lichen growth, as growth rates in *Alectoria* and *Bryoria* are comparatively rapid, with annual rates > 10% (Stevenson & Coxson 2003) and up to 1 mg g⁻¹ day⁻¹ (Phinney *et al.* 2021). Stevenson & Coxson (2007) found that stand-level *Bryoria* loadings tripled over a seven-year period.

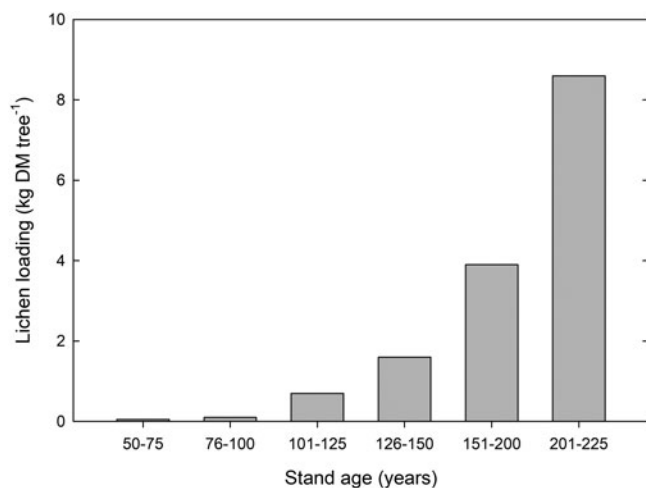


Figure 2. Lichen abundance (kg DM tree⁻¹) by stand age in Wells Gray Provincial Park, with biomass expressed as dry mass (DM). Adapted from Edwards *et al.* (1960).

Understanding the mechanisms that shape old-growth dependency in *Alectoria* and *Bryoria* hyperabundance is of increasing importance at a time when DSC habitat is being severely fragmented by industrial logging. In particular, it seems pertinent to examine the often implicit assumption that the onset of stand-level hair lichen hyperabundance might be accelerated by partial-cut harvesting treatments and related silvicultural protocols (e.g. Stevenson 1979, 1990; Rominger & Oldemeyer 1989; Stevenson & Enns 1992; Terry *et al.* 2000; Serrouya *et al.* 2011; Boutin & Merrill 2016). In an early paper on the distributional ecology of *Bryoria* within the range of DSC, Goward (1998) hypothesized that the establishment of stand-level hair lichen hyperabundance is necessarily an outcome of certain structural features peculiar to trees in old-growth forests and therefore not amenable to acceleration. Our first of three objectives in this paper is to examine this hypothesis in light of recent quantitative and qualitative insights into *Bryoria* ecophysiology, while our second objective is to provide a mechanistic explanation of (a descriptive model for) the delayed onset of *Bryoria* hyperabundance. Finally, our third objective is to draw on both ecophysiological studies and field observation to lay the conceptual foundation for a parallel model pertinent to *Alectoria sarmentosa* (Ach.) Ach., an exercise with considerable potential importance for efforts at DSC conservation. Our current emphasis on *Bryoria* derives from both its overall greater importance to DSC as a winter forage source (Rominger *et al.* 1996; Serrouya *et al.* 2007) and, compared to *Alectoria*, from its less complex, more readily modelled three-dimensional distribution within the canopies of conifers (Goward 1998).

Deep-Snow Caribou Winter Habitat

The current range of DSC largely coincides with the geographical extent in BC of Caribou Rainforest or Inland Temperate Rainforest (Coxson *et al.* 2020), a region where orographic uplift of Pacific storm systems creates a zone of elevated precipitation (DellaSala *et al.* 2021). At high elevations this uplift leads to deep winter snowpacks, allowing caribou in late winter to forage on canopy lichens from a 2–3 m settled snowpack (Stevenson *et al.* 2001; Dery *et al.* 2014). The main tree species in these high elevation forests are *Picea engelmannii* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir), which together make up the Engelmann spruce-subalpine fir (ESSF) biogeoclimatic zone

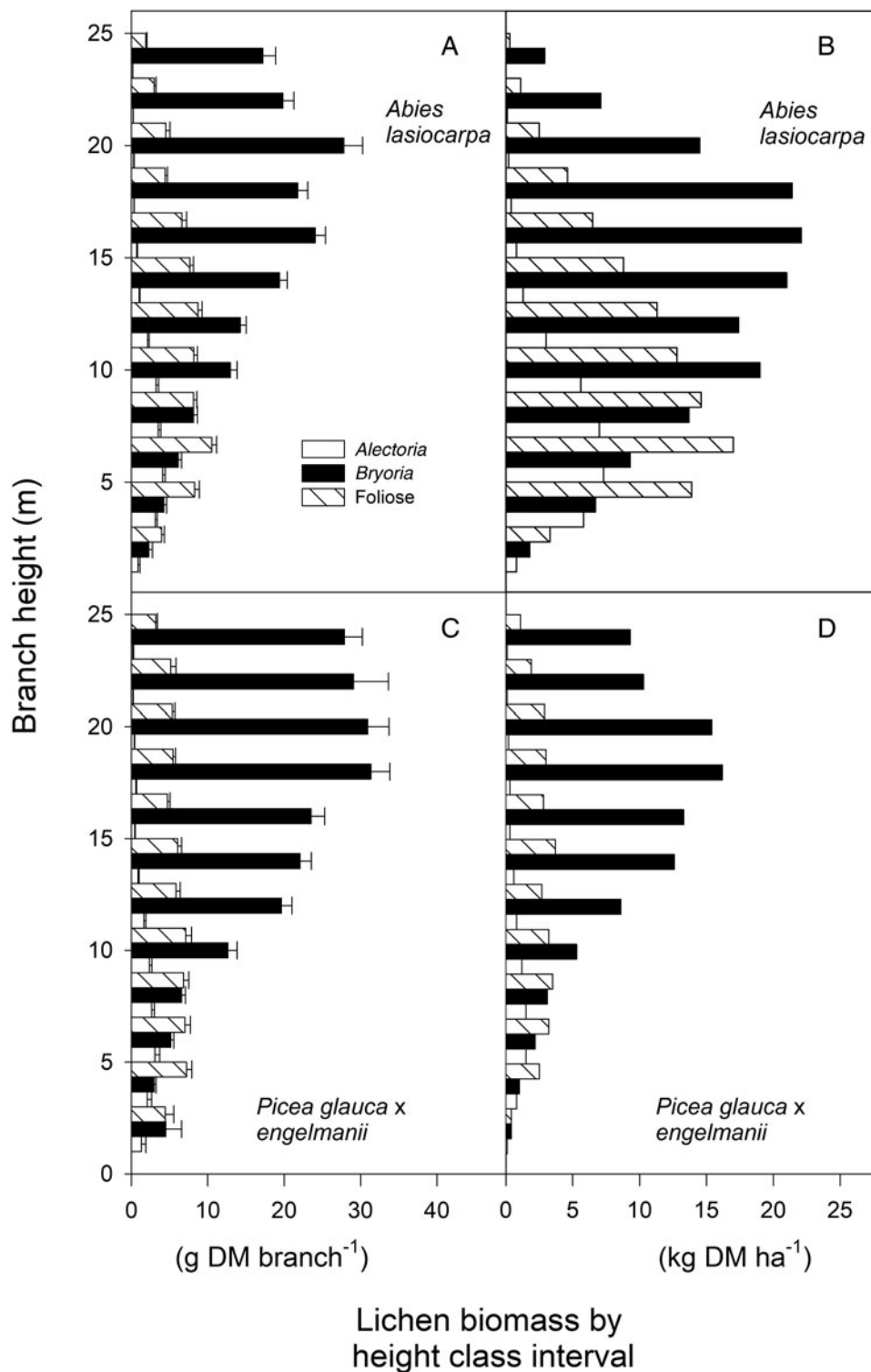


Figure 3. Lichen biomass by tree height class interval on a per branch basis (g DM branch^{-1} ; see A & C) and on a per area basis (kg DM ha^{-1} ; see B & D), with biomass expressed as dry mass (DM). Measurements were taken at Pinkerton Mountain, British Columbia, for each of *Alectoria*, *Bryoria* and foliose lichen functional groups in *Abies lasiocarpa* (A & B) and *Picea engelmannii* trees (C & D). Each bar represents the mean \pm 1 SE for branches within 2 m height class intervals. Adapted from Campbell & Coxson (2001).

(Meidinger & Pojar 1991). Mature trees in the ESSF are typically 20–30 m in height with a characteristically narrow, spire-like canopy architecture (Meidinger & Pojar 1991). Downward-leaning branches of mature *Picea engelmannii* and *Abies lasiocarpa*, shaped by deep winter snowpacks, can reach 2–3 m in length in

the lower canopy, providing an abundant substratum for hair lichens (Campbell & Coxson 2001).

Natural range-of-variability estimates suggest that upwards of 80% of the Caribou Rainforest (area: 13 301 km^2) was formerly covered by old-growth forests (Delong 2007). Stand-level

replacement was accordingly largely a function of single-tree gap dynamics after windthrow or insect outbreaks, leading to multi-aged stands (Benson & Coxson 2002). At tree scale, Campbell & Coxson (2001) provide structural characteristics for a 300-year-old ESSF stand in which mean branch length (*c.* 2.5 m) was greatest between 4 and 5 m above ground, branch diameter (3.5–4 cm) was greatest at mid-canopy, and branch density (9–12/m⁻¹) was greatest in the upper third of the canopy.

In recent decades, the Caribou Rainforest has been heavily fragmented by industrial forestry, with a 95% reduction in the area of primary core forests, recently leading to an IUCN ranking of critically endangered for the Caribou Rainforest as a whole (DellaSala *et al.* 2021). The corresponding loss of DSC habitat, mostly at lower and middle forested elevations (Palm *et al.* 2020), has also led to a dramatic decline in DSC populations (COSEWIC 2014), which have dwindled from *c.* 2500 animals in 18 herds in 1995 (Wittmer *et al.* 2005b) to *c.* 1150 caribou in 12 herds in 2020 (British Columbia Ministry of Environment and Climate Change Strategy 2023). Although a few DSC herds still linger south of the Caribou Rainforest in the Interior Wetbelt (DellaSala *et al.* 2021) (Fig. 1), it now seems clear that the Caribou Rainforest will represent their final sanctuary (Apps & McLellan 2006).

Distributional Ecology of High-Biomass *Bryoria* spp. Within the Range of DSC

Bryoria is a genus of brownish to blackish hair lichens (*sensu* Goward *et al.* 2022) restricted primarily to the branches of trees, especially conifers, at cool temperate and boreal latitudes (Brodo & Hawksworth 1977). Of the *c.* 10 species known to occur within the range of DSC (Goward 1994), only two (*B. fremontii* (Tuck.) Brodo & D. Hawksw. and *B. pseudofuscescens* (Gyeln.) Brodo & D. Hawksw.) regularly reach stand-level hyperabundance, although *Nodobryoria oregana* (Tuck.) Common & Brodo sometimes attains moderate abundance (Goward 2003a). Goward & Campbell (2005) referred to these as the high-biomass *Bryoria* spp., in contrast to the low-biomass *Bryoria* spp. including *B. fuscescens* (Gyelnik) Brodo & D. Hawksw., *B. glabra* (Motyka) Brodo & D. Hawksw. and *B. lanestris* (Ach.) Brodo & D. Hawksw.

It is worth noting here that *B. fremontii* differs markedly from *B. pseudofuscescens*, both in thallus morphology and in ecological expression. While the first is a rather robust species consisting of pliant branches often somewhat thickened and 20 or even 40 cm long, the second (here including *B. inactiva* Goward *et al.* and *B. pikei* Brodo & D. Hawksw.; see Boluda *et al.* 2019; Myllys *et al.* 2011) is a comparatively delicate lichen with thinner and more brittle branches usually < 15 cm long. *Bryoria fremontii* occurs in summer-dry regions beyond the ecological tolerance of *B. pseudofuscescens* (Rambo 2010). In winter, presumably owing to their relatively high protein content (Rominger *et al.* 1996), both species are preferentially foraged by DSC compared to *A. sarmentosa* (Rominger *et al.* 2000).

Vertical Zonation of the High-Biomass *Bryoria* spp. in the Forest Canopy

A marked pattern of vertical zonation can be distinguished in *Bryoria* abundance in old subalpine forest canopies within the range of DSC (Fig. 3). On both *Abies lasiocarpa* and *Picea engelmannii*, *Bryoria* reaches its greatest abundance between 15 and 20 m above ground, being by far the most abundant lichen

morphogroup (compared to *Alectoria* and foliose lichens) within these forest canopies. These mid- to upper-canopy *Bryoria* spp. become available to foraging DSC in three contexts: episodically when trees fall (Serrouya *et al.* 2007), periodically as litterfall, and more or less continuously by means of the manna hypothesis described below.

At a finer scale, this vertical gradient in *Bryoria* abundance is shaped by complex branch-scale three-dimensional responses to changes in moisture exposure and canopy ventilation. Establishing a causal relationship between increasing forest age and stand-level *Bryoria* hyperabundance requires an understanding of these micro- and mesoscale responses. We therefore highlight three recurring patterns first reported by Goward (1998): 1) *Bryoria* is absent from conifer branches subject to prolonged burial by snow; 2) *Bryoria* is largely absent from the outer foliated portions of conifer branches yet can occur in hyperabundance in the inner defoliated portions of the same branches; 3) *Bryoria* biomass in mid-successional forests tends to be disproportionately higher on stands growing in wind-exposed sites than in more sheltered stands. These and other observations led Goward (1998) to infer that the tree- and stand-level occurrence of the high-biomass *Bryoria* spp. reflects a complex integration of sensitivity to prolonged wetting on the one hand, and a positive response to rapid drying after wetting on the other hand.

It is now possible to examine this inference in light of recent results on hair lichen ecophysiology. Coxson & Coyle (2003) demonstrated a decline in net photosynthesis in *Bryoria* after prolonged hydration, while Campbell & Coxson (2001) found that increased exposure to ventilation and light accelerates growth while at the same time reducing thallus die-back (see also Coxson & Coyle 2003). Esseen *et al.* (2017) postulated that *Bryoria*'s sensitivity to prolonged wetting may reflect a pronounced capacity for external water storage. This phenomenon, apparently linked to the water-binding properties of melanin pigments (Beilinson *et al.* 2022), both extends photosynthetic activity after wetting and reduces photosynthetic efficiency owing to suprasaturation (Lange *et al.* 1993). In support of this suggestion, growth rates in *Bryoria*, unlike those of *A. sarmentosa*, do not increase with increasing rainfall (Phinney *et al.* 2021).

Goward (2003a) identified three vertical canopy zones of *Bryoria* abundance in high-elevation old-growth forests (Fig. 4). Nearest the ground is Zone A, where prolonged snow cover precludes the growth of hair lichens, and the upper trimline corresponds to the settled depth of the winter snowpack (Zone A in Fig. 4, Fig. 5D). Above Zone A is Zone B, the zone of periodic *Bryoria* die-back (Fig. 5A), where the high-biomass *Bryoria* spp. occur in low abundance and/or vigour, presumably a consequence of physiological damage during prolonged wetting (Gauslaa 2023). Note that Zone B can be lacking on solitary trees situated in highly wind-exposed localities, where the B/C trimline is replaced by an A/C trimline, as in Fig. 5D. Above Zone B is Zone C, characterized as the region of maximum ventilation, whether in the middle and/or upper canopy (Fig. 5B) or along forest margins (Goward & Campbell 2005). This is the zone of *Bryoria* hyperabundance, where thallus die-back is infrequent, thallus growth is accelerated (see below), and the high-biomass *Bryoria* spp. achieve their heaviest loadings (Fig. 5C & D).

The heavy *Bryoria* loadings associated with Zone C have been examined by Esseen *et al.* (2017), who showed that high-biomass *Bryoria* spp. branch more abundantly in the upper forest canopy

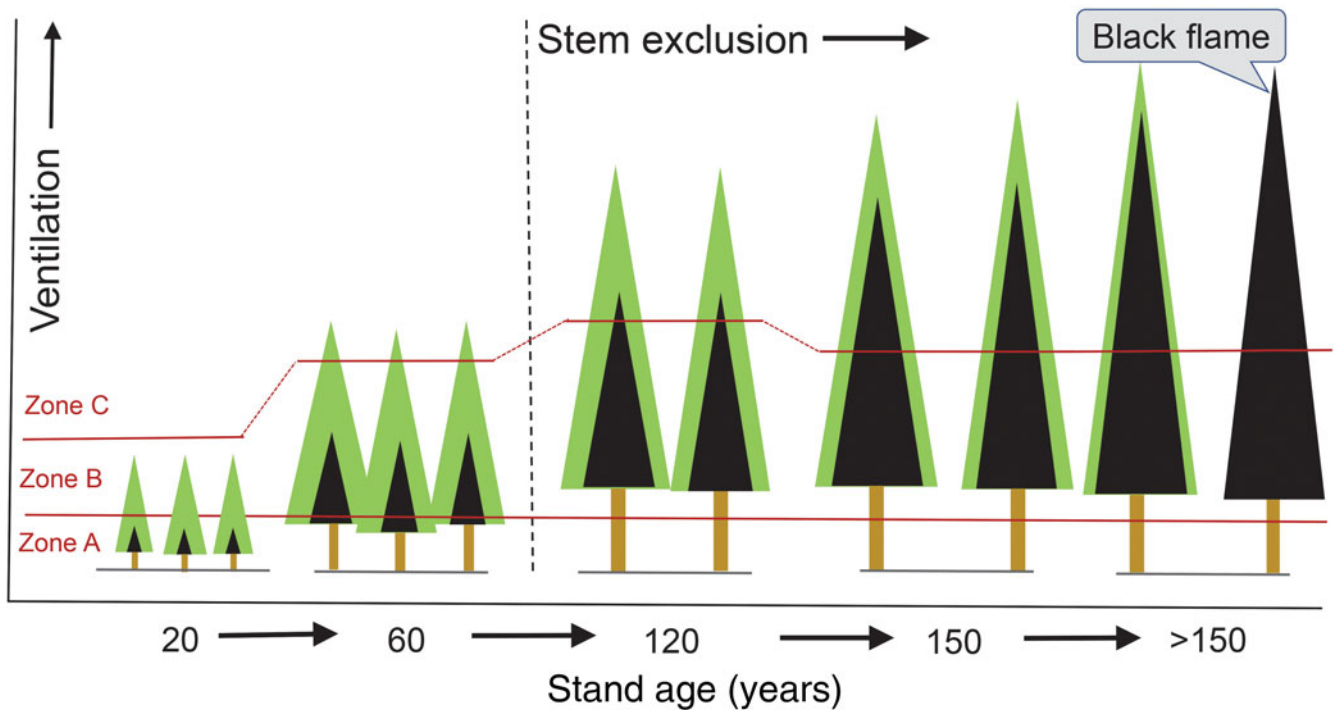


Figure 4. Schematic diagram showing five age-class stages in the development of tree-level hyperabundance in *Bryoria fremontii* and *B. pseudofuscenscens* (= the high-biomass *Bryoria* spp.) with increasing stand age within the range of Deep-Snow Mountain Caribou. The inner black canopy represents the defoliated zone where hair lichens establish and thrive above the settled depth of the winter snowpack (the A/B trimline), whereas the outer pale sleeve shows the foliated part of the canopy branches, which decreases geometrically with increasing tree age. The Y axis denotes increasing height above the ground and thus increasing ventilation. Zone A = prolonged snow cover precluding hair lichens; Zone B = zone of periodic *Bryoria* die-back; Zone C = the region of maximum ventilation and *Bryoria* hyperabundance. See text for further details on Zones A, B and C. After die-off of old trees occurs, a 'black flame' phase can be seen, where *Bryoria* is abundant throughout the vertical canopy profile. The development of hyperabundance in *Alectoria sarmentosa* is similar, albeit extending upwards into the upper canopy only in humid forest settings. In colour online.

(Fig. 4, Zone C) than in the lower canopy (Fig. 4, Zone B). Presumably this reflects their massively interweaving morphology and resulting enhanced capacity for interstitial water storage after rain or fog. In this scenario, the outer parts of the lichen dry rapidly compared with internal sections, causing water to be wicked outward from the less well illuminated thallus interior toward the thallus exterior. Here light is favourable for photosynthesis, whereas prolonged moderate hydration enhances net carbon fixation and thereby promotes increased branching. The likely outcome is a positive feedback loop, according to which enlargement of the interstitial water reservoir with progressive increase in thallus volume tends to accelerate the rate of overall biomass accrual, a phenomenon consistent with, and presumably contributing to, *Bryoria* hyperabundance in Zone C (Fig. 4, Zone C).

The disparate microclimatic conditions associated with Zone B versus Zone C are also reflected in thallus morphology (Goward 2003a). Thus, while the high-biomass *Bryoria* spp. exhibit a distinctly narrowly tapering (comb tooth-like) profile in the former zone (Fig. 5A), in the latter they are more broadly tapering (pennant-like) (Fig. 5C), a distinction readily observed from 10 or even 20 m. The tapering morphology prevalent in Zone B results from periodic thallus die-back that tends to prevent lateral growth along the surface of the supporting conifer branches; no such die-back occurs in Zone C, so that thalli become laterally more broadly attached and hence pennant-like. This distinction in thallus morphology facilitates recognition of the zone of upward transition from Zone B to Zone C, hereafter referred to as the B/C trimline, which in turn provides a

measure of relative stand-level potential for *Bryoria* hyperabundance: low in cases where the B/C trimline is positioned high in the canopy, and increasingly higher as it approaches the ground (Goward 2003a).

The Manna Effect: a Sustained-Yield System for DSC Winter Forage

In common with many other hair lichens, *Alectoria* and the two high-biomass *Bryoria* spp. exhibit indeterminate growth, that is, their branches can in principle elongate indefinitely. In practice this means that branch elongation must at some point be offset by fragmentation (Stevenson 1979, 1988; Renhorn & Esseen 1995; Goward 2003b), resulting in the periodic release of thallus fragments into lower portions of the forest canopy. Consistent with this, Stevenson & Coxson (2003) found that around half of annual biomass increase in *Bryoria* is lost to litterfall. While most of the resulting thallus fragments presumably fall to the ground as litterfall (Esseen 1985; Coxson & Curteanu 2002; Goward 2003b), some inevitably lodge in the defoliated cone, inoculating and thereby contributing to the ongoing replenishment of Zone B hair lichen biomass following episodic die-back, a process that, once begun, maintains stand-level *Bryoria* loadings at or near full potential indefinitely.

Stated more formally, this is the 'Manna Effect', according to which thallus fragments derived from massive standing crops of high-biomass *Bryoria* spp. in Zone C and *Alectoria* in Zone B continuously become available to wintering DSC as 1) litterfall

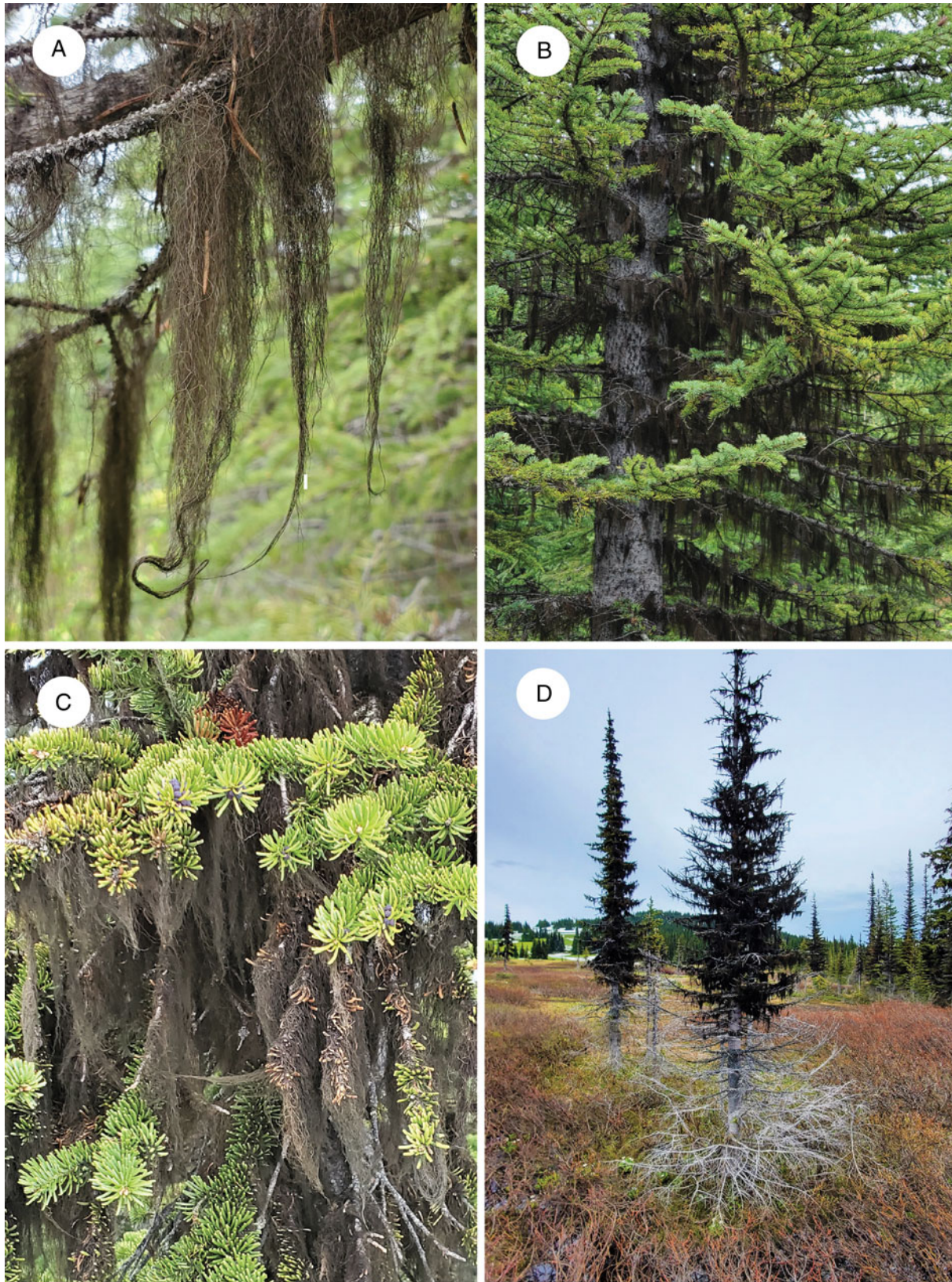


Figure 5. A, close-up of high-biomass *Bryoria* spp. showing the narrow, comb-tooth tapering profile associated with Zone B as well as the early stages of die-back at the thallus tips where branches have lost their flexibility and form \pm agglutinated ‘moustaches’ (see text). B, high-biomass *Bryoria* spp. already well established within the defoliated cone of this 40-year-old subalpine fir. These lichens will gradually disappear as upward and outward tree growth in this plantation stand reduces light penetration into the lower canopy while at the same time retarding evaporation after wetting. C, close-up of high-biomass *Bryoria* hyperabundance on a wind-exposed *Abies lasiocarpa*, showing the broad, pennant-like tapering profile characteristic of Zone C. D, two recently dead *Picea engelmannii* have transitioned to black flame trees in a wind-exposed subalpine meadow. Note the copious presence of high-biomass *Bryoria* spp. above (Zone C) and their absence below (Zone A). The trimline that separates Zones A (branches without hair lichens) and C (branches covered in black *Bryoria*) marks the settled depth of the winter snowpack. In colour online.

on the snow surface, 2) thalli lodged within foraging reach on the branches of standing trees, and 3) episodically, as recently fallen trees (Antifeau 1987). From this perspective, DSC can thus be understood as a beneficiary of an old-growth-forest-mediated sustained-yield system of winter forage production; this system, because it operates in the middle and upper canopy beyond their foraging reach, is resistant to degradation from excessive foraging (Edwards & Ritcey 1960).

The Development of *Bryoria* Hyperabundance with Increasing Forest Age: a Descriptive Model

In this section we propose a mechanistic model for the delayed onset of *Bryoria* hyperabundance with increasing stand age. We start with the observation (Goward 1998) that the (outer) foliated portions of conifer branches do not support *Bryoria* establishment, while the (inner) defoliated portions of the same branches are the primary habitat of this genus. In this way, progressive annual needle cast is necessarily a key contributor to *Bryoria* hyperabundance insofar as it results in an inner cone of defoliated branches enveloped by an outer sleeve of foliated branch tips (Fig. 5B). Crucially, and with increasing age of the tree, the proportion of total canopy volume occupied by the defoliated cone increases geometrically relative to the foliated sleeve, a phenomenon briefly described below and schematically illustrated in Fig. 4.

After 20 years, the inner defoliated cone occupies *c.* 20% of total canopy volume. Depending on the depth of the winter snow-pack relative to the height of the tree, the defoliated zone may now either support a few small *Bryoria* thalli or, at subalpine elevations where hair lichens near the ground are excluded by annual burial in snow (Goward 1998), lack *Bryoria* altogether. In any event, *Bryoria* growth rates in trees of this age are expected to be low and offset by periodic die-back.

At 60 years, and especially in open stands (Benson & Coxson 2002; Coxson & Coyle 2003; Goward *et al.* 2022), the defoliated cone now sustains a full complement of *Bryoria* species, with the occasional exception of *B. fremontii*, whose pliancy and comparative tensile strength often yield rather coarse thallus fragments resistant to efficient wind dispersal (T. Goward, personal observation). At the same time, and because conditions conducive to Zone C do not yet (within the range of DSC) overlap with well-developed portions of the defoliated cone, the high-biomass *Bryoria* spp. continue to experience periodic die-back during prolonged wet weather (Goward 1998). *Alectoria sarmentosa* at this stage can also be present in low abundance (Gauslaa & Goward 2023).

By 120 years, stem exclusion (Oliver & Larson 1996) is underway, and the stand is now more open than before, resulting in increased light in the lower canopy as well as, higher in the canopy, increased exposure to the drying effects of ventilation. The defoliated cone is now well developed into the middle and upper canopies, and the high-biomass *Bryoria* spp. have begun to establish a permanent and ever-increasing biomass reservoir within Zone C. Meanwhile, diminishing rates of tree growth (Bigler & Veblen 2009) create a comparatively stable forest environment favourable to the hair lichens (Esseen *et al.* 2016b).

By 150 years, the defoliated branch zone accounts for *c.* 95% of canopy volume, providing a fully developed scaffolding for hair lichens into the middle and upper canopies. Meanwhile, the portion of this scaffolding that intersects with Zone C now often sustains *B. fremontii* and *B. pseudofuscescens* in hyperabundance,

resulting in high rates of thallus fragmentation and litterfall. While much of this litterfall reaches the ground or snow surface (Campbell & Coxson 2001), some catches in the lower canopy branches within Zone B where, again, it can accumulate to heavy loadings subject, however, to periodic die-back. The net outcome of this forest maturation is a massive *Bryoria* reservoir that in suitable localities and/or topographic positions can occur across large expanses of forest.

As the dying tree (200+ years) sheds the needles that constitute its outer foliated sleeve, the newly defoliated branch tips become available for colonization by high-biomass *Bryoria* spp. At this point, and especially in open stands, increased lichen growth rates rapidly transform the entire tree into a 'black flame' of hair lichens (Fig. 5D). Typically, this black flame phase, which persists until sloughed off during bark exfoliation, is still intact when the host tree finally collapses, thereby furnishing DSC with a much sought-after feeding platform (Edwards *et al.* 1960; Antifeau 1987; Terry *et al.* 2000). In this context, it seems reasonable to suggest that the current trend of increasing subalpine tree mortality, a by-product of climate change (e.g. Smith *et al.* 2015; Andrus *et al.* 2021), might translate to a temporary boost in late winter forage availability.

In summary, the available evidence supports the hypothesis (Goward 1998) that the century-long delay in stand-level onset of hyperabundance in *B. fremontii* and *B. pseudofuscescens* within the range of DSC reflects the late development of certain structural features favourable to their growth and peculiar to old-growth forests. Four such features can be recognized: 1) a fully realized tree-scale (and stand-scale) development of the defoliated cone (Goward 2003a); 2) relative environmental stability associated with age-related reduction in tree growth (Bigler & Veblen 2009); 3) increased stand spacing (Campbell & Coxson 2001; Benson & Coxson 2002) associated with stem exclusion (Oliver & Larson 1996); 4) related to this, rapid post-wetting desiccation associated with high ventilation in at least the upper portions of the defoliated cone (Esseen *et al.* 2017). Taken together, these prerequisites of *Bryoria* hyperabundance challenge the often implicit assumption (Serrouya *et al.* 2011; Boutin & Merrill 2016) that its onset might in principle be appreciably accelerated by selection logging or other silvicultural protocols.

Here it is worth noting that stand-level *Bryoria* biomass in unmanaged forests may continue to increase into the fourth century post disturbance (Stevenson & Coxson 2003), a finding consistent with the modelling exercise of Dettki & Esseen (2003), who showed that even rotations of 200 years would yield far less *Bryoria* biomass than uncut stands. From this we infer that our use of 120–150 years as onset for *Bryoria* hyperabundance should be regarded as a minimum interval after disturbance.

Finally, we stress that the above model describes the behaviour of the high-biomass *Bryoria* spp. within the range of DSC; there is no reason to believe that *B. fremontii* or *B. pseudofuscescens* can achieve hyperabundance throughout their respective distributions, as implicit in the findings of Rambo (2010). Our field experience suggests that stand-level abundance in these species varies according to degree of overlap in at least eight interacting climatic and edaphic variables, namely: 1) base-poor soils (Gauslaa *et al.* 2021); 2) acidic tree bark (James *et al.* 1977); 3) a general absence of within-canopy nutrient enrichment (Goward & Arsenault 2003); 4) high atmospheric purity (Häffner *et al.* 2001) including low nitrogen deposition (Esseen *et al.* 2016a); 5) cool climatic regimes combined with moderate continentality (*sensu* Tuhkanen 1984) (Esseen *et al.* 2016a); 6) moderate precipitation

(Esseen *et al.* 2016a; Phinney *et al.* 2021); 7) frequent wetting by dew or mist (Gauslaa 2014; Bidussi & Gauslaa 2015; Strother *et al.* 2021) followed by 8) rapid desiccation (Goward 1998; Esseen *et al.* 2017). Even within the range of DSC the divergent hair lichen biomass estimates reported for old-growth subalpine forests, from 300–500 kg ha⁻¹ (Rominger *et al.* 1994; Campbell & Coxson 2001) to > 3000 kg ha⁻¹ (Edwards *et al.* 1960), might simply reflect differing degrees of overlap in the above variables.

Alectoria sarmentosa Within the Range of Deep-Snow Mountain Caribou

Eight species of *Alectoria* are currently recognized in North America (Esslinger 2021), although only *A. sarmentosa* is of importance to DSC. This pendent hair lichen has rather coarse, pale yellowish green branches (cortical usnic acid) that can sometimes bear apothecia (Brodo & Hawksworth 1977). Compared with *Bryoria*, *A. sarmentosa*, henceforth referred to as *Alectoria*, has high tensile strength; in favourable habitats, it can measure up to 110 cm long (Goward & Ahti 1992), although 30–50 cm is more typical (Esseen 2006, 2019). *Alectoria* provides an important source of forage for DSC in late autumn and early winter, when other food sources are buried out of reach by snow (Rominger *et al.* 2000), and before the winter snowpack lifts them to within foraging reach of Zones B and C. In late winter, however, DSC forage less on *Alectoria* than on *Bryoria* (Rominger *et al.* 1996).

While important insights into the ecophysiology and distributional ecology of *Alectoria* continue to come to light (Esseen 2019; Phinney *et al.* 2021; Gauslaa & Goward 2023), little effort has yet been given to characterizing the main features of its micro- and toposcale occurrence within the range of DSC. Nonetheless, our goal here is to discuss factors responsible for the delayed development of *Alectoria* hyperabundance into the second century following stand initiation, a discussion that seems merited at this time for three reasons pertinent to DSC conservation: 1) DSC depend on *A. sarmentosa* as a near-exclusive source of early winter forage (Rominger & Oldemeyer 1990); 2) industrial forestry continues to fragment the old-growth forests that sustain its heaviest loadings (Palm *et al.* 2020); 3) in contrast to the high-biomass *Bryoria* spp., the onset of hyperabundance in *Alectoria* appears in some cases to be amenable to acceleration using silvicultural approaches (see below). The following discussion may help to guide future research on the distributional ecology of this wide-ranging hair lichen.

Goward (1998) listed seven micro- and toposcale features pertinent to the distributional ecology of the high-biomass *Bryoria* spp. within the range of DSC. Four of these features are shared with *Alectoria*: 1) an inability to colonize branches subject to annual burial in the winter snowpack; 2) a disproportionately higher biomass in the (inner) defoliated cone than in the (outer) foliated sleeve; 3) a disproportionately lower biomass on vigorously growing trees than on trees subject to slower rates of growth; 4) an ability to persist in stands sheltered from frequent exposure to direct sunlight (i.e. in common with *B. pseudofuscescens* but not with *B. fremontii*) (T. Goward, personal observation). In addition, *Alectoria* and the high-biomass *Bryoria* spp. also tend to achieve maximum biomass in localities adjacent to open water and/or subject to frequent mist or fog. Four points of ecological variance with the high-biomass *Bryoria* spp. can also be noted. Therefore, *Alectoria*: 5) tends to be resistant to periodic die-back (T. Goward, personal observation); 6) is generally restricted to

lower portions of the forest canopy (Coxson & Coyle 2003; Esseen 2019); 7) occurs in greater overall abundance in cold subalpine forests than in warmer forests at valley and especially middle elevations (T. Goward, personal observation; see also Esseen *et al.* 2016a); 8) is more widely distributed in wetter regions and more localized in drier regions (Benson & Coxson 2002). Taken together, and in contrast to the high-biomass *Bryoria* spp., these last four patterns support the theory that *Alectoria* is a rather hygrophytic species (8) in which enhanced tolerance for prolonged wetting (5, 6) operates in tandem with comparative intolerance to rapid desiccation (7, 8).

Recent advances in understanding the ecophysiology of *Alectoria* suggest that the microscale and toposcale distribution of this species is shaped by at least two constraints. The first constraint concerns a sensitivity to direct sunlight while in the dry condition, a phenomenon attributed by Färber *et al.* (2014) to the poor sun-screening efficiency of its cortical pigment usnic acid, which affords the photobiont limited protection against high light. The second constraint appears to involve an inherent requirement for frequent and/or prolonged wetting (e.g. Phinney *et al.* 2021), presumably an adaptation for sustaining metabolic repair mechanisms against light damage (Färber *et al.* 2014). Consistent with these constraints, and in contrast to the high-biomass *Bryoria* spp., *Alectoria* achieves maximum net carbon uptake in the lower forest canopy (Coxson & Coyle 2003), where partial shelter from solar radiation combined with reduced ventilation prolong photosynthetic activity after rain (Stevenson & Coxson 2007).

These factors are reflected in the vertical distribution of *Alectoria* within forests in DSC habitat (Fig. 3). *Alectoria* biomass peaks between 5 and 10 m above ground level, diminishing rapidly in abundance at greater heights within the canopy (Fig. 3). In the tree-scale zonal classification developed for the high-biomass *Bryoria* spp. by Goward (2003a), the vertical amplitude of *Alectoria* broadly overlaps with *Bryoria* Zone B (T. Goward, personal observation), that is, the portion of the forest canopy where *B. fremontii* and *B. pseudofuscescens* are subject to periodic die-back. Since Zone B is typically confined to the lower canopy (Fig. 4), it follows that the stand-level biomass achieved by *Alectoria* is generally much lower, certainly in old-growth forests, than that of the high-biomass *Bryoria* spp., which not only reach their heaviest loadings in Zone C in the middle and upper canopies (Fig. 3), but also continuously inoculate the lower canopy, Zone B, with their thallus fragments.

It is important to note, however, that Zone B can also extend into the middle and upper canopies, especially in perhumid areas of the Caribou Rainforest, where moderate loadings of *Alectoria* have been shown to occur > 30 m above ground (Edwards *et al.* 1960). Such a wide vertical amplitude greatly increases the potential for stand-level hyperabundance, resulting in values that in some cases approximate those of the high-biomass *Bryoria* spp. (Benson & Coxson 2002). Crucially, and as with *B. fremontii* and *B. pseudofuscescens*, the onset of such heavy tree-scale loadings is necessarily constrained by the late development of the defoliated cone into the middle and upper portions of the forest canopy (Fig. 6A & D).

Our understanding of the reproductive ecology of *Alectoria* is limited owing to uncertainty concerning its capacity for long-distance dispersal via fungal spores versus short-distance dispersal via fragmentation. What is clear, however, is that its tensile strength results in rather coarse thallus fragments (Stevenson 1988) resistant to efficient wind dispersal (Dettki *et al.* 2000; Goward 2003b). A feature of many mid-successional stands is

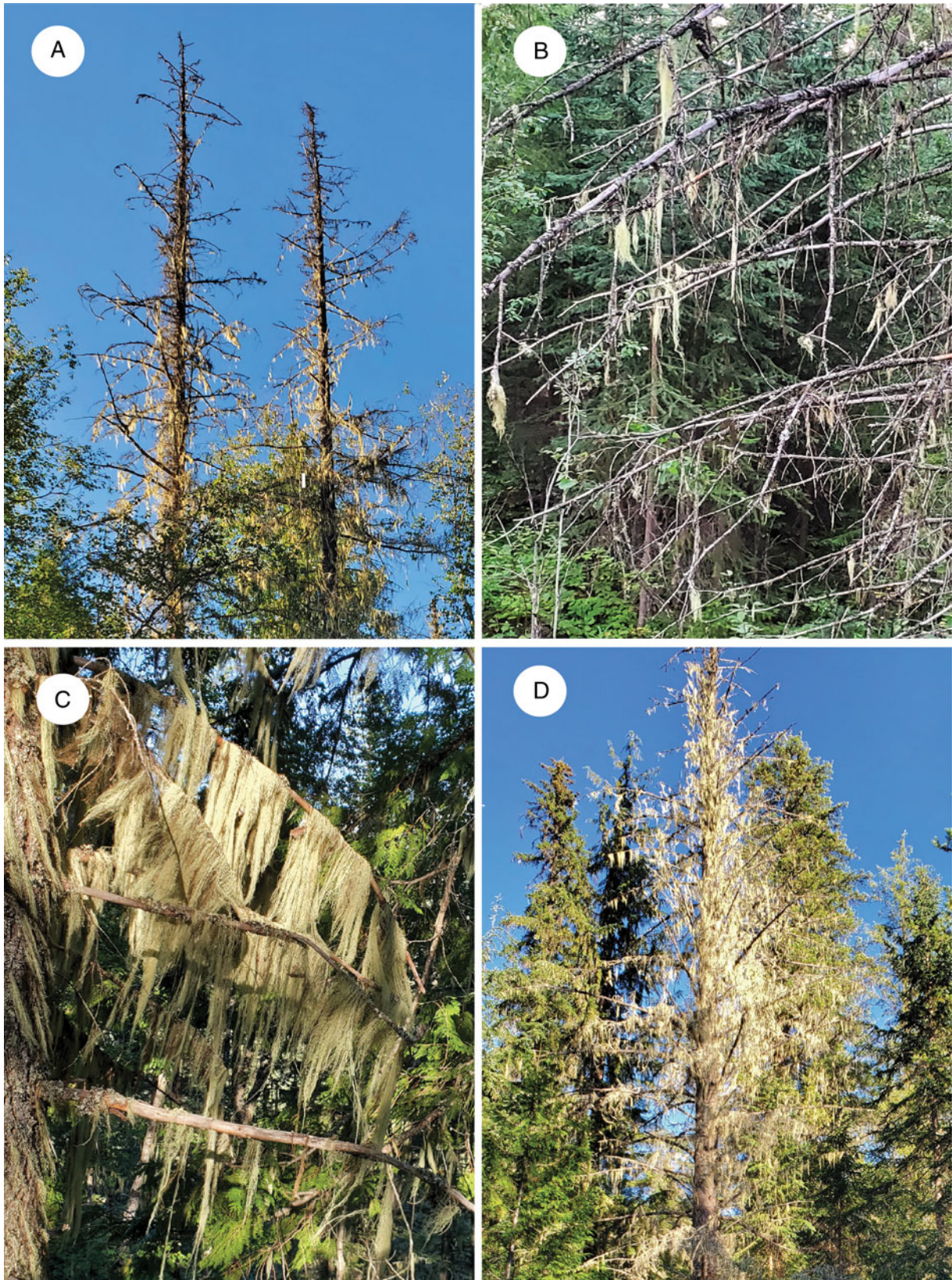


Figure 6. A, recently defoliated *Pseudotsuga menziesii*, showing early colonization of *Alectoria sarmentosa* (Zone B) grading upwards to high-biomass *Bryoria* spp. in the more wind-exposed upper canopy (Zone C). B, scattered elongated clumps of *A. sarmentosa* characteristic of the lower canopy of regenerating conifer forests, here aged 90 y. C, close-up of *A. sarmentosa* hyperabundance derived through litterfall from the upper canopy of low-elevation 120 y *P. menziesii*. This stand is situated in a hilltop fog belt near a large lake. D, a recently dead *P. menziesii* situated near a river and bearing copious *A. sarmentosa*, hence a yellow flame tree. In colour online.

the stand-level occurrence of *A. sarmentosa* at once robust and intermittently distributed (Fig. 6B), consistent with relatively infrequent thallus fragmentation in wind-sheltered forests.

To summarize, stand-scale *Alectoria* biomass within the range of DSC is generally negligible during the first century following disturbance (Goward & Campbell 2005; Goward *et al.* 2022), an observation that applies even in the lower portions of the forest canopy where fully developed defoliated cones become established early on. Only after *c.* 100 years, following the onset of stem exclusion (Oliver & Larson 1996) and consequent increased canopy openness, does *A. sarmentosa* begin to occur in hyperabundance (Fig. 6C), albeit usually only in the lower portions of the canopy (T. Goward, personal observation). Presumably this pattern in part reflects a corresponding increase in light penetration into the lower canopy (Campbell & Coxson 2001).

Implications for Forest Management

We have shown that the late development of heavy *Bryoria* loadings in forest succession is necessarily associated with structural attributes peculiar to old-growth forests and hence not conducive to acceleration by stand thinning or other silvicultural treatments. In particular, the late development of a defoliated cone into the middle and upper canopies precludes the occurrence in plantation stands of *Bryoria* loadings relevant to DSC until the second century after disturbance. Furthermore, silvicultural systems designed to mimic the characteristics of old-growth forest ecosystems face three challenges pertinent to DSC winter ecology: 1) partial cutting significantly and permanently reduces stand-level hair lichen loadings compared to unmanaged stands of similar age (Stevenson 2001; Stevenson & Coxson 2003; Waterhouse *et al.* 2007); 2) any temporary increase in hair lichen biomass on residual trees, a function of canopy openness favouring high light and increased ventilation (Campbell & Coxson 2001), will be lost once post-logging regeneration begins to close the forest canopy; 3) the comparatively closed stands that result are unlikely ever to be used by caribou (Terry *et al.* 2000; Apps *et al.* 2013).

These challenges notwithstanding, the findings summarized here suggest that *Alectoria* hyperabundance may be more amenable to artificially induced acceleration, at least in stands of sufficient age to support fully developed defoliated cones in the lower and middle canopies: firstly, because *Alectoria* is well adapted for growth and persistence in the lower forest canopy (Zone B) in conditions unfavourable for the high-biomass *Bryoria* spp., and secondly, because branch colonization in this species often lags far behind the establishment of a suitable defoliated cone, a consequence of its high tensile strength and resultant inefficient vegetative dispersal (Dettki 1998). Stevenson & Enns (1992) discussed the possibility that stem girdling might be used to generate hair lichen forage for black-tailed deer. Since trees killed by girdling remain standing, a judicious application of this approach in DSC early winter habitat could in principle promote 'yellow flame' trees (Fig. 4D) that not only release abundant *Alectoria* litterfall, but also function as propagule sources for the surrounding forest. Further research is warranted.


Old-Growth Forests and Conservation Strategies for Deep-Snow Mountain Caribou

To date, conservation strategies for DSC have focused on predator control (Serrouya *et al.* 2019) and maternity penning (Ford *et al.*

2022), together with partial protection of late winter habitat at sub-alpine elevations (British Columbia Ministry of Environment 2009). Importantly, none of these initiatives serve to mitigate the adverse effects of ongoing fragmentation of DSC early winter habitat at lower and middle forested elevations. Since DSC avoid mid-seral stands where they do not have ready sightlines to facilitate avoidance of predators (Wittmer *et al.* 2007; Blagdon & Johnson 2021), isolated patches of old-growth forest fragmented by mid-seral plantation forests will largely be inaccessible to them. Thus, the avoidance behaviour of these caribou ensures that the progressive loss of old-growth forest habitat necessarily initiates a corresponding loss of winter forage greatly exceeding the areal extent of the clearcuts involved (see Johnson *et al.* 2015). Additionally, edge effects in fragmented old-growth forest patches can lead to reduced canopy lichen loading, given the sensitivity of hair lichens to wind scouring (Coxson & Stevenson 2005). The emerging consensus is that long-term survival of DSC requires the continued existence of large, extensively replicated tracts of old-growth forests at all forested elevations, consistent with their dietary requirements during well-documented dual annual migrations (Edwards & Ritcey 1959; Apps *et al.* 2001; Kinley *et al.* 2007).

Looking ahead, and putting predator relationships aside, it seems inevitable that an ongoing loss of winter forage availability must at some point place DSC at risk of episodic malnutrition: firstly, because the metabolic costs of increased search effort (Stevenson 1979) will exceed the potential for energy input through foraging (Rominger *et al.* 1996), and secondly, because winter forage availability is itself subject to considerable interannual variation (Kinley *et al.* 2007).

Conservation efforts that target predator control and maternity penning at the expense of habitat conservation across the full elevational range of DSC will not save these caribou (Environment Canada 2014; Nagy-Reis *et al.* 2021). Even allowing that predation has to date been the primary proximal cause of DSC decline (Johnson *et al.* 2022), it seems unwise to assume that malnutrition will not at some point play a role in their ongoing herd-by-herd extirpation (Government of Canada 2018). In this paper, we have shown that post-logging habitat restoration for DSC is necessarily a long-term commitment requiring more than a century. In such a scenario, it seems reasonable to urge that future efforts at DSC conservation give particular attention to maintaining the sustained-yield system of winter forage production that surely brought this subspecies of barren-ground caribou into existence in the first place.

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