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ORIGINAL ARTICLE

# Lichenological evidence for the recognition of inland rain forests in western North America

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## ABSTRACT

**Aim** The coastal temperate rain forests of north-western North America are internationally renowned as the archetypal expression of the temperate rain forest biome. Less well documented is the existence of somewhat similar forests 500–700 km inland on the windward slopes of the Columbia and Rocky Mountains. Here we attempt to show that these inland 'wetbelt' forests warrant rain forest status.

**Location** North-western North America.

**Methods** We use tree-dwelling macrolichens to assess the degree of environmental congruence between the coastal temperate rain forests and their inland counterparts.

**Results** We report three key findings: (1) 40% of oceanic, epiphytic macrolichens found in Pacific coastal rain forests occur also in inland regions; (2) epiphytic species richness decreases with decreasing latitude, such that roughly 70% of disjunct oceanic species are restricted to regions north of 51° N; and (3) the southward decline in lichen diversity is correlated with a parallel decrease in summer precipitation, but not with mean annual precipitation.

**Main conclusions** These observations are consistent with the recognition of an inland rain forest formation between 50 and 54° N. Inland rain forests represent a small, biologically significant ecosystem whose continued fragmentation and conversion to tree plantations warrant close scrutiny.

**Keywords**

**British Columbia, climate, epiphytes, lichens, summer moisture deficit, temperate rain forests.**

## INTRODUCTION

The temperate rain forest biome is a highly disjunct, globally rare vegetation type accounting for < 0.5% of the world's land surface (Ecotrust, Pacific GIS & Conservation International, 1995). Alaback (1991) and others have recognized eight temperate rain forest formations worldwide, including portions of north-western North America, south-western South America, New Zealand, Tasmania, Japan, north-western Europe, the southern Alps, and the eastern Black Sea coast. Most of these regions are located in proximity to the open ocean, and all are subject to high annual precipitation owing to the moisture-capturing effects of nearby mountain ranges.

By far the largest temperate rain forest, in area accounting for nearly half of the biome, lies within the Pacific region of North America. As circumscribed by Schoonmaker *et al.* (1997), the Pacific North American rain forest extends 3600 km from the Kenai Peninsula of Alaska (60° N) south to the Bay area of California (38° N). This is a biologically rich region supporting not only some of the world's largest conifer species (*Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, etc.) but also, within their canopies, some of the world's richest epiphytic lichen and bryophyte assemblages (Pike *et al.*, 1975; Rhoades, 1995). The ongoing fragmentation of these rain forests as a result of industrial-scale forestry has in recent decades stimulated intense international debate (Norse, 1990).

Forest ecologists have long recognized the existence of a second, much less extensive 'rain forest' region in western North America (Rowe, 1959). Located 500–700 km inland on the western, windward slopes of the Columbia and Rocky

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Mountains, this region is popularly known as the 'interior wetbelt' (Daubenmire, 1952; Bell, 1964). The interior wetbelt consists of a broad, discontinuous band of humid forest types extending roughly 1000 km from Purden Lake (54° N) in east-central British Columbia south to the Bitterroot Mountains of Montana and the Salmon River Mountains of Idaho (45° N). In Canada the interior wetbelt is classified as belonging to the Interior Cedar–Hemlock Biogeoclimatic Zone (ICH; Meidinger & Pojar, 1991), while in the United States its forests are referred to as habitat types of the western redcedar or western hemlock series (Pfister *et al.*, 1977; Cooper *et al.*, 1991; see also Spribille, 2002).

Numerous studies have called attention to the presence in the interior wetbelt of many plant and animal species more characteristic of coastal regions. Perhaps most widely known are accounts of coastal vascular plants occurring as disjuncts in Idaho, Montana and southern inland British Columbia (Daubenmire, 1969; Johnson & Steele, 1978; Lorain, 1988). Coastal disjuncts have also been documented among this region's mosses (Schofield, 1976, 1992; Tan, 1980), as well as among its lichens (McCune, 1984; Goward, 1994).

In recent years there has been a growing trend to recognize the interior wetbelt as an inland counterpart of the coastal temperate rain forest formation. Veblen & Alaback (1995) were apparently the first authors to mention these forests within a broader discussion of the temperate rain forest biome. Five years later, Arsenault & Goward (2000) in inland British Columbia and Alaback *et al.* (2000) in Idaho expanded upon this theme by highlighting several structural and successional congruences between coastal and inland regions. The former authors also provided a map of the 'inland rain forest', which they interpreted as corresponding to the wettest subzones of the ICH.

The main objective of this paper is to test the hypothesis that at least some portions of the interior wetbelt actually warrant recognition as rain forest. Our approach will be typological, that is, we will argue that the term temperate rain forest should be restricted to regions sharing key biological characteristics with the 'type' region, which we take to be the coastal temperate rain forests of western North America (Alaback, 1991). To achieve this end, we adopt epiphytic (tree-dwelling) lichens as a key rain forest discriminator. Our decision to use lichens in this way has its basis in the well documented sensitivity of lichens to even minor shifts in environmental conditions (Gauslaa, 1985; Kershaw, 1985; Goward & Arsenault, 2000b). Lichens are dual organisms: part fungus and part alga. In order to exist, a lichen must simultaneously satisfy the physiological requirements of both of its partners (Lange *et al.*, 1986; Palmqvist, 2000). For most species this imposes severe constraints on the range of habitats available for colonization. Not surprisingly, most lichens are adapted to a rather narrow range of ecological conditions – a fact that recommends their use as highly sensitive tools for tracking spatial and temporal shifts in environmental conditions, especially climate (Degelius, 1935; Schöller, 1991; Wirth, 1992).

## MATERIALS AND METHODS

### Study area

The study area includes British Columbia north to 55° N, with a slight northward extension to 56° N in the well-studied Kispiox region (Goward & Pojar, 1998). It extends southward to Washington, Oregon, Idaho and Montana west of 113° W. This is a physiographically diverse region, in which a succession of mountain ranges oriented parallel to the coastline creates a strong east–west continentality gradient. Reflecting the onshore flow of moist air from the Pacific Ocean, the western side of each mountain range is comparatively wet, and the eastern side dry. The seasonal apportioning of precipitation varies latitudinally, with a southward trend to proportionately wetter winters and drier summers. Northward the trend is reversed and summers are relatively moist, especially north of about 51° N. Owing to the moderating effect of the Pacific Ocean, coastal areas experience cool oceanic conditions characterized by a narrow seasonal temperature range [continentality values of about 5–29 in the system of Conrad (1946)]. Inland of the coastal mountains, temperatures fluctuate much more widely, and continentality registers about 30–40 (Goward, 1999). A more detailed account of regional climate is provided by Demarchi *et al.* (1990) for British Columbia, and by Franklin & Halpern (2000) and Lahey (1979) for the Pacific Northwest.

### Data collection

To standardize our data set across the study area, we placed three constraints on our species selection. The first constraint required that only epiphytic macrolichens (*sensu* Goward *et al.*, 1994; Goward, 1999) be used, in recognition of the comparative lack of information on epiphytic microlichens. Reports of epiphytic species from deciduous trees or mossy boulders were excluded, as were specimens from the spray zones of waterfalls, which benefit from extremely high year-round humidity not representative of regional climate. The second constraint dictated that only 'oceanic' lichens be included. 'Oceanic', as used here, refers to species clearly adapted to cool, humid climates, as revealed by a tendency to occur predominantly in coastal regions. We emphasize that the final list of oceanic lichens adopted in this study (Appendix 1) was distilled from the phytogeographical analysis of a much larger list of epiphytic macrolichens (Spribille & Goward, unpubl. data).

Finally, the third constraint directed that only lichen species known to colonize conifers be included (see below). Our decision specifically to employ epiphytic macrolichens of conifers is based on five considerations: (1) the rain forests of western North America are largely dominated by conifers (Alaback, 1991); (2) no other substrate colonized by lichens has received more attention from lichenologists (McCune *et al.*, 1997); (3) epiphytic lichens are more likely than other floristic elements to be present throughout their full ecological ranges (Björk & Goward, unpubl. data); (4) owing to their occurrence on trees, epiphytic lichens are less likely than other floristic elements to be affected by local edaphic factors; and (5) lichens of conifers have already been shown to provide a powerful signal of regional climatic conditions in western North America (Goward & Arsenault, 2000a).

Discrepancies in lichen species concepts among workers in different parts of our study area obliged us to adopt broad concepts for some species. *Sphaerophorus globosus* and *S. tuckermannii* were combined as *S. globosus* s. lat., while *Bryoria trichodes* subsp. *trichodes* and subsp. *americana* were lumped as *B. trichodes*. In other regards, our taxonomy and nomenclature follow Esslinger (1997).

The distributions of all selected species were plotted across the entire study area. For British Columbia, we used the dot maps of Goward *et al.* (1994) and Goward (1999), augmented by unpublished maps in the case of several species. Lichen occurrences in Washington and Oregon were obtained from maps provided by the US Forest Service lichen air quality monitoring programme (http://www.nacse.org/lichenair), and were supplemented by herbarium records from OSC, WTU and the private collection of Martin Hutten (Port Angeles, Washington). Lichen distributions in inland Washington and Oregon as well as Montana and Idaho were based on unpublished dot maps developed from collections in the herbaria COLO, MONTU, OSC, WTU and UBC, and supplemented by data collected during field work in south-eastern British Columbia, northern Idaho, and western Montana.

### Data analysis

The resulting distributions were plotted on regional maps overlain by a grid system in which the individual cells measured 1° of latitude by 1° of longitude. A list of species occurring in each cell was tabulated and linked with a spatial display in a Geographic Information System (ArcView 3.2; Environmental Systems Research Institute, Inc., Redlands, CA, USA). We were thus able to display spatial patterns of three parameters: total richness of oceanic macrolichen species, total richness of oceanic chlorolichens (species with a green algal photobiont) and total richness of oceanic cyanolichens (species with a cyanobacterial photobiont). Cyanolichen species richness is of particular interest owing to the well documented requirement of cyanolichens for water in the liquid form; many other lichens can become physiologically active, at least at cool temperatures, when exposed to elevated atmospheric humidity alone (Lange *et al.*, 1986).

We attempted to account for the above spatial patterns by comparing them against known climatic gradients, with emphasis on inland regions. Data for 26 climate stations within the range of inland cedar–hemlock forests were obtained from the British Columbia Ministry of Forests (unpubl. data), Environment Canada (http://www.smc.ec.gc.ca/climate) and NOAA (1982a,b). Four climatic variables were used: (1) mean annual precipitation (MAP), (2) mean summer precipitation (MSP, May–September), (3) mean temperature of the warmest month (MTWM, July) and (4) mean precipitation of the warmest month (MPWM). Because moisture deficits are expected to be detrimental to many oceanic lichens (e.g. Gauslaa & Solhaug, 1998), and because the most pronounced moisture deficits are presumed to occur in July, we gave this month special emphasis in our analysis. All variables were examined for correlation with total oceanic species richness and total richness of cyanolichens per latitudinal belt. Owing to a lack of climatic data for half of the inland quadrats, coupled with an uneven occurrence of climate stations in the other half, we were unable to analyse correlations at the quadrat level.

## RESULTS

Oceanic epiphytic lichens are most diverse along the Pacific coast (Fig. 1), where all 89 species incorporated in our study are known to occur. Fifty of these are chlorolichens, while the remaining 39 are cyanolichens. Inland regions, by contrast, are much less species-rich, with only 36 oceanic species (40% of the total), 14 of which are chlorolichens and 22 cyanolichens.

Maximum species richness in inland regions occurs between 50 and 54° N, where as many as 20 species were recorded in some quadrats (Table 1). South of 50° N, species richness declines sharply; here most quadrats support only three to six species. Consistent with these trends, more than three-quarters of all oceanic species have ‘northern’ distributions, that is, they are restricted to regions mostly or entirely north of 50° N (Table 1). Of the remaining species, five (*Hypogymnia enteromorpha*, *Nephroma helveticum*, *Platismatia herrei*, *Pseudocyphellaria anomala* and *S. globosus*) are ‘widespread’, and four (*Hypogymnia apinnata*, *H. inactiva*, *Platismatia stenophylla* and *Pseudocyphellaria anthraspis*) are ‘southern’, being found primarily south of 50° N (Table 1). Most of the southern species extend much farther north in coastal localities.

Latitudinal trends in chlorolichen and cyanolichen species richness differ significantly between coastal and inland regions. Along the Pacific coast, both groups are well represented and widespread, with only a slight northward increase in cyanolichen diversity and a slight southward increase in chlorolichens, centering on about 51° N (Table 2). In inland regions, latitudinal trends are much more obvious, with a sharp decline in oceanic species south of about 50° N. Among the cyanolichens, for example, only 4 of 22 inland species occur southward to Montana and Idaho (Table 1). This trend is much less conspicuous among the chlorolichens, owing in large part to a southward addition of several species not present in the north (Table 2).

The southward decline in oceanic species richness in the interior wetbelt is consistent with a trend to an increasingly Mediterranean-type climate. Mean July temperatures, for example, increase with decreasing latitude, and summer precipitation decreases (Fig. 2a). South of 50° N, where oceanic lichen diversity is lowest, summer precipitation is generally < 250 mm. Assuming a loss to evaporation of 2 mm of precipitation per 1 °C (Walter, 1955; Walter & Lieth, 1967), this results in a continuous moisture deficit during the

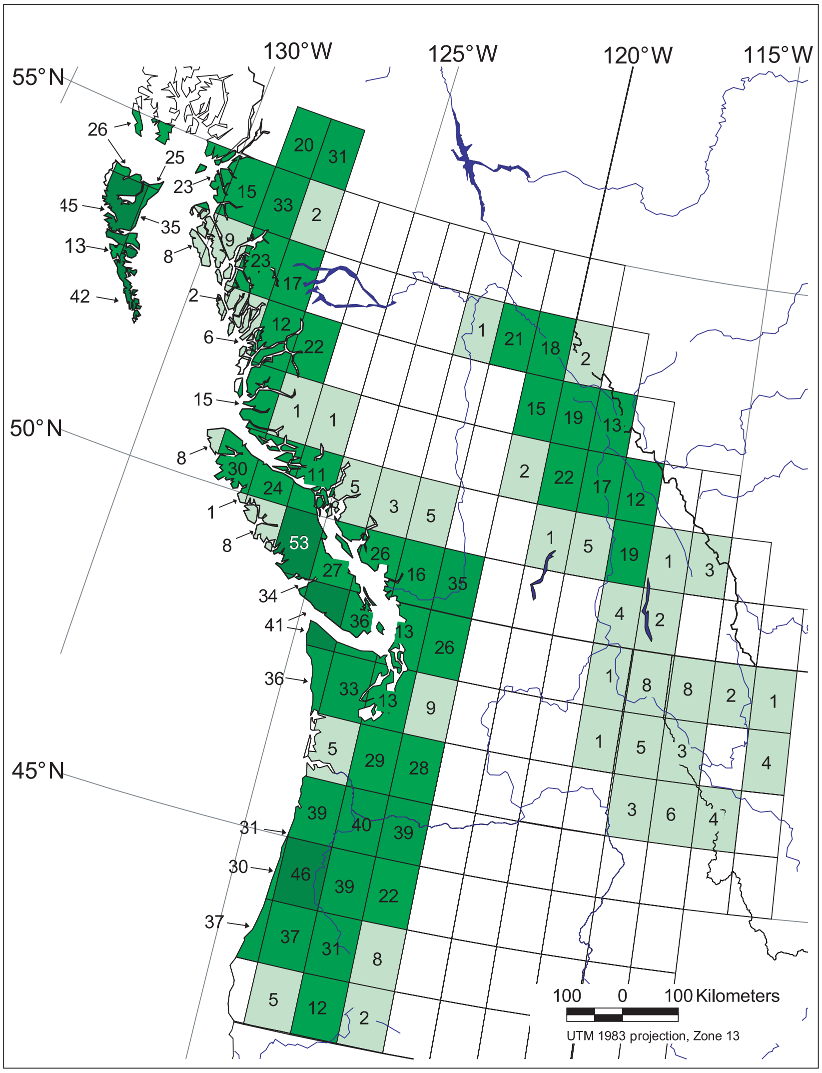

**Figure 1** Density of oceanic lichens in coastal and inland western North America. Numbers refer to the total number of oceanic lichens mapped per quadrat.

summer months. North of 50° N, by contrast, a moisture surplus occurs even in July (Fig. 2a). It should be noted, however, that total annual precipitation does not vary significantly from north to south, although considerable local variation does occur (Fig. 2b).

## DISCUSSION

The northern two-thirds of our study area was occupied by glacial ice until about 12,000–10,000 years BP (e.g. Pielou, 1991). By contrast, the remainder of the interior wetbelt south of 48° N escaped glaciation, thereby providing a refugium for many of the plants and animals now occupying the northern interior wetbelt. Following from this, it would be tempting to hypothesize that the epiphytic lichens of inland British Columbia must have migrated directly northward from their Pleistocene refugia. In the case of oceanic species, however, there are at least two reasons for questioning this assumption. First, the most productive forests for these species are dominated by *Thuja plicata* and *Tsuga heterophylla*, neither of which was present in glaciated portions of the interior wetbelt prior to about 2000–3000 years BP, that is, long after their establishment in coastal regions (Hebda, 1995). Secondly, relictual inland populations south of about 51° N are lacking for a large majority of oceanic cyanolichens.

Lorain (1988) has proposed several scenarios to account for the establishment, in post-Pleistocene times, of vascular plant disjunctions between coastal regions and the interior wetbelt. One of these scenarios pertains to glaciated regions, including the northern two-thirds of the present study area. Lorain (1988) suggests that colonization took place in stepwise fashion, first north along the coast from refugia south of the ice, and then inland from coastal regions via two primary migration routes, i.e. the Skeena and Fraser river valleys.

Recent palynological research indicates that climatic conditions were relatively warm and/or dry until about 4000 years BP (Hebda, 1995). Presumably the onset of cooler, more humid conditions at around that time favoured the development, not only of modern forest community structure (Hebda, 1995), but also of the epiphytic lichen assemblages currently

**Table 1** Distribution of oceanic macrolichens in inland north-western North America

| Quadrat coordinates | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Latitude (north of ° N) | 53 | 53 | 53 | 53 | 52 | 52 | 52 | 51 | 51 | 51 | 51 | 50 | 50 | 50 | 50 | 50 | 49 | 49 | 48 | 48 | 48 | 48 | 48 | 47 | 47 | 47 | 47 | 46 | 46 | 46 |
| Longitude (east of ° W) | 123 | 122 | 121 | 120 | 121 | 120 | 119 | 121 | 120 | 119 | 118 | 120 | 119 | 118 | 117 | 116 | 118 | 117 | 118 | 117 | 116 | 115 | 114 | 118 | 117 | 116 | 114 | 117 | 116 | 115 |
| **Northern species** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Chlorolichens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Bryoria trichodes s.lat.* | | + | + | | | | + | | | | + | | | | | | | | | | | | | | | | | | | |
| *Cavernularia hultenii* Degel. | | + | | | + | + | | | + | | | | | | | | | | | | | | | | | | | | | |
| *Cetrelia cetrarioides* (Delise ex Duby) Culb. & C. Culb. | | | | + | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Hypogymnia oceanica* Goward | | | | | + | + | | | + | | | | | + | | | | | | | | | | | | | | | | |
| *Loxosporopsis corallifera* Brodo, Henssen & Imshaug | | | | | + | + | | | | + | | | | | | | | | | | | | | | | | | | | |
| *Parmelia pseudosulcata* Gyelnik | | + | | | + | + | | | + | | | | + | | | | | | | | | | | | | | | | | |
| *Platismatia norvegica* (Lynge) Culb. & C. Culb. | | + | + | | + | + | | | + | | | | | + | | | | | | | | | | | | | | | | |
| *Usnea longissima* Ach. | | | | | | | | | | + | | | | | | | | | | | | | | | | | | | | |
| Cyanolichens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Collema auriforme* (With.) Coppins & Laundon | | + | | | | | | | + | | | | | | | | | | | | | | | | | | | | | |
| *Fuscopannaria ahlneri* (P.M. Jørg.) P.M. Jørg. | | | + | | | | | | + | | | | | | | | | | | | | | | | | | | | | |
| *Fuscopannaria leucostictoides* (Ohlsson) P.M. Jørg. | | | | | | | | | + | | | | | | | | | | | | | | | | | | | | | |
| *Fuscopannaria mediterranea* (Tav.) P.M. Jørg. | | + | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Fuscopannaria ramulina* P.M. Jørg. & Tønsberg | | | + | | + | + | + | | + | + | + | | | + | | | | | | | | | | | | | | | | |
| *Leptogium cyanescens* (Rabenh.) Körber | | | | + | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Lichinodium canadense* Henssen | | | + | | | | + | | + | + | + | | + | + | | | | | | | | | | | | | | | | |
| *Lobaria hallii* (Tuck.) Zahlbr. | + | | + | | + | + | + | + | + | + | + | | | | | | | | | | | | | | | | | | | |
| *Lobaria retigera* (Bory) Trevisan | | + | + | | | + | | | + | | | | | + | | | | | | | | | | | | | | | | |
| *Lobaria scrobiculata* (Scop.) DC. | | + | + | | | + | | | + | + | + | | | + | | + | + | | | | | | | | | | | | | |
| *Nephroma isidiosum* (Nyl.) Gyelnik | | + | + | | + | | + | | | + | + | | | + | | | | | | | | | | | | | | | | |
| *Nephroma occultum* Wetm. | | + | + | | + | + | | | + | + | + | | | + | | | | | | | | | | | | | | | | |
| *Parmeliella parvula* P.M. Jørg. | | | + | | | | + | | | + | | | | + | | | | | | | | | | | | | | | | |
| *Polychidium dendriscum* (Nyl.) Henssen | | | + | | | + | + | | + | + | | | | + | | | | | | | | | | | | | | | | |
| *Spilonemella americana* Henssen & Tønsberg | | + | + | | | | + | | | + | | | | + | | | | | | | | | | | | | | | | |
| *Sticta fuliginosa* (Hoffm.) Ach. | | + | + | | + | + | + | | + | + | + | + | | + | | | | | | | | | | | | | | | | |
| *Sticta limbata* (Sm.) Ach. | | + | + | | | + | | | | | | | | + | | | | | | | | | | | | | | | | |
| *Sticta oroborealis* Goward & Tønsberg | | + | + | | + | + | + | | + | + | + | | | + | | | | | | | | | | | | | | | | |
| *Sticta wrightii* Tuck. | | + | + | | | + | + | | + | + | | | | + | | | | | | | | | | | | | | | | |
| **Widespread species** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Chlorolichens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Hypogymnia enteromorpha* (Ach.) Nyl. | | + | | | + | | | | | | | | + | | | | | + | | + | + | | | | | | | | + | + |
| *Platismatia herrei* (Imsh.) Culb. & C. Culb. | | | | | | + | | | | | | | + | + | | | | | | + | + | | | | | | | + | | |
| *Sphaerophorus globosus* s.lat. | | + | | | + | + | | | + | + | + | | + | + | + | | + | | | | + | | | | + | + | | | + | |
| Cyanolichens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Nephroma helveticum* Ach. | | + | + | | + | + | + | | + | + | + | | | + | | + | + | | | + | + | + | + | | | + | + | | | |
| *Pseudocyphellaria anomala* Brodo & Ahti | | + | + | | + | + | + | + | + | + | + | | | + | | + | | | | + | + | | | | + | | + | | + | + |

**Table 1** *continued*

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Southern species** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Chlorolichens | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Hypogymnia apinnata* Goward & McCune | | | + | | | | | | | | | | | | | | + | + | | + | + | + | | | + | + | + | | + | + |
| *Hypogymnia inactiva* (Krog) Ohlsson | | | | | | | | | | | | | | | | | | | | + | + | | | | + | | + | | + | |
| *Platismatia stenophylla* (Tuck.) Culb. & C. Culb. | | | | | | | | | | | | | | | | | | | | + | + | | | | | | | + | | + |
| Cyanolichen | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pseudocyphellaria anthraspis* (Ach.) Magn. | | | | | | | | | | | | | | | | | | | + | + | | | | + | + | | | + | + | |
| Total chlorolichens | 0 | 6 | 3 | 1 | 7 | 7 | 1 | 0 | 5 | 3 | 2 | 0 | 4 | 4 | 1 | 0 | 2 | 2 | 0 | 5 | 6 | 1 | 0 | 0 | 3 | 2 | 2 | 2 | 4 | 3 |
| Total cyanolichens | 1 | 13 | 17 | 1 | 8 | 12 | 12 | 2 | 15 | 14 | 10 | 1 | 1 | 15 | 0 | 3 | 2 | 0 | 1 | 3 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 |
| Total species in quadrat | 1 | 19 | 20 | 2 | 15 | 19 | 13 | 2 | 20 | 17 | 12 | 1 | 5 | 19 | 1 | 3 | 4 | 2 | 1 | 8 | 8 | 2 | 1 | 1 | 5 | 3 | 4 | 3 | 6 | 4 |

+, Species present in quadrats as epiphytes.

inhabiting them. Based on the existing evidence, therefore, cyanolichen recolonization probably occurred, as Lorain suggests, from source areas along the Pacific coast.

It is less certain that cyanolichens migrated eastward from coastal British Columbia following specific migration corridors in the Skeena and Fraser river valleys. As a group, lichens are usually considered to be highly efficient at long-distance dispersal (Degelius, 1935), possibly accounting for their remarkably wide, often circumpolar distributions, at least at boreal and temperate latitudes (Ahti, 1977). Notwithstanding recent molecular studies suggesting that some lichen species are probably dispersal-limited (Printzen *et al.*, 2003; Walser *et al.*, 2005), the presence of a rich lichen flora on, for example, the mid-Atlantic island of Tristan da Cunha (Jørgensen, 1977) leaves little doubt as to the ability of lichens to disperse over thousands of kilometres. A similar observation can be made for mosses, ferns, clubmosses, and other plant groups dispersing via spores or spore-sized diaspores (Preston & Hill, 1999). Most vascular plants, with their heavy seeds, are much more dispersal-limited; their global ranges are often comparatively restricted (Jørgensen, 1977).

Based on the foregoing, it seems unlikely that the absence of a well developed oceanic epiphytic lichen flora in the southern interior wetbelt results from dispersal limitations. In our view, a more likely explanation is that oceanic lichen distribution is controlled by a southward trend to increasingly summer-dry conditions: a factor clearly disadvantageous to lichens adapted to cool, rather humid growing conditions. In broad outline, this conclusion accords with the earlier findings of Goward & Ahti (1997), who discussed distributional trends among cladoniiform lichens in north-western North America. These authors reported a strong latitudinal gradient in species diversity, with maximum floristic richness occurring between 52 and 56° N. South of 52° N, *Cladonia* was found to decline at a rate of roughly three to five species per degree of latitude. Goward & Ahti argued that this decline could be explained by a parallel southward trend from summer-moist conditions to summer-dry. We conclude that epiphytic cyanolichen distribution follows a similar pattern.

At a general level, then, the results of this study are consistent with a close causal relationship between macroclimate and oceanic lichen distribution. In our view, summer drought is likely to be the single most important factor limiting oceanic lichen occurrence in inland regions. While acknowledging the ecological significance of other environmental variables – temperature, substrate chemistry, etc. – we suggest that July moisture deficits offer a convenient and widely available correlate on which to base predictive models of oceanic lichen distribution.

In summary, our study has yielded three key findings. First, 40% of oceanic epiphytic macrolichens occurring in coastal temperate rain forests are present also in the interior wetbelt. Secondly, a majority of these species are restricted, in inland regions, to areas north of about 50° N – a distributional pattern exhibited to a much greater extent by cyanolichens than by chlorolichens. Thirdly, the greater richness of oceanic lichens north of 50° N is strongly correlated with high summer

**Table 2** Latitudinal trends of oceanic epiphytic macrolichens in coastal and inland regions of north-western North America

| Latitudinal belt (° N) | Coastal |  | Inland |  |
|---|---|---|---|---|
|  | Chlorolichens | Cyanolichens | Chlorolichens | Cyanolichens |
| 55–56 | 13 | 19 | – | – |
| 54–55 | 32 | 21 | – | – |
| 53–54 | 36 | 21 | 10 | 19 |
| 52–53 | 34 | 14 | 9 | 13 |
| 51–52 | 14 | 3 | 9 | 16 |
| 50–51 | 28 | 20 | 6 | 15 |
| 49–50 | 40 | 21 | 3 | 1 |
| 48–49 | 44 | 18 | 6 | 3 |
| 47–48 | 26 | 19 | 3 | 3 |
| 46–47 | 23 | 11 | 6 | 2 |
| 45–46 | 38 | 15 | – | – |
| 44–45 | 40 | 16 | – | – |
| 43–44 | 38 | 15 | – | – |
| 42–43 | 12 | 4 | – | – |

precipitation and a concomitant positive summer evapotranspiration budget. For convenience, the 50° N threshold can be used as a dividing line between the northern interior wetbelt to the north and the southern interior wetbelt to the south.

In recent global surveys of the coastal temperate rain forest formation, Alaback (1991) and others restricted the term 'temperate rain forest' to regions satisfying five climatic and ecological attributes. As revealed in Table 3, four of these attributes are captured by the northern interior wetbelt, although the fifth – mean annual precipitation > 1400 mm – is not. To judge, however, from the poor correlation between MAP and oceanic species richness, MAP seems to be of relatively little importance to epiphytic lichens in our area. A more significant correlate is summer precipitation, which exceeds 140 mm throughout the interior wetbelt, and is more than double this in northern regions (Appendix 2). In contrast to the northern interior wetbelt, the southern interior wetbelt satisfies only two of Alaback's five criteria, and appears to be too warm, too dry, and too prone to fire to qualify for rain forest status (Table 3).

The temperate rain forest of coastal western North America is divisible into three latitudinal zones (Alaback, 1991), two of which – the perhumid rain forest zone and the seasonal rain forest zone – largely overlap with our study area. The dividing line between these two zones is situated in the vicinity of the transition from the northern to the southern interior wetbelts, at 51° N. Following from this, it would be tempting to recognize two parallel phases of the inland rain forest formation: a perhumid phase in the north, and a seasonal phase in the south. And indeed, Alaback *et al.* (2000) recently proposed rain forest status for the Aquarius Research Natural Area of north-central Idaho. This site is located at 47° N, that is, well within the southern interior wetbelt. According to Alaback, the inclusion of the Aquarius site in the seasonal rain forest zone can be justified on physiognomic and ecological characteristics of the tree and shrub layers.

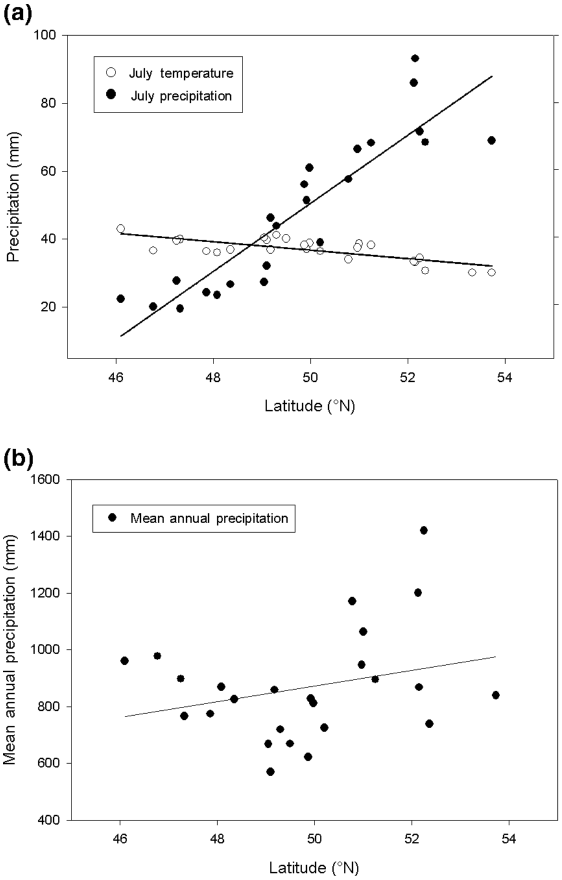

**Figure 2** Precipitation and temperature normals for 26 climate stations in the interior cedar–hemlock zone of north-western North America, arranged south to north. (a) Mean daily precipitation and temperature for the month of July, with 1 °C scaled to match 2 mm of precipitation as in Walter climate diagrams, indicating moisture deficit and surplus. Mean July daily temperature: $r^2 = 0.56$, $P < 0.001$; mean July precipitation: $r^2 = 0.82$, $P < 0.001$. (b) Mean annual precipitation (n.s.). For station locations see Appendix 2.

The lichenological evidence, however, does not support this proposal. In a recent survey of the Aquarius site, only five species of oceanic epiphytic macrolichens were encountered (Spribille, unpubl. data). This represents < 7% of oceanic lichens present in seasonal coastal temperate rain forests of the same latitude – a figure apparently consistent with the occurrence of oceanic lichens in the southern interior wetbelt as a whole. In marked contrast, the northern interior wetbelt supports nearly half of coastal epiphytic lichens occurring north of 51° N. We emphasize, however, that many portions of the southern interior wetbelt remain poorly explored for lichens. It is entirely possible that patches of lichen-rich rain forest will eventually be found. Such patches, if they exist, are likely to take the form of small and climatically sheltered 'islands' in a much larger 'ocean' of summer-dry forest habitat. Further work is needed, especially with respect to the use of oceanic microlichens as indicators of rain forest conditions.

**Table 3** Apportioning of temperate rain forest attributes in the northern and southern interior wetbelts of western North America

| Temperate rain forest attribute | Northern interior wetbelt | Southern interior wetbelt |
|---|---|---|
| Mean July temperature < 16 °C | Yes, in part | No |
| Mean annual precipitation > 1400 mm | No | No |
| Mean summer precipitation > 140 mm | Yes | Yes |
| Low frequency of wildfire | Yes | No |
| Cool dormant season | Yes | Yes |

Source: Alaback (1991), Veblen & Alaback (1995).

## Conservation significance

The inland rain forest formation represents a small, discontinuous ecosystem combining coastal and boreal biotic elements. In the past, a predominance of small-scale gap regeneration, coupled with infrequent wildfire, has permitted many stands to attain great age (Delong, 1998). Industrial-scale logging of old cedar–hemlock forests southward from the Robson Valley, at 54° N, to the Incomappleux Valley, at about 51° N, is now converting many of the oldest and biologically richest stands to early successional status. We emphasize that the inland rain forests of British Columbia are unique in the world: first in terms of their combination of thermal continentality and hygric oceanity; secondly, until recently, in terms of their undisturbed nature. As the tremendous biological diversity of these forests begins to be glimpsed, it is reasonable to ask how much additional habitat fragmentation can be sustained by an epiphytic lichen flora that includes a significant number of rare species (Goward & Arsenault, 2000a). At the very least, potential impacts on viability of epiphytic lichen populations should be carefully considered in the development of future management plans within this ecosystem.

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**Appendix 1** Oceanic epiphytic macrolichens of north-western North America used in the analysis.

*Alectoria vancouveriensis* (Gyelnik) Gyelnik ex Brodo & D. Hawksw., *Bryocaulon pseudosatoanum* (Asah.) Kärnefelt, *Bryoria bicolor* (Ehrh.) Brodo & D. Hawksw., *Bryoria carlottae* Brodo & D. Hawksw., *Bryoria cervinula* Mot. ex Brodo & D. Hawksw., *Bryoria pseudocapillaris* Brodo & D. Hawksw., *Bryoria trichodes s.lat., Bryoria subcana* (Nyl. ex Stizenb.) Brodo & D. Hawksw., *Bunodophoron melanocarpum* (Sw.) Wedin, *Cavernularia hultenii* Degel., *Cavernularia lophyrea* (Ach.) Degel., *Cetrelia cetrarioides* (Duby) Culb. & C. Culb., *Collema auriforme* (With.) Coppins & J. R. Laundon, *Erioderma sorediatum* D. J. Galloway & P. M. Jørg., *Fuscopannaria ahlneri* (P. M. Jørg.) P. M. Jørg., *Fuscopannaria alaskana* P. M. Jørg. & Tønsberg, *Fuscopannaria laceratula* (Hue) P. M. Jørg., *Fuscopannaria leucostictoides* (Ohlsson) P. M. Jørg., *Fuscopannaria mediterranea* (Tav.) P. M. Jørg., *Fuscopannaria pacifica* P. M. Jørg., *Fuscopannaria ramulina* P. M. Jørg. & Tønsberg, *Heterodermia japonica* (Sato) Swinscow & Krog, *Heterodermia leucomela* (L.) Poelt, *Heterodermia sitchensis* Goward & W. Noble, *Hypogymnia apinnata* Goward & McCune, *Hypogymnia duplicata* (Ach.) Rass., *Hypogymnia enteromorpha* (Ach.) Nyl., *Hypogymnia heterophylla* L. Pike, *Hypogymnia inactiva* (Krog) Ohlsson, *Hypogymnia oceanica* Goward, *Hypotrachyna riparia* McCune, *Hypotrachyna sinuosa* (Sm.) Hale, *Kaernefeltia californica* (Tuck.) Thell & Goward, *Leioderma sorediatum* D. J. Galloway & P. M. Jørg., *Leptogium brebissonii* Mont., *Leptogium cyanescens* (Rabenh.) Körber, *Lichinodium canadense* Henssen, *Lobaria hallii* (Tuck.) Zahlbr., *Lobaria oregana* (Tuck.) Müll. Arg., *Lobaria retigera* (Bory) Trevisan, *Lobaria scrobiculata* (Scop.) DC., *Lobaria silvae-veteris* (Goward & Goffinet) Goward & Goffinet, *Loxosporopsis corallifera* Brodo, Henssen & Imshaug, *Menegazzia terebrata* (Hoffm.) A. Massal., *Nephroma helveticum* Ach., *Nephroma isidiosum* (Nyl.) Gyelnik, *Nephroma laevigatum* Ach., *Nephroma occultum* Wetmore, *Pannaria malmei* Dodge, *Parmelia pseudosulcata* Gyelnik, *Parmelia squarrosa* Hale, *Parmeliella parvula* P. M. Jørg., *Parmotrema arnoldii* (Du Rietz) Hale, *Parmotrema chinense* (Osbeck) Hale & Ahti, *Parmotrema crinitum* (Ach.) M. Choisy, *Platismatia herrei* (Imshaug) Culb. & C. Culb., *Platismatia norvegica* (Lynge) Culb. & C. Culb., *Platismatia stenophylla* (Tuck.) Culb. & C. Culb., *Polychidium contortum* Henssen, *Polychidium dendriscum* (Nyl.) Henssen, *Pseudocyphellaria anomala* Brodo & Ahti, *Pseudocyphellaria anthraspis* (Ach.) H. Magn., *Pseudocyphellaria crocata* (L.) Vainio, *Pseudocyphellaria mallota* (Tuck.) H. Magn., *Pseudocyphellaria perpetua* McCune & Miadłikowska, *Pseudocyphellaria rainierensis* Imshaug, *Ramalina menziesii* Taylor, *Ramalina subleptocarpha* Rundel & Bowler, *Sphaerophorus globosus* s.lat., *Spilonemella americana* Henssen & Tønsberg, *Sticta beauvoisii* Delise, *Sticta fuliginosa* (Hoffm.) Ach., *Sticta limbata* (Sm.) Ach., *Sticta oroborealis* Goward & Tønsberg, *Sticta wrightii* Tuck., *Sulcaria badia* Brodo & D. Hawksw., *Teloschistes flavicans* (Sw.) Norman, *Usnea ceratina* Ach., *Usnea chaetophora* Stirton, *Usnea cornuta* Körber, *Usnea esperantiana* Clerc, *Usnea fragilescens* Hav. ex Lynge, *Usnea hesperina* Mot., *Usnea longissima* Ach., *Usnea madeirensis* Mot., *Usnea nidulans* Mot., *Usnea rubicunda* Stirton, *Usnea wirthii* Clerc, *Vermilacinia cephalota* (Tuck.) Spjut & Hale.

**Appendix 2** Selected climatic data from interior wetbelt stations in north-western North America. Stations arranged from north to south. MAP, mean annual precipitation; MSP, mean summer precipitation (May–September); MTWM, mean temperature of the warmest month (July); MPWM, mean precipitation of the warmest month. Data derived from British Columbia Ministry of Forests (unpubl. data), Environment Canada (http://www.smc.ec.gc.ca/climate) and NOAA (1982a,b)

| Station | Latitude (N) | Longitude (W) | Elevation (m) | MAP (mm) | MSP (mm) | MPWM (mm) | MTWM (°C) |
|---|---|---|---|---|---|---|---|
| British Columbia | | | | | | | |
| Dome Creek | 53°44′ | 120°05′ | 648 | 839.8 | 374.3 | 69.0 | 14.7 |
| Teare LW | 53°02′ | 120°08′ | 1329 | * | 328.2 | * | 14.7 |
| Horsefly Lake | 52°22′ | 121°02′ | 777 | 739.4 | 401.0 | 68.5 | 15.0 |
| Blue River North | 52°09′ | 119°01′ | 689 | 867.7 | 439.3 | 93.1 | 16.3 |
| Blue River A | 52°08′ | 119°01′ | 679 | 1199.8 | 365.6 | 86.0 | 16.4 |
| Mica Dam | 52°03′ | 118°35′ | 579 | 1419.0 | 331.0 | 71.6 | 16.9 |
| Seymour Arm | 51°15′ | 118°05′ | 351 | 894.9 | 336.3 | 68.3 | 18.8 |
| Revelstoke | 51°00′ | 118°12′ | 456 | 1063.7 | 325.0 | * | 19.0 |
| Revelstoke A | 50°58′ | 118°11′ | 443 | 946.6 | 274.9 | 66.5 | 18.4 |
| Sidmouth | 50°47′ | 118°01′ | 430 | 1170.9 | 309.2 | 57.6 | 16.7 |
| Lardeau | 50°12′ | 116°58′ | 550 | 725.2 | 229.1 | 39.1 | 17.9 |
| New Denver | 49°59′ | 117°23′ | 564 | 812.2 | 272.9 | 61.0 | 19.1 |
| Kaslo | 49°55′ | 116°55′ | 588 | 828.0 | 250.0 | 51.4 | 18.2 |
| Fauquier | 49°52′ | 118°04′ | 472 | 621.8 | 254.5 | 56.1 | 18.8 |
| Nelson 2 | 49°03′ | 117°17′ | 603 | 668.9 | 216.3 | * | 19.8 |
| Castlegar A | 49°18′ | 117°38′ | 494 | 719.0 | 234.4 | 43.9 | 20.3 |
| Salmo BCFS | 49°11′ | 117°48′ | 685 | 858.7 | 299.5 | 46.3 | 18.1 |
| Creston | 49°06′ | 116°31′ | 597 | 568.9 | 199.9 | 32.1 | 19.6 |
| Columbia Gardens | 49°03′ | 117°36′ | 433 | 666.9 | 214.8 | 27.4 | 19.9 |
| Idaho | | | | | | | |
| Priest River ES | 48°21′ | 116°05′ | 725 | 824.7 | 219.0 | 26.7 | 18.1 |
| Saint Maries | 47°19′ | 116°34′ | 654 | 766.3 | 193.0 | 19.6 | 19.7 |
| Avery RS 2 | 47°15′ | 115°55′ | 728 | 897.6 | 251.9 | 27.7 | 19.5 |
| Elk River 1S | 46°46′ | 116°11′ | 889 | 977.4 | 226.0 | 20.1 | 18.0 |
| Fenn RS | 46°06′ | 115°33′ | 483 | 959.6 | 275.3 | 22.4 | 21.2 |
| Montana | | | | | | | |
| Heron 2 NW | 48°05′ | 116°00′ | 683 | 868.9 | 245 | 23.6 | 17.7 |
| Trout Creek RS | 47°52′ | 115°37′ | 718 | 774.4 | 200 | 24.4 | 17.9 |

*Data not available.