

## Cyanolichens and conifers: implications for global conservation

Trevor Goward<sup>1</sup> and André Arsenault<sup>2</sup>

<sup>1</sup> Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6G 2B1, Canada (Mailing address: Enlivened Consulting Ltd., Edgewood Blue, Box 131, Clearwater, B.C. V0E 1N0, Canada)  
tgoward@wellsgray.net

<sup>2</sup> British Columbia Forest Service, 515 Columbia Street, Kamloops, B.C. V2C 2T7, Canada  
Andre.Arsenault@gems8.gov.bc.ca

### Abstract

Based on a survey of 935 herbarium specimens collected from British Columbia, the substrate ecology and “lifezone” distribution of 48 species of epiphytic cyanolichens are broadly summarized. Conifers belonging to the Pinaceae provide habitat, in coastal regions, for at least 43 cyanolichen species, 12 of which occur exclusively on conifers. Hardwoods support a similar number of cyanolichens, but provide exclusive habitat for only four species. Cyanolichen diversity on conifer branches is shown to increase along a gradient of increasing summer precipitation.

It is suggested that the occurrence of cyanolichens on conifer branches (i.e., the “CC phenomenon”) was formerly well developed in many parts of Europe, but has declined in response to increasing acid precipitation. According to this hypothesis, existing epiphytic lichen assemblages in Europe no longer express their full pre-industrial ecological amplitude. In contrast, conifers in Pacific North America apparently still support “pristine” epiphytic communities; this region should be accorded special emphasis for global cyanolichen conservation. The CC phenomenon may offer a highly sensitive early warning system of broad-scale acidification in eastern North America and other regions where industrial activity is increasing.

Keywords: British Columbia, Canada, lichens, epiphytes, cyanolichens, conifers, oldgrowth, conservation

## 1 Introduction

As a group, lichens tend to be adversely affected by human activity. During the twentieth century, logging, mining, agriculture, suburban sprawl, and long-range air pollution have all exacted a heavy toll on lichen diversity and abundance in many regions of the world (WOLSELEY 1995). This has led to increasing international concern among scientists, who often view lichens as surrogates for less conspicuous taxonomic groups.

Most studies conducted to date suggest that not all lichen species are equally vulnerable to human activity. One group that has been especially singled out as an indicator of environmental degradation are the epiphytic, or tree-dwelling, cyanolichens. Cyanolichens can be described as species in which the photosynthesizing partner is a cyanobacterium. Representative epiphytic cyanolichen genera include *Collema*, *Erioderma*, *Fuscopannaria*, *Leioderma*, *Leptogium*, *Lichinodium*, *Lobaria*, *Nephroma*, *Pannaria*, *Parmeliella*, *Peltigera* (*collina* only), *Polychidium*, *Pseudocyphellaria*, and *Sticta*.

Recent work on substrate selection by cyanolichens reveals a physiological requirement for nutrient-rich substrates. In the case of epiphytic cyanolichens, it is now well established

that these species are most abundant over bark or wood with a pH of between about 5.0 and 6.0 (JAMES *et al.* 1977; GAUSLAA 1985, 1995; but see WIRTH 1995). Surfaces more acidic than this tend not to support cyanolichens.

It is also widely accepted that gymnospermous trees (conifers) are less base-rich than most angiospermous trees ("hardwoods"). From this it would seem to follow that epiphytic cyanolichen diversity ought to be much higher on the latter substrates than on the former. Indeed, this pattern has been well documented in many regions of Europe. Yet the situation is certainly more complex than this, as conifers along the Pacific coast of North America are known to support a wide array of cyanolichens (PIKE *et al.* 1975; GOWARD *et al.* 1994; GOWARD 1999). Clearly it would be useful to gain deeper insight into the nature of this apparent discrepancy.

The objectives of this paper are threefold: first, to conduct a detailed survey of the occurrence of epiphytic cyanolichens in the forests of British Columbia; second, to contrast the resulting patterns, especially with respect to conifers, with corresponding patterns in other regions of the world at similar latitudes; and third, to organize these observations into a summarizing hypothesis regarding circumpolar epiphytic cyanolichen distribution.

## 2 Materials and methods

This study is based exclusively on herbarium material on deposit at the University of British Columbia (UBC). More specifically, we recorded substrate and distributional data for 935 specimens belonging to the Peltigerineae and Lichinaceae (*sensu* TEHLER 1996). Our decision to limit this study to herbarium material proceeds from two assumptions concerning the representativeness of the lichen holdings at UBC. Our first assumption is that these collections accurately portray the relative frequency occurrence of cyanolichens on different tree species. Our second assumption is that they provide an accurate cross-section of cyanolichen distribution on a regional scale. Here it is pertinent to observe that the lichen holdings at UBC now include a rich collection of specimens collected in connection with studies specifically designed to record cyanolichen diversity and phorophyte selection (Goward, various reports and publications). Indeed, more than half of the available material has derived from such studies. For an up-to-date summary of lichen-collecting localities in British Columbia, see Map 1 in GOWARD (1999).

Our study was further limited, insofar as possible, to cyanolichens occurring on twigs and branches. Specimens growing on the trunks or boles of trees often benefit from highly localized chemical and microclimatic conditions mediated by the trunks themselves (BARKMAN 1958). For this reason, their presence in a given stand cannot always reliably be taken as representative of regional macroclimatic conditions. The situation is very different in the case of lichens colonizing twigs and branches. Being smaller and more exposed than trunks, these substrates provide epiphytic habitats much more representative of forest mesoclimate and regional macroclimate.

We have also assembled data on the occurrence of cyanolichens on conifer branches in other parts of the world at temperate and boreal latitudes. Some of this information was gleaned from the literature, but most has been kindly supplied by colleagues specializing in epiphytic lichen ecology.

The resulting data were organized first by lifezone (see below), and second according to the host trees (identified to genus only). For completeness, relevant data have been included for all tree genera occurring under natural conditions in British Columbia. In our analysis,

however, we have incorporated only those tree genera belonging to the Pinaceae, i.e., *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*; the occurrence of cyanolichens on members of the Cupressaceae and Salicaceae will be discussed elsewhere (GOWARD and ARSENAULT, in prep.). Data are also provided for epiphytic cyanolichens restricted locally to the spray zones of waterfalls. Once again these data are included only for completeness; our analyses will be presented in a future paper.

Our taxonomy and nomenclature follow ESSLINGER and EGAN (1995) in most regards. Three species not appearing in that publication are discussed by GOWARD (1999): *Spilonema* sp. 1, Unknown 1, and Unknown 2.

### 3 Study area

The primary study area is British Columbia: a physiographically diverse (DEMARCHI *et al.* 1990), sparsely populated province located in the cordilleran region of western North America. A majority of British Columbia's ecosystems remain more or less intact, providing a superb field laboratory for the study of lichen distributional ecology. This province comprises several roughly longitudinal mountain ranges separated by narrow valleys and broad volcanic plateaux. The mountains are oriented roughly parallel to the Pacific coast, thus tending to interrupt the prevailing onshore flow of moist Pacific air. Their existence gives rise to four sharply demarcated and highly distinctive continentality regions, or "lifezones", i.e., the "hypermaritime", "maritime", "intermontane", and "boreal" (GOWARD 1999). Within each of these lifezones, precipitation is controlled largely by topographic position, being heavier on the windward slopes, and lighter on the leeward slopes. The interplay among these climatic factors creates a repeating complex of humidity sectors expressed across the breadth of the province.

The forests of British Columbia support 18 genera of trees, nine of which belong to the Pinaceae and Cupressaceae. The latter tree families make up roughly 90% of the province's forest cover, as follows: *Pinus* (27%); *Picea* (25%); *Abies* (17%); *Pseudotsuga* and *Larix* (9%); *Tsuga* (7%); and *Chaemycyparis* and *Thuja* (5%) (Anonymous 1995). Nine hardwood genera are also present, and collectively make up the remaining 10% of forest cover. These are *Acer*, *Alnus*, *Arbutus*, *Betula*, *Populus*, *Pyrus*, *Quercus*, *Rhamnus*, and *Salix* (op. cit.).

## 4 Results and discussion

### 4.1 Breakdown of the data

Nine hundred and thirty-five specimens of epiphytic cyanolichens were examined during the course of this study. Six hundred and forty-six of these were collected from conifers, while 289 were derived from hardwoods. Initially this would seem to imply a strong bias in favour of conifers. As noted above, however, hardwoods comprise only about 10% of the forest cover of British Columbia; these genera are thus actually overrepresented in the data set. Here it can be noted that *Tsuga* alone, with 262 specimens, supports nearly as many cyanolichen species ( $n = 33$ ) as do all hardwood genera taken together ( $n = 38$ ).

## 4.2 Phorophyte selection by cyanolichens in British Columbia

Figure 1 provides a summary of phorophyte selection for 48 epiphytic cyanolichen species occurring in British Columbia. Among the conifers, *Picea*, *Tsuga*, and *Abies* support the richest cyanolichen floras, with 34, 33, and 31 species, respectively. *Thuja*, with 22 species, and *Pseudotsuga*, with 15 species, also provide important substrates for this group. *Chamaecyparis*, by contrast, supports only two species, while *Pinus* supports one species, and *Juniperus* and *Larix* support none at all. Among the hardwoods, *Alnus* and *Acer* provide the most favourable substrates, supporting 26 and 23 cyanolichen species, respectively. Other hardwood genera are much less rich, with between 17 and nine species.

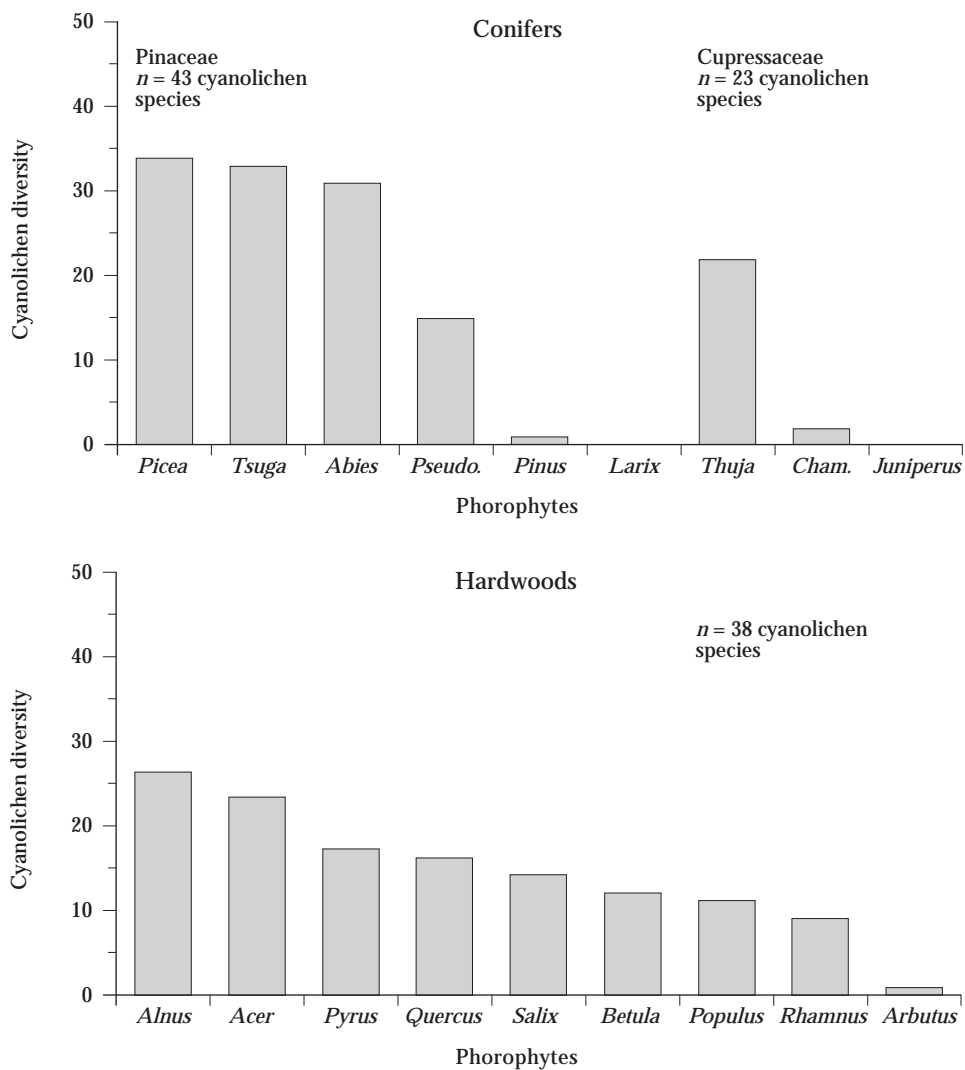


Fig. 1. Phorophyte selection in 48 epiphytic cyanolichens in British Columbia (genus only). Legend: *Pseudo.* = *Pseudotsuga*; *Cham.* = *Chamaecyparis*.

Cyanolichen diversity on conifers, with 43 species, marginally exceeds that on hardwoods, with 38 species (Table 1). Nine cyanolichens actually appear to be restricted to conifers in British Columbia, i.e., *Erioderma solediatum*, *Leioderma solediatum*, *Lichinodium canadense*, *Lobaria silvae-veteris*, *Parmeliella parvula*, *Polychidium contortum*, *Pseudocyphellaria rainierensis*, *Sticta wrightii*, and Unknown 1. Another 14 species occur predominantly on conifers, and are rarely observed on hardwoods. By contrast, only four species (*Collema auriforme*, *Leptogium brebissonii*, *L. pseudofurfuraceum*, and *L. polycarpum*) are restricted to hardwoods, while three additional species clearly favour them, i.e., *Collema furfuraceum*, *C. nigrescens*, and *C. subflaccidum*. These observations strongly suggest that conifers in British Columbia are crucial to the maintenance of cyanolichen diversity.

Table 1. Phorophyte selection by 48 epiphytic cyanolichens in British Columbia. Legend. AB = *Abies*, LA = *Larix*, PC = *Picea*, PN = *Pinus*, PS = *Pseudotsuga*, TS = *Tsuga*, CH = *Chamaecyparis*, JU = *Juniperus*, TH = *Thuja*, AC = *Acer*, AL = *Alnus*, AR = *Arbutus*, BE = *Betula*, PO = *Populus*, PY = *Pyrus*, QU = *Quercus*, RH = *Rhamnus*, SA = *Salix*.

Phorophyte	(n)	Pinaceae							Cupressaceae				Hardwood trees									
		AB	LA	PC	PN	PS	TS	All	CH	JU	TH	All	AC	AL	AR	BE	PO	PY	QU	RH	SA	All
Cyanolichens																						
<i>Collema</i>																						
<i>auriforme</i>	2						0			1	1						1					1
<i>furfuraceum</i>	7	1		1			2					3	1					1				5
<i>nigrescens s. lat.</i>	10			1			1					1					1					9
<i>subflaccidum</i>	10			1			1	2				4	2					1			1	8
<i>Erioderma</i>																						
<i>solediatum</i>	4			2			2	4														0
<i>Fuscopannaria</i>																						
<i>ahlneri</i>	20	1		2			15	18			1	1	1									1
<i>laceratula</i>	10			9			9							1								1
<i>leucostictoides</i>	14	3		1		1	3	8			2	2				1	1					4
<i>mediterranea</i>	7						4	4				2				1						3
<i>saubinetii</i>	5	1					1	2	1		1	2		1								1
<i>Leioderma</i>																						
<i>solediatum</i>	1			1																		0
<i>Leptogium</i>																						
<i>brebissonii</i>	1						0														1	1
<i>burnetiae</i>	14	2		4		1	7					2	2		1	1	1					7
<i>pseudofurfuraceum</i>	3						0					1		2							2	3
<i>polycarpum</i>	1						0					1										1
<i>saturninum</i>	21	1		6		2	9				3					7						12
<i>Lichinodium</i>																						
<i>canadense</i>	5	1					4	5														0
<i>Lobaria</i>																						
<i>hallii</i>	36	5		10		1	2	18			1	1	4	4		1	3	2	2		1	17
<i>oregana</i>	43	10		8		4	11	33			3	3	2	2		1		2				7
<i>pulmonaria</i>	82	8		11	1	6	16	42			5	5	5	5		2	3	3	9	1	7	35
<i>retigera</i>	20	4		1			11	16			3	3					1					1
<i>scrobiculata</i>	43	10		10			12	32				3	1					1	4		2	11
<i>silvae-veteris</i>	12	2					10	12														0
<i>Nephroma</i>																						
<i>bellum</i>	44	10		9		1	13	33				2	4			3	1					11
<i>helveticum</i>	53	12		6		2	21	41			2	2	3	2				2	2		1	10
<i>isidiosum</i>	24	3		7		1	8	19			3	3	1	1								2
<i>laevigatum</i>	24	4		1		2	5	12					3	1				1	5	1	1	12
<i>occultum</i>	27	7		5			14	26								1						1
<i>parile</i>	28	4		7			9	20						3		1	2	1			1	8
<i>resupinatum</i>	27	3		7		1	1	12			2	2	1	5		1	1		3		2	13



Bark chemistry can also be strongly influenced by regional variation in environmental chemistry. For example, it has been postulated that regional variation in bedrock geology can translate to broadscale differences in overall bark pH (GAUSLAA and HOLIEN 1998). It has also been shown that acidic precipitation can affect epiphytic lichen community structure over distances measuring thousands of kilometres (WOLSELEY 1995). Such influences doubtless exert a profound influence on regional cyanolichen community structure. We return to these observations in Section 4.5.

#### 4.4 Regional Patterns of Cyanolichen Diversity in British Columbia

Overviews of epiphytic cyanolichen distribution in various “lifezones” are provided in Table 2 and Figure 2. The available data suggest that cyanolichen diversity, at least on members of the Pinaceae, increases with increasing summer precipitation. Epiphytic cyanolichens are absent altogether from semi-arid and dry inland regions (not shown). Even in dry maritime localities, only five species are known to occur. In comparison, 11 species have been collected in moist intermontane regions, and 25 species in wet and very wet intermontane regions. Cyanolichen richness peaks at 35 species in maritime portions of the province described as moist and wet, and then declines to 28 species in very wet hypermaritime regions. We emphasize that these patterns accord well with our field experience over many years; they are unlikely to be mere artifacts of differential sampling intensity.

Table 2. Epiphytic cyanolichen distribution in six “lifezones” in British Columbia (see text). Occurrences denoted by an exclamation mark are predominantly oldgrowth-associated in the lifezones indicated. Occurrences in parentheses are restricted to the spray zones of waterfalls. Based on NOBLE (1982), GOWARD and AHTI (1992), GOWARD *et al.* (1994), JØRGENSEN and GOWARD (1994), THOMSON and AHTI (1994), GOWARD (1995, 1996), GEISER *et al.* (1998), GOWARD and POJAR (1998), GOWARD (1999), and collections at UBC. Legend. <sup>1</sup>See Figure 1. <sup>2</sup>See MEIDINGER and POJAR (1991). <sup>3</sup>Hypermaritime. <sup>4</sup>Maritime. <sup>5</sup>Intermontane. <sup>6</sup>Occurring on conifer branches (Pinaceae only). <sup>7</sup>Occurring on hardwood trees. <sup>8</sup>*Sensu* GOWARD (1999).

Lifezone <sup>1</sup> Subzone(s) <sup>2</sup> Cyanolichens	Hypermaritime <sup>3</sup> Very wet		Maritime <sup>4</sup> Dry		Maritime Moist, Wet		Intermontane <sup>5</sup> Moist		Intermontane Wet, Very wet		Boreal Moist, Wet	
	conif	hardw <sup>7</sup>	conif	hardw	conif	hardw	conif	hardw	conifi	hardw	conifi	hardw
<i>Collema</i>												
<i>auriforme</i>	+								+			
<i>furfuraceum</i>				+	+	+	+	+	+			+
<i>nigrescens</i>				+		+		+		+		+
<i>subflaccidum</i>	+					+		(+)	(+)	(+)		+
<i>Erioderma</i>												
<i>sorediatum</i>	+											
<i>Fuscopannaria</i>												
<i>ahlneri</i>	+				+	+				+		
<i>laceratula</i>	+	+										
<i>leucostictoides</i>	+	+		+	+					+		
<i>mediterranea</i>				+	+			(+)	(+)	(+)		
<i>saubinetii</i>	+	+			+							
<i>Leioderma</i>												
<i>sorediatum</i>	+											
<i>Leptogium</i>												
<i>brebissonii</i>		+										
<i>burnetiae</i>	+			+	+	+		(+)	+	+	+	
<i>pseudofurfuraceum</i>				+								
<i>polycarpum</i>				+	+							
<i>saturninum</i>				+	+	+		+	+	+	+	+
<i>Lichinodium</i>												
<i>canadense</i>					+					+		

Table 2 continued.

Lifezone <sup>1</sup> Subzone(s) <sup>2</sup>	Hypermaritime <sup>3</sup> Very wet		Maritime <sup>4</sup> Dry		Maritime Moist, Wet		Intermontane <sup>5</sup> Moist		Intermontane Wet, Very wet		Boreal Moist, Wet	
	conif	hardw <sup>7</sup>	conif	hardw	conif	hardw	conif	hardw	conifi	hardw	conifi	hardw
Cyanolichens												
<i>Lobaria</i>												
<i>hallii</i>				+	+	+			+	+		
<i>oregana</i>	+		+!		+!	+			(+)			
<i>pulmonaria</i>	+	+		+	+	+	+		+	+		
<i>retigera</i>					+!	+			+	+!		
<i>scrobiculata</i>	+			+	+	+			+	+		
<i>silvae-veteris</i>					+	+						
<i>Nephroma</i>												
<i>bellum</i>	+	+			+	+	+	+	+	+		+
<i>helveticum</i>	+	+		+	+	+	+		+			
<i>isidiosum</i>					+!	+	(+)		+!	+		
<i>laevigatum</i>	+	+		+								
<i>occultum</i>					+!	+			+!			
<i>parile</i>					+	+	+	+	+	+		
<i>resupinatum</i>	+			+	+	+	+	+	+	+		+
<i>Pannaria</i>												
<i>rubiginosa</i>	+!											
<i>Parmeliella</i>												
<i>parvula</i>					+				(+)			
<i>triptophylla</i>					+	+	+	+	+	+		+
<i>Peltigera</i>												
<i>collina</i>	+	+		+	+	+	(+)		+	+		
<i>Polychidium</i>												
<i>contortum</i>	+!				+!							
<i>dendriscum</i>					+!		(+)		+!	+!		
<i>Pseudocyphellaria</i>												
<i>anomala</i>	+	+	+	+	+	+	+		+			
<i>anthraspsis</i>	+	+	+			+						
<i>crocata</i>	+	+	+	+	+				(+)			
<i>rainierensis</i>	+!	+			+							
<i>Spilonema</i>												
sp. 1 <sup>8</sup>	+!				(+)							
<i>Sticta</i>												
<i>beauvoisii</i>	+!		+		+!	+						
<i>fuliginosa</i>	+	+		+	+	+	+		+	+		
<i>limbata</i>	+	+		+	+!	+	(+)	(+)	+!	+!		
<i>oroborealis</i>					+!	+			+!			
<i>weigeli</i>					+!	+						
<i>wrightii</i>					+!	+			+!			
Unknown 1 <sup>8</sup>					+!				(+)			
Unknown 2 <sup>8</sup>	+!											
Total species	28	15	5	19	35(1)	27	12(6)	9(4)	25(6)	15	3	5

Diversity on hardwoods follows a similar pattern, with the exception that cyanolichens are more diverse in dry maritime regions than in any other lifezone except the moist and wet maritime. The occurrence in the dry maritime of numerous cyanolichens constitutes an obvious distributional anomaly: based on the patterns reported for conifers, the dry maritime ought to support fewer, not more, cyanolichen species. One plausible explanation would involve the architecture of hardwoods. In brief, hardwoods have a centripetal structure which causes rainwater to be directed inwards toward the bole (BARKMAN 1958). Here environmental conditions are humid: first owing to poor ventilation (GEIGER 1965), and second because thick bark in this portion of a tree can retain moisture for prolonged periods. Both of these phenomena probably favour the establishment and growth of hygrophytic cyanolichens – even under macroclimatic conditions that would otherwise not support them.



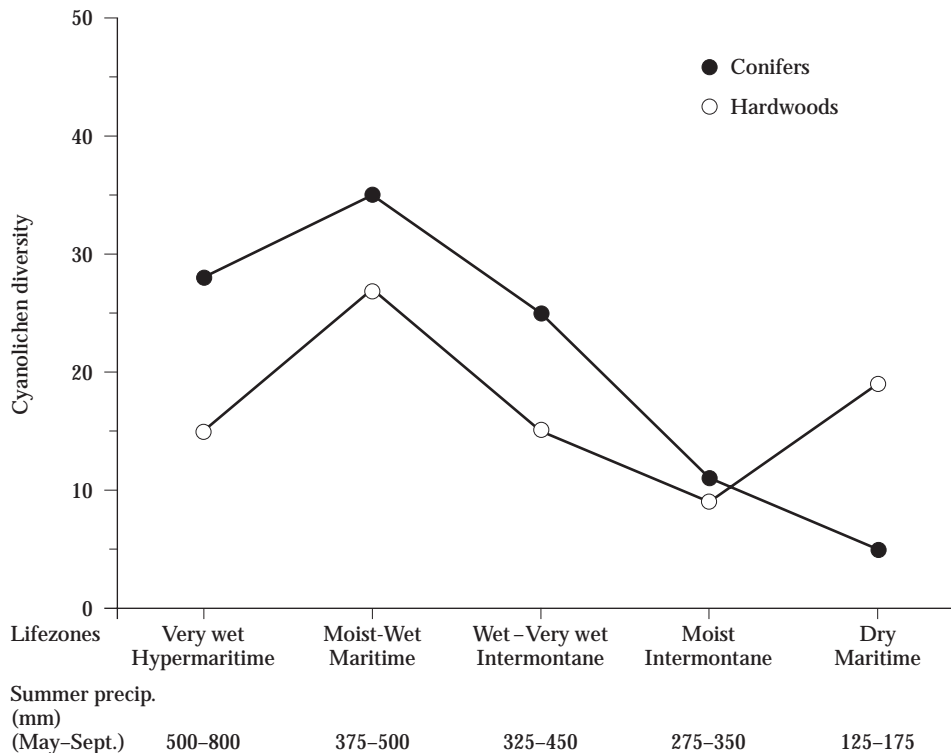


Fig. 2. Epiphytic cyanolichen diversity: conifers versus hardwoods (see text).

If epiphytic cyanolichen diversity is truly correlated with summer moisture, as would appear, then these species should occur in maximum numbers in regions designated here as very wet hypermaritime. Yet the available data suggest that hypermaritime regions support fewer cyanolichens than moist and wet maritime regions (see Fig. 2). Possibly forested ecosystems in the hypermaritime are too continuously humid to permit wetting and drying at intervals sufficient for the maintenance of epiphytic cyanolichens. Also, salt spray along the Pacific coast appears to favour the development of epiphytic mosses (HONG and GLIME 1997), which in turn tend to exclude cyanolichens from otherwise suitable habitats. It may be pertinent to observe that early growth in many cyanolichen species is comparatively very slow (SCHEIDEGGER 1995). Given that many cyanolichen species are well developed (in exposed sites) near the open ocean, it seems unlikely that salt spray *per se* is a significant limiting factor.

In Figure 3, the ratio of cyanolichen diversity on conifers as compared with that on hardwoods is summarized for five lifezones. The relative importance of conifer branches as substrates for cyanolichens is seen to increase several-fold along a gradient of increasing summer precipitation. More specifically, cyanolichen diversity in the hypermaritime is nearly two times greater on conifers than on hardwoods. In contrast, conifers in the dry maritime support only roughly one-quarter of the cyanolichen species supported by hardwoods. These patterns accord well with the observation that hardwoods are much scarcer in humid regions of British Columbia than in drier regions (KRAJINA *et al.* 1982). They also agree with well-documented successional patterns in Pacific North America, where conifers tend to dominate

forest canopies with increasing stand age (WARING and FRANKLIN 1979; MACKINNON and VOLD 1998); oldgrowth forests, in other words, are much more widespread in humid regions than in drier regions prone to wildfire. Finally, the disproportionate occurrence of hardwoods in dry maritime regions almost certainly translates to an enhanced availability of substrates well buffered against summer drought (see above). Such substrates are well suited to colonization by cyanolichens.

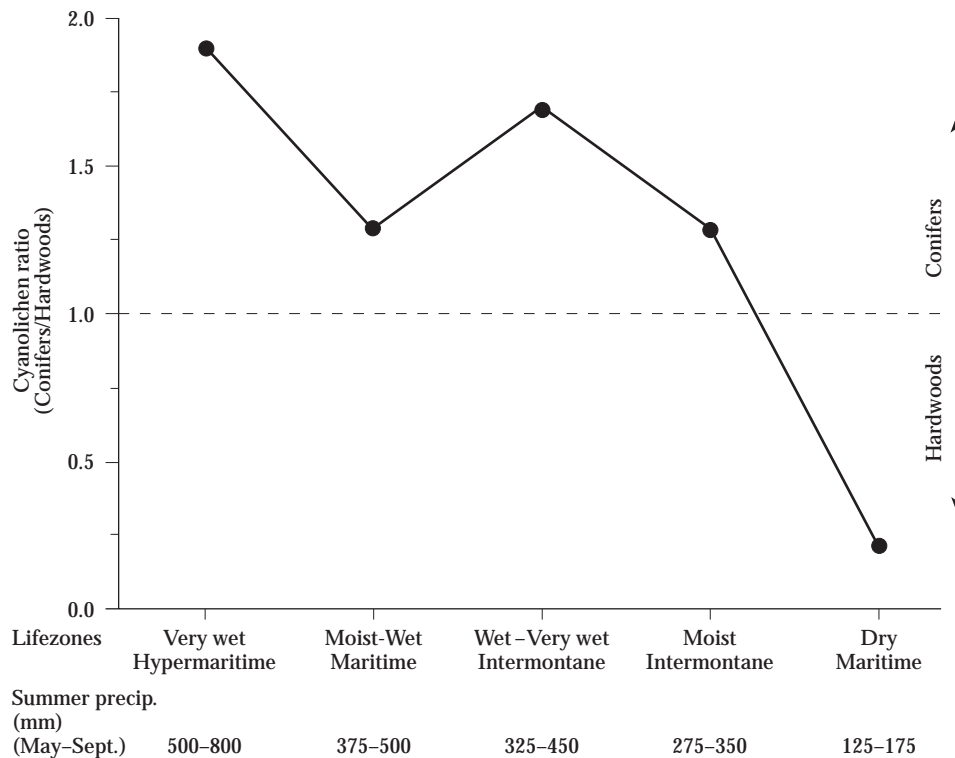


Fig. 3. The relative apportioning of epiphytic cyanolichens across five "lifezones" in British Columbia: conifers versus hardwoods (see text).

#### 4.5 Circumtemperate patterns of cyanolichen occurrence on conifers

Figure 4 summarizes the reported and "potential" (i.e. pre-industrial) distribution of cyanolichens on members of the Pinaceae at temperate and boreal latitudes. For convenience, the occurrence of cyanolichens on conifer branches will henceforth be referred to as the "CC phenomenon". The patterns displayed in Figure 4 permit five observations regarding the CC phenomenon: 1) it can be largely captured within the distribution areas of four conifer genera, i.e., *Abies*, *Picea*, *Pseudotsuga*, and *Tsuga*; 2) it is confined to cool regions, with summer mean temperatures (May through September) below about 15 °C; 3) it is limited to humid regions, where measurable precipitation (including fog-induced "occult precipitation") occurs on at least sixty days each summer; 4) it is not excluded by high continentality *per se* (*sensu* TUHKANEN 1984); and 5) it extends northward only as far as the middle subzone of the boreal bioclimatic zone (*sensu* TUHKANEN 1984).

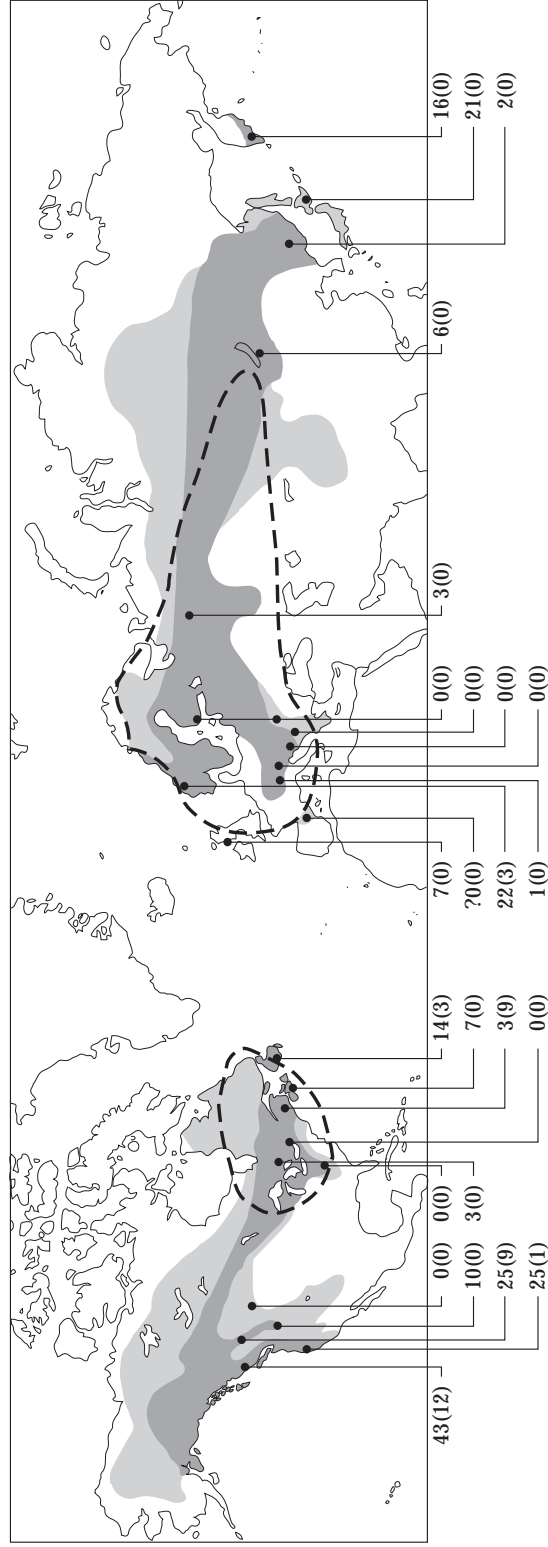


Fig. 4. Reported and "potential" occurrence of cyanolichens on conifer branches at middle latitudes in the northern hemisphere. Greyed area: distribution area of Pinaceae, excluding Larix and Pinus (from FLORIN 1963; JALAS and SUOMINEN 1973; BROCKMAN 1979; HULTEN and FRIES 1986). Blackened area: potential distribution area of cyanolichens on conifer branches (see text). Dotted lines: distribution area of "acid rain effect" on lichens (from WOLSELEY 1995). Paired numbers indicate cyanolichen occurrence on conifers in selected regions (and

cyanolichen species restricted to conifers). Regional sources: T. Ahti (Finland), I.M. Brodo (central Canada), S.R. Clayden (eastern Canada), B. Coppins (Britain), J. Etayo (Spain), B. Goffinet (Alberta), H. Holien (Norway), G. Inarov (Russia), H. Kashiwadani (Japan), S. Kondratyuk (Ukraine), B. McCune (Montana), W. Maass (eastern Canada), S. Ozimec (Croatia), J. Prügger (Slovenia), C. Scheidegger (Switzerland), S. Sillett (Pacific United States), T. Tønsberg (general), R. Türk (Austria), G. Urbanavichyus (Russia), M. Zhurbenko (Russia).

As thus circumscribed, the CC phenomenon is likely to be well developed in only four regions of the northern hemisphere, i.e., northwestern North America (especially north of California), northeastern North America (north of New Hampshire), western Europe (excluding Mediterranean regions), and eastern Asia (northeast China and southeast Russia). For practical purposes, its distribution area might be predicted to correspond roughly with the core ranges of several widely distributed hygrophytic lichens, including *Cladonia umbricola*, *Parmotrema arnoldii*, *Peltigera britannica*, *P. horizontalis*, and *Usnea longissima*.

Figure 4 further suggests that the CC phenomenon declines sharply with increasing distance from the continental coastlines. This trend is well expressed on the eastern margins of the continents. On the western margins, however, this situation is more complex. For example, the inland "rainforests" of south-central British Columbia, situated 400–500 km from the Pacific coast, support at least 25 epiphytic cyanolichens. Admittedly conditions are thermally rather oceanic in this region (GOWARD 1994), although winter temperatures as low as  $-40^{\circ}\text{C}$  have been recorded. Farther south, in slightly drier, but otherwise corresponding portions of Idaho and Montana, the CC phenomenon is limited to only ten species. In Europe, the Pyrenees of northern Spain, with 11 species, constitute another inland "hot spot" for the CC phenomenon (Fig. 4).

Even in thermally highly continental regions, instances of the CC phenomenon are to be found (Fig. 4). For example, the northern Ural Mountains support three such species, whereas six species are present in the vicinity of Lake Baikal. Included here are *Collema*, *Leptogium*, *Lobaria*, and *Nephroma*. Presumably the ability of such lichens to establish in some of the world's most continental climates is linked to a prevalence of cool, humid weather during the summer months. From this it follows that not all epiphytic cyanolichens should be classified as "oceanic", at least in the thermal sense (ROSE 1988).

The relative importance of conifers to cyanolichens appears to vary significantly in different regions of the world (Figure 4). In coastal British Columbia, for example, at least 12 epiphytic cyanolichens occur exclusively on this substrate, i.e., *Collema auriforme*, *Erioderma solediatum*, *Leioderma solediatum*, *Lichinodium canadense*, *Lobaria oregana*, *Lobaria silvae-veteris*, *Pannaria rubiginosa*, *Parmeliella parvula*, *Polychidium contortum*, *P. dendriscum*, Unknown 1 and Unknown 2. Farther east, the inland rainforests of southern British Columbia support nine such species. In contrast, conifers in coastal Oregon and California are known to provide exclusive habitat for only one species. Elsewhere again, in southeastern Newfoundland, only three cyanolichens depend entirely on conifers, while no species at all belong in this category in most parts of Eurasia, with the exception of west-central Norway, where three cyanolichens are restricted to *Picea abies*.

A unique feature of the late twentieth century has been broadscale environmental deterioration resulting from acid precipitation (RICHARDSON 1991). Ecosystem acidification is especially detrimental to epiphytic lichens. WOLSELEY (1995) has provided a global map summarizing lichen decline in response to acid precipitation. When her map is compared against our Figure 4, a clear correspondence between acid rain and low epiphytic cyanolichen diversity on conifers emerges. This correspondence is especially apparent in western Europe, where the CC phenomenon is almost entirely absent, even in areas supporting extensive conifer forests. Only in west-central Norway – one of the least polluted parts of Europe (GAUSLAA and HOLIEN 1998) – do conifers support a wide array of cyanolichens. These correlations, in our opinion, are unlikely to be coincidental.

That the ecological amplitude of epiphytic cyanolichens in Europe has contracted during the past century is well documented (ROSE 1988; FARMER *et al.* 1991; GAUSLAA and HOLIEN 1998). Species formerly abundant on a wide variety of hardwood trees now occupy only a few phorophyte species exceptionally well buffered against acidification. It is hardly surprising that conifers, which are poorly buffered even under pristine atmospheric conditions, support

almost no cyanolichens at all. Yet this may not always have been the case. Indeed, the CC phenomenon might once have been well developed in some parts of Europe, just as it continues to be in some parts of western North America, where conifers actually support a higher cyanolichen diversity than hardwoods. Of course it could be argued that no (or very few) records are available in support of this hypothesis. In our opinion, however, that is to be expected: first, because cyanolichens probably disappeared from conifers long before they began to decline on hardwood trees; and second, because no thorough examination of old herbarium specimens appears to have been undertaken. We suggest, then, that the present-day absence of the CC phenomenon in much of Europe might well represent an ecological anomaly: an artifact of industrialization.

There is growing evidence that the putative decline of the CC phenomenon in Europe is now being repeated in northeastern North America. In maritime regions of eastern Canada, for example, Wolfgang Maass (pers. comm.) has accumulated data to show that cyanolichens have disappeared from forests in which they were abundant only a few decades ago. Though a causal relationship with acid rain remains to be demonstrated, it is doubtless significant that this region is situated within the "pollution zone" indicated in WOLSELEY (1995).

In this paper, we have attempted to show that epiphytic cyanolichens can occur regularly on the bark of conifers growing in humid regions not subject to acid rain. We suggest that regions in which the CC phenomenon is well developed might be characterized as environmentally "pristine", at least in the sense that epiphytic cyanolichens still occupy their original, pre-industrial ecological amplitude. In contrast, epiphytic cyanolichen assemblages in regions affected by acid precipitation are more appropriately viewed as "relictual", that is, they are confined to a considerably reduced assemblage of phorophytes.

Notwithstanding current ameliorating trends (SEAWARD 1997), ecosystem acidification will probably continue to exert a profound influence on cyanolichen distribution over large areas of the world. Owing, however, to its proximity to the Pacific Ocean, northwest North America is well positioned to remain a stronghold of cyanolichen diversity expressed at pre-industrial levels. We predict that this region, centering on British Columbia, will be pivotal to future efforts by the international community to maintain "primeval" lichen communities at north temperate and low boreal latitudes. At the same time, we suggest that the CC phenomenon, or rather its decline, holds promise as a sensitive early-warning-system of broadscale acidification. In bringing these observations and conjectures to the attention of our colleagues, we wish only to point to a highly complex field of lichen phytogeography that in our opinion deserves more detailed study.

#### **Acknowledgements**

We are grateful to Carla Rydholm and Olivia Lee for providing distributional data on cyanolichens on deposit at UBC. We are also grateful to the following colleagues for supplying information on the CC phenomenon in different parts of the world: Teuvo Ahti, Irwin Brodo, Stephen Clayden, Brian Coppins, Javier Etayo, Bernard Goffinet, Håkon Holien, Gregory Insarov, Hiroyuki Kashiwadani, Sergey Kondratyuk, Bruce McCune, Wolfgang Maass, Sinisa Ozimec, Johannes Prügger, Christoph Scheidegger, Steve Sillett, Tor Tønsberg, Roman Türk, Gena Urbanavichyus, and Mikhail Zhurbenko. Adolf Ceska, Stephen Clayden, Andy MacKinnon, Wilf Schofield, and Dave Spittlehouse kindly provided important literature. Håkon Holien, Wolfgang Maass, Palmer Palmer, Carla Rydholm, and Kenneth G. Wright are especially thanked for stimulating discussion. We are also thankful to Russ Walton and Sherri Brimacombe for assistance with some of the figures. The manuscript was reviewed by Håkon Holien, Carla Rydholm, Christoph Scheidegger, Kenneth G. Wright, and one anonymous reviewer. Funding was provided by Forest Renewal British Columbia (FRBC) through the British Columbia Ministry of Forests.

## 5 References

- Anonymous, 1995: Forest, range and recreation resource analysis, 1994. Victoria, British Columbia Ministry of Forests, Research Branch. 308 pp.
- BARKMAN, J.J., 1958: Phytosociology and ecology of cryptogamic epiphytes. Assen, van Gorcum. 628 pp.
- BROCKMAN, C.F. 1979: Trees of North America: a field guide to the major native and introduced species north of Mexico. New York, Golden Press. 280 pp.
- BRODO, I.M., 1974 ("1973"): Lichen ecology. In: AHMADJIAN, V.; HALE, M.E. (eds) The lichens. New York, Academic Press Inc. 401–441.
- CARLISLE, A.; BROWN, A.H.F.; WHITE, E.J., 1967: The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland. J. Ecol. 55: 614–627.
- COXSON, D.S.; NADKARNI, N.M., 1995: Ecological roles of epiphytes in nutrient cycles of forest ecosystems. In: LOWMAN, M.D.; NADKARNI, N. (eds) Forest Canopies. New York, Academic Press. 495–543.
- DEMARCHI, D.A.; MARSH, R.D.; HARCUMBE, A.P.; LEA, E.C., 1990: The environment. In: CAMPBELL, R.W.; DAWE, N.K.; MCTAGGART C.I.; COOPER, J.M.; KAISER, G.W.; MCNALL, M.C.E. (eds) The birds of British Columbia. Volume 1. Victoria, Royal British Columbia Museum. 55–144.
- ESSLINGER, T.L.; EGAN, R.S., 1995: A sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada. The Bryologist 98: 467–549.
- FARMER, A.M.; BATES, J.W.; BELL, J.N.B., 1991: Ecophysiological effects of acid rain on bryophytes and lichens. In: BATES, J.W.; FARMER, A.M. (eds) Bryophytes and lichens in a changing environment. New York, Oxford University Press. 284–313.
- FLORIN, R., 1963: The distribution of conifer taxad genera in time and space. Acta Horti Bergiani 20: 121–312.
- GAUSLAA, Y., 1985: The ecology of *Lobarion pulmonariae* and *Parmelion caperatae* in *Quercus* dominated forests in south-west Norway. Lichenologist 17: 117–140.
- GAUSLAA, Y., 1995: The *Lobarion*, an epiphytic community of ancient forests threatened by acid rain. Lichenologist 27: 59–76.
- GAUSLAA, Y.; HOLIEN, H., 1998: Acidity of boreal *Picea abies*-canopy lichens and their substratum, modified by local soils and airborne acidic depositions. Flora 193: 249–257.
- GEIGER, R., 1965: The climate near the ground. Cambridge, Massachusetts, Harvard University Press. 611 pp.
- GEISER, H.; DILLMAN, K.L.; DERR, C.C.; STENSVOLD, M.C., 1998: Lichens of southeast Alaska. In: GLENN, M.G.; HARRIS, R.C.; DIRIG, R.; COLE, M.S. (eds.) Lichenographia Thomsoniana: North American lichenology in honor of John W. Thomson. Ithaca, New York, Mycotaxon, Ltd. 201–243.
- GILBERT, O.L., 1970: Further studies on the effect of sulphur dioxide on lichens and bryophytes. New Phytol. 69: 605–627.
- GILBERT, O.L., 1986: Field evidence for an acid rain effect on lichens. Environ. Pollut. (series A) 40: 227–231.
- GOUGH, L.P., 1975: Cryptogam distributions on *Pseudotsuga menziesii* and *Abies lasiocarpa* in the Front Range, Boulder County, Colorado. The Bryologist 78: 124–145.
- GOWARD, T., 1994: Notes on oldgrowth-dependent epiphytic macrolichens in the humid oldgrowth forests in inland British Columbia, Canada. Acta Bot. Fenn. 150: 31.
- GOWARD, T., 1995: *Nephroma occultum* and the maintenance of lichen diversity in British Columbia. Mitt. Eidgenöss. Forsch.anst. WSL 70: 93–101.
- GOWARD, T., 1996: Lichens of British Columbia: rare species and priorities for inventory. Victoria, Research Branch, British Columbia Ministry of Forests, and Habitat Protection Branch, British Columbia Ministry of Environment, Lands and Parks, British Columbia. Working Paper 08. 34 pp.



- GOWARD, T., 1999: The lichens of British Columbia: illustrated keys. Part 2 – Fruticose species. British Columbia Ministry of Forests Special Report Series 9: 1–319.
- GOWARD, T.; AHTI, T., 1992: Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. *Acta Bot. Fenn.* 147: 1–60.
- GOWARD, T.; ARSENAULT, A., 2000: Cyanolichen distribution in young unmanaged forests: a dripzone effect? *The Bryologist* 103: 28–37.
- GOWARD, T.; MCCUNE, B.; MEIDINGER, D., 1994: The lichens of British Columbia: illustrated keys. Part 1 – Foliose and squamulose species. British Columbia Ministry of Forests Special Report Series 8: 1–181.
- GOWARD, T.; POJAR, J., 1998: Antique forests and epiphytic macrolichens in the Kispiox Valley. Forest Sciences Extension Note 33. Smithers, British Columbia Ministry of Forests, Prince Rupert Forest Region. 11 pp.
- HONG, W.S.; GLIME, J.M., 1997: Comparison of phrophyte communities on three major tree species on Ramsay Island, Queen Charlotte Islands, Canada: bryophyte vs lichen dominance. *Lindbergia* 22: 21–30.
- HULTÉN, E.; FRIES, M., 1986: Atlas of North European vascular plants north of the Tropic of Cancer. Volume 1. Königstein, Germany, Koeltz Scientific Books.
- JALAS, J.; SUOMINEN, J., 1973: Atlas Florae Europaea: distribution of vascular plants in Europe. Volume 2. Helsinki, Finland, The Committee for Mapping the Flora of Europe, and Societas Biologica Fennica Vanamo.
- JAMES, P.W.; HAWKSWORTH, D.L.; ROSE, F., 1977: Lichen communities in the British Isles: a preliminary conspectus. In: SEAWARD, M.R.D. (ed) *Lichen ecology*. London, Academic Press. 295–413.
- JØRGENSEN, P.-M.; GOWARD, T., 1994: Two new *Leptogium* species from western North America. *Acta Bot. Fenn.* 150: 75–78.
- KRAJINA, V.J.; KLINKA, K.; WORRALL, J., 1982: Distribution and ecological characteristics of trees and shrubs of British Columbia. Vancouver, Faculty of Forestry, University of British Columbia. 131 pp.
- KUUSINEN, M., 1996: Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist* 28: 443–463.
- MACKINNON, A.; VOLD, T., 1998: Old-growth forests inventory for British Columbia, Canada. *Natural Areas Journal* 18: 309–318.
- MEIDINGER, D.; POJAR, J., 1991: Ecosystems of British Columbia. British Columbia Ministry of Forests Special Report Series 6. Victoria, Research Branch, Ministry of Forests. 330 pp.
- NOBLE, W.J.; 1982: The lichens of the coastal Douglas-fir Dry Subzone of British Columbia. Ph.D. Thesis. Vancouver, British Columbia, University of British Columbia. 942 pp.
- PIKE, L.H.; DENISON, W.C.; TRACY, D.M.; SHERWOOD, M.A.; RHOADES, F.M., 1975: Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *The Bryologist* 78: 389–402.
- RICHARDSON, D.H.S., 1991: Lichens as biological indicators – recent developments. In: JEFFREY, D.W.; MADDEN, B. (eds) *Bioindicators and environmental management*. Toronto, Academic Press. 263–272.
- ROSE, F., 1988: Phytogeographical and ecological aspects of *Lobarion* communities in Europe. *Bot. J. Linn. Soc.* 96: 69–79.
- SCHEIDEGGER, C., 1995: Early development of transplanted isidioid soredia of *Lobaria pulmonaria* in an endangered population. *Lichenologist* 27: 361–274.
- SEAWARD, M.R.D., 1997: Urban deserts bloom: a lichen renaissance. *Bibliographica Lichenologica* 67: 297–309.
- SIGAL, L.L.; JOHNSTON, J.W., 1986: Effects of acid rain and ozone on nitrogen fixation and photosynthesis in the lichen *Lobaria pulmonaria* (L.) Hoffm. *Environ. Exp. Bot.* 26: 59–64.
- TEHLER, A., 1996: Systematics, phylogeny and classification. In: NASH, T.H. (ed) *Lichen biology*. Cambridge, Cambridge University Press. 217–239.
- THOMSON, J.W.; AHTI, T., 1994: Lichens collected on an Alaska Highway Expedition in Alaska and Canada. *The Bryologist* 96: 138–157.

- TUHKANEN, S., 1984: A circumboreal system of climatic-phytogeographical regions. *Acta Bot. Fenn.* 127: 1–50.
- WARING, R.H.; FRANKLIN, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204: 1380–1386.
- WIRTH, V., 1995: *Die Flechten Baden-Württembergs*. Stuttgart, Germany, Eugen Ulmer. 1006 pp.
- WOLSELEY, P., 1995: A global perspective on the status of lichens and their conservation. *Mitt. Eidgenöss. Forsch.anst. WSL* 70: 11–27.