

Observations on the Ecology of the Lichen Genus *Bryoria* in High Elevation Conifer Forests

TREVOR GOWARD

Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6G 2B1, Canada
(Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0, Canada)

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The distributional ecology of the tree-dwelling "hair lichens" *Bryoria fremontii* and *B. pseudofuscescens* is examined, based on observations in high elevation conifer forests of inland British Columbia. Seven obvious microscale and mesoscale patterns are reported for one or both of these species: (1) a failure to successfully colonize branches occurring below the upper limit of the winter snowpack; (2) an occurrence in much lower abundance over the outer, foliated portions of branches than over the inner, defoliated portions of the same branches; (3) a tendency to periodic die-off in the outer, foliated branches, but not in the inner, defoliated branches; (4) a development of disproportionately heavier loadings over old, senescent trees than over young, vigorously growing trees of similar size; (5) an ability to colonize all levels of the forest canopy, including the upper crowns of trees; (6) an anomalously higher biomass in young stands growing in exposed sites than in young stands growing in sheltered sites; and (7) a development of considerable biomass in poorly illuminated stands that are nevertheless well ventilated. Based on these observations, the main distributional features of these species, and of *Bryoria* as a whole, are assumed to reflect a pronounced sensitivity to prolonged wetting, especially as a result of snowmelt. Other environmental factors are apparently less important, at least in the study area.

Key Words: *Bryoria fremontii*, *Bryoria pseudofuscescens*, arboreal lichens, conifer forests, British Columbia.

Few lichens are more familiar to biologists than *Alectoria*: an assemblage of hair-like species adapted especially to inhabiting the trunks and branches of conifers. Traditionally, *Alectoria* has been interpreted as a large "form genus" encompassing a majority of tree-dwelling "hair lichens". More recently, however, Brodo and Hawksworth (1977) and Common and Brodo (1995) have shown that the brownish and blackish species are not closely related to the greenish species, and should be assigned to various segregate genera, including *Bryoria*. The name *Alectoria* is thus currently reserved for a small assemblage of greenish hair lichens that contain usnic acid. Whatever their circumscription, these lichens are widespread and common in Canada's northern boreal woodlands, and are abundant also in the montane forests of British Columbia. In the latter region, they provide an important winter food for various ungulates, especially including the Woodland Caribou (*Rangifer tarandus caribou*) (Edwards and Ritcey 1960; Antifeaux 1987). Not surprisingly, *Alectoria* and *Bryoria* are of considerable interest to wildlife biologists.

It is now generally accepted among lichenologists that some lichen species are associated predominantly, or even exclusively, with late successional or old-growth forests (e.g., Rose 1976, 1992; Tibell 1992; Neitlich 1993; Goward 1994; Selva 1994). Though few physiological data are available to account for this phenomenon, oldgrowth dependency is usually assumed to be a function of various attributes pecu-

liar to oldgrowth ecosystems. Such attributes might include, for example, humid microclimatic conditions, availability of bark and wood in various stages of soundness and decay, relative environmental stability, and the existence of microsites not available in younger forest ecosystems.

An unusual form of "oldgrowth dependency" is exhibited in the high elevation conifer forests of northwestern North America by *Alectoria* and *Bryoria*. Though most species belonging to these genera colonize at a rather early phase in forest succession, they usually do not achieve appreciable biomass until much later (Lesica et al. 1991; McCune 1993; Esseen and Renhorn 1996). By the time a forest has attained oldgrowth status, hair lichen biomass may be truly spectacular, with loadings of more than 3000 kg per hectare having been recorded in southern inland British Columbia (Edwards et al. 1960). Such loadings are apparently unequalled in other parts of the world (Rhoades 1995).

During the past four decades, considerable work has been undertaken on the ecological behaviour of *Alectoria* and *Bryoria* in the high elevation forests of southern inland British Columbia and adjacent Idaho (e.g., Edwards et al. 1960; Ahti 1962*; Stevenson 1979, 1990; Antifeau 1987; Rominger et al. 1994). Most of this work has been performed by wildlife

*See Documents Cited section.

Most of this work has been performed by wildlife biologists, and all of it has been prompted by concern for the welfare of this region's Woodland Caribou. In part because these animals depend on the availability of large quantities of hair lichens, Caribou populations in southern British Columbia tend to be adversely affected by the loss of old-growth forests through logging and other agents of disturbance (for further discussion, see Stevenson and Hatler 1985).

Eleven hair lichens have been reported from British Columbia's high elevation inland conifer forests (see for example Goward and Ahti 1992). However, only three of these species — *Alectoria sarmentosa* (Ach.) Ach., *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw. and *B. pseudofuscens* (Gyelnik) Brodo & D. Hawksw. — may be said to contribute significantly to total hair lichen biomass; most of the remaining species occur in much lesser abundance. Given, however, that the combined ecological amplitude of these three species more or less embraces that of hair lichens as a whole in these forests, considerable insight may be gained through a study of their microscale and mesoscale distributions.

In recent years, the British Columbia forest industry has attempted to mitigate the impacts of logging on Caribou by designing silvicultural prescriptions intended to accelerate the development of hair lichen loadings. Unfortunately, most of the work conducted to date appears to have been performed in the absence of a general hypothesis on the distributional ecology of these lichens. The purpose of the present paper is to propose such a hypothesis for the genus *Bryoria*, based on the behaviour of *B. fremontii* and *B. pseudofuscens*. It is hoped the ideas expressed here may help to direct future quantitative studies on hair lichens and, not less, to guide future forest management practices within the range of British Columbia's Woodland Caribou. A future paper will discuss the distributional ecology of *Alectoria sarmentosa* (Goward, in preparation).

Ecological observations on hair lichens, including *Bryoria*, are notoriously resistant to precise quantification: first owing to their occurrence over trees: a three-dimensional habitat (McCune 1990; Stevenson and Enns 1993); second owing to their three-dimensional growth form (Goward and Arsénault 1997); and third owing to their tendency to reproduce through fragmentation (Brodo and Hawksworth 1977). Because fragments of *Bryoria* are regularly distributed throughout the forest canopy by wind or other agents of dispersal, detailed quantitative studies — including studies of biomass, microclimate, and physiological response — cannot be relied upon to convey ecologically unambiguous information. In response to these difficulties, and in the belief that careful observation has much to teach about lichen

ecology, the methods adopted in the present study are largely qualitative. They especially involve the detection of obvious microscale and mesoscale distributional patterns in *Bryoria*.

The observations reported here are based on incidental field studies carried out over a period of five 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). The forests under study occur at an elevation between 1450 m and 2100 m, and are dominated by *Abies lasiocarpa* and *Picea engelmannii*; they belong to the Engelmann Spruce - Subalpine Fir Biogeoclimatic Zone (hereafter "ESSF") of Meidinger and Pojar (1991), as well as to the Upper Oroboreal and Orohemiarctic Subzones of Tuhkanen (1984; see also Goward and Ahti 1992). Climatic conditions are cold and humid. Mean monthly temperatures exceed 10°C during only one or two months of the year, and snow covers the ground during seven to eight months of the year. In the lower portions of the ESSF, the forest canopy is more or less continuous, and the understory tends to be dominated by various shrubs, including *Menziesia ferruginea*, *Rhododendron albiflorum*, *Ribes lacustre*, *Vaccinium membranaceum* and *Vaccinium ovalifolium*. In the upper portions, in which stand structure is much more open, shrubs are less common, and the understory is characteristically dominated by herbs, including *Erigeron peregrinus*, *Lupinus arcticus*, *Valeriana sitchensis* and *Veratrum viride*. For a more complete description of the vegetation, see Pojar and Meidinger (1991).

Distributional Patterns

Throughout most, and possibly all, of the ESSF, *Bryoria* displays at least seven obvious microscale and mesoscale patterns of distribution. These will be briefly discussed below.

1) Relations to Winter Snowpack

In boreal and oroboreal regions subject to deep winter snowpacks, hair lichens, including *Bryoria*, are typically absent from the lowermost branches of the lower canopy. In the study area, indeed, these lichens develop a distinct lower trimline at between 1.5 m and 2.5 m above the ground. That this trimline approximates the average maximum depth of the winter snowpack led Stevenson et al. (1994) to attribute it to mechanical damage exerted by the snowpack as it settles. While mechanical damage cannot be ruled out as a contributing factor, my own repeated observations suggest that *Bryoria* is excluded primarily through physiological sensitivity to prolonged exposure to snow.

This assertion is supported by the observation that fallen thalli lodged in the surface of the snow soon become matted, giving a moribund appearance. It is

also consistent with the observation that young trees in the ESSF generally support no *Bryoria* at all until they have become sufficiently tall to protrude through the surface of the winter snowpack — usually at twenty to fifty years of age, but in many cases much later still (Parish 1997). Given that diaspore availability is clearly not limiting to *Bryoria* dispersal in this zone (Goward, in preparation), and given that mechanical damage alone is unlikely to account for the complete absence of hair lichens over young trees, this pattern must be explained on other grounds. The most reasonable explanation would seem to involve an inherent inability to withstand prolonged burial within the winter snowpack. These observations must of course be confirmed by detailed studies of *Bryoria* ecophysiology.

2) Relation to Foliated Branches and Defoliated Branches

A striking and highly intriguing microdistributional pattern observed repeatedly among hair lichens is their general inability to successfully colonize the foliated portions of conifer branches. By contrast, these lichens regularly develop heavy loadings over defoliated portions of the same branches, often only a few centimetres away. This observation appears to be critical to an understanding of *Bryoria* ecology in the ESSF. In attempting to account for it, it is helpful to divide the canopy branches of a tree into two concentric zones: (1) an inner zone of brownish, defoliated branches; and (2) an outer zone of green, foliated branches. These zones will henceforward be referred to as the “defoliated zone” and the “foliated zone”, respectively. Both zones may of course be expressed along different portions of a single branch.

That *Bryoria* biomass is invariably much heavier in the defoliated zone than in the foliated zone may at first appear to be related to differences in age, the former zone having been available for colonization much longer than the latter zone. However, biomass discrepancies between these zones are generally much too pronounced and too sharp to be explained entirely on this basis: the transition between copious lichen loading on the one hand, and meagre lichen loading on the other hand often occurs over a horizontal distance of only 10 to 20 cm. What is more, it is difficult to reconcile these discrepancies with the prevalence of fragmentation as a mechanism of dispersal in *Bryoria*. Thallus fragments are continuously being redistributed through the canopy as a result of wind, snow clumping, and bird and mammal movements. Given the existence of such on-going “transplant experiments”, and given that conifer needles in the ESSF generally persist for a decade or more, it is inconceivable that at least some thallus fragments should not accumulate to conspicuous loadings among the needles of the foliated zone. This comment of course applies equally to the foliated zone of young sapling conifers, in which the ter-

minial branches have not yet protruded above the surface of the winter snowpack (see pattern 1, above).

During the early stages of this study, bark chemistry and/or bark texture was assumed to provide a plausible explanation for the relative absence of *Bryoria* over foliated branches. This explanation, however, appears to be inconsistent with the observation that hair lichens actually do routinely colonize foliated branches in certain (rather localized) habitats. Solitary trees growing in open bogs, for example, often support heavy mats of hair lichens over both the defoliated and foliated portions of branches. In some instances, indeed, lichen loadings may be sufficiently heavy to occasion the death of the branches. Trees growing in rather exposed situations along ridgecrests provide a similar instance, though foliated branches in this case are seldom killed. Taken together, these observations suggest either that bark chemistry and texture are not limiting to *Bryoria*, or, if they are, that their influence may be overridden by other factors. Stevenson (1985) reached a similar conclusion in her study of hair lichen ecology in coastal forests.

The evidence thus strongly suggests the existence of an active mechanism of *Bryoria* exclusion in the foliated zones of most trees. Here it may be observed that conifers, having a centrifugal architecture, tend to shed water outward, in the direction of the foliated zone (Barkman 1958). Given that the branches of the foliated zone thus remain wet much longer than the branches of the defoliated zone (see also the discussion under pattern 3, below), it is proposed that prolonged wetting may be at least partly responsible for the exclusion of *Bryoria* in the former zone.

Such a wetting effect is especially pronounced during the winter months, when the foliated zone becomes blanketed with snow. In exposed or well-illuminated sites, the snow typically ablates rather rapidly, as a result either of wind or of direct warming by the sun. In sheltered or poorly illuminated sites, by contrast, the snow is likely to disappear more gradually, usually as a consequence of melting. Because the weight of the snow depresses the branches, it ensures that snowmelt is directed away from the trunk of the tree, in the direction of the branch tips (see Smith 1974). The extent to which a given foliated zone is subject to prolonged wetting doubtless depends on various complex details of architecture and exposure; but generally speaking, foliated branches positioned in sheltered situations may be expected to retain snowmelt much longer than other portions of a tree. The interception of rain, however, apparently operates according to very different principles (Satterlund and Haupt 1967).

By contrast, branch surfaces in the defoliated zone both receive less snow than their counterparts in the more exposed foliated zone, and provide comparatively meagre platforms for snow accumulation; they

therefore tend to shed snow comparatively rapidly. What is more, the dark colouration associated with *Bryoria* doubtless absorbs considerable heat, at least in illuminated sites, thus creating comparatively warm microclimatic conditions conducive to rapid snow melt. Viewed from this perspective, the existence of heavy hair lichen loadings over the defoliated, inner branches of a tree may be interpreted as an artifact of the ecologically "drier" conditions here.

3) *Periodic Die-backs*

During the spring and summer of 1997 — an anomalously wet period in southern British Columbia (Ralph Adams, personal communication) — *Bryoria* suffered a pronounced die-back in the study area. Most heavily affected were thalli that had become established over the foliated zone — presumably a result of thallus fragmentation. Thalli growing in the defoliated zone, by contrast, were largely unaffected by die-back. On branches over which both zones are expressed, it was possible to discern a continuum of thallus vigour consisting of at least three nodes: (1) an inner node of "healthy" thalli, in which the tips of the strands are divergent or at least discrete; (2) an intermediate node of apparently moribund thalli, in which the strand tips adhere to one another in a long, narrow, tapering "mustache"; and (3) an outer node of dead thalli, in which the strands are matted and clumped more or less throughout. Depending on aspect and degree of exposure, nodes 2 and 3 were restricted mostly to the foliated zone, though in sheltered sites node 2 was often found to extend inward to the outer portions of the defoliated zone. It would be interesting to discover whether, as seems likely, growth rates in *Bryoria* typically decrease outward along a branch in tandem with this continuum.

The situation was very different in the case of dead branches lacking a foliated zone. Here generally little evidence of *Bryoria* die-back was observed, even in the apical portions of the branches. This is an interesting observation. If, as seems likely, the apical portions of dead branches and the apical portions of living branches are subject to comparable levels of illumination, temperature, wind, and precipitation, then none of these factors seems likely to account for the observed differences in *Bryoria* loadings. Once again the most probable limiting factor, active solely in the foliated zone, would appear to be prolonged wetting.

Kershaw (1985) has already pointed to the existence in tree canopies of a "complex seasonal series of three-dimensional evaporative patterns" (his emphasis). Presumably as a result of these patterns, *Bryoria* undergoes seasonal readjustments to the prevailing climatic conditions: during periods of relative physiological drought, wind-dispersed fragments successfully colonize outward onto the foliated zone, whereas during the rest of the year, especially win-

ter, this genus tends to die back in the direction of the inner portions of the defoliated zone. Such trends must profoundly affect *Bryoria* growth rates in different portions of the canopy, with optimum rates doubtless shifting inward toward the trunk and outward toward the branch tips at different times during the course of a year.

4) *Relation to Old Trees*

A striking characteristic of old trees in the ESSF is their distinctly dark green colouration, as compared with the medium green colouration of adjacent younger trees. This colour difference extends to the forest itself, and may be discerned at considerable distances. Initially this discrepancy was assumed to be related to age-related differences in needle colour. Subsequent observation has revealed, however, that it in fact derives primarily from age-related differences in background *Bryoria* loadings. As already discussed in pattern 2, above, the development and extent of *Bryoria* loadings in a maturing tree closely parallel the development and extent of its inner defoliated zone. For convenience, the trajectory of both of these trends may be described in terms of the life history of a single branch.

In the earliest years of life, a branch is comprised entirely of a foliated zone; in the absence of a defoliated zone, it supports few if any colonies of *Bryoria*. After about ten or twelve years of age, however, the inner portion of the branch undergoes a degree of needle cast, thereby initiating a defoliated zone. From this point onward, the defoliated zone occupies an increasingly larger proportion of total branch length. Eventually the associated increasing dominance of hair lichens begins to cause a gradual darkening of the tree canopy. When eventually the branch dies, the foliated zone disappears. In its place the branch now consists entirely of a defoliated zone, over which a heavy loading of *Bryoria* soon becomes established. This trend to increasing dominance of hair lichens over the branch mirrors in microcosm the gradual increase in *Bryoria* over the tree as a whole. It is important to stress that the extent of *Bryoria* colonization on any given branch, and hence on any given tree, is dependent on the age of the branch, rather than on its size. Hence the observation, made on several separate occasions, that *Bryoria* loadings tend to be much heavier on old trees than on younger trees of similar size.

5) *Occurrences in the Upper Crowns of Old Forests*

As a rule, oldgrowth-dependent epiphytic lichens tend to be restricted to the lower canopy, in which within-stand microclimatic conditions are presumably favourable to their colonization; for a discussion, see McCune (1993) and Goward (1995). By contrast, few if any *Bryoria* species display a similar pattern in the oldgrowth forests of the ESSF. Here *Bryoria* loadings are routinely very heavy even when growing fully exposed to prevailing macroclimatic

conditions, as in the upper canopy of exposed trees. From this observation alone, it seems unlikely that the development of a heavy *Bryoria* biomass will be found to depend on special within-stand microclimatic conditions associated with oldgrowth forests. Instead, the positive correlation between increasing forest age and increasing hair lichen biomass appears to reflect the development of various structural features of ageing trees. In general, *Bryoria* appears to "read" the substrates associated with older trees as being less "humid" than those provided by younger trees. Thus, it is generally the age of individual trees, and not that of the forests in which they occur, which is of overriding importance to *Bryoria* loadings.

6) Relations to Young Trees in Exposed Sites

Heavy *Bryoria* loadings are usually associated with trees older than 100 to 150 years in age. Under some conditions, however, heavy loadings may develop in forest stands aged 70 years or even younger; see also Stevenson 1985. These younger stands are typically situated on ridgecrests or at the edges of clearings, though they may also occur in forests in which canopy structure is anomalously open. In either event the existence of heavy *Bryoria* loadings on young trees is invariably associated with sites exposed to high ventilation. Such observations strongly suggest that *Bryoria* growth rates are relatively rapid in the ESSF, and are unlikely by themselves to account for discrepancies in lichen biomass, at least in trees older than about 70 years; see also Renhorn and Esseen (1995).

7) Relation to Illumination

Repeated observation suggests that at least some species of *Bryoria* are able to persist at rather low levels of illumination. *Bryoria fuscescens*, for example, has been observed to occur in all but the most heavily shaded stands. In highly ventilated sites, such as isolated "tree islands" in the upper portions of the ESSF, *B. capillaris* and *B. pseudofuscescens* may likewise achieve considerable loadings over branches subject to little direct sunlight. These observations suggest that low illumination per se is probably able to exclude these lichens only under exceptional conditions, and should thus not be considered limiting to *Bryoria* as a whole. On the other hand, shaded microsites subject to poor ventilation appear to favour *Alectoria sarmentosa* over *Bryoria* (Goward, in preparation).

A "Prolonged Wetting Hypothesis" for *Bryoria*

Stevenson (1985) has proposed that frequency of wetting and drying may play an important role in *Bryoria* ecology. By contrast, the observations recorded here suggest that duration of wetting is likely to be much more significant than frequency of wetting, at least in the ESSF. Indeed, the existing field evidence strongly supports the hypothesis that

the main features of *Bryoria* distribution and biomass may be accounted for by a sensitivity to prolonged wetting. More specifically, this hypothesis is supported by patterns 1, 2 and 3, and is consistent with patterns 4, 5, 6 and 7. What is more, patterns 2, 3, 5 and 7 seem to provide various lines of evidence in support of the reciprocal hypothesis, namely that other environmental factors — temperature, illumination, frequency of wetting and drying, substrate texture, substrate chemistry — are by themselves *not* limiting to *Bryoria* in the ESSF. The possibility does exist, of course, that such factors may in combination override duration of wetting as a dominant ecological force under at least some conditions. Even so, it is difficult to avoid the conclusion that prolonged wetting is of considerable importance in the ecology of these lichens in the ESSF as a whole.

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