Inland Old-Growth Rain Forests: Safe Havens for Rare Lichens?

Trevor Goward[1]
Herbarium, Department of Botany, University of British Columbia, Vancouver, BC, V6G 2B1, Canada

André Arsenault
British Columbia Ministry of Forests, Kamloops Forest Region
515 Columbia Street, Kamloops, BC, V2C 2T7, Canada

ABSTRACT

Lichens in which a cyanobacterial partner occurs can be referred to as "cyanolichens." Such species are potentially important contributors to the nitrogen budgets of some conifer forest ecosystems. In the intermontane forests of British Columbia, 31 epiphytic (tree-dwelling) cyanolichens are known to colonize conifers, including 12 species that can be considered rare or infrequent in the province as a whole. In this paper we present a simple key for predicting stand-level epiphytic cyanolichen diversity on conifers. The key is based on several readily mappable environmental factors and is useful at an operational scale. Maximum cyanolichen diversity is shown to occur in lowland old-growth rain forests established over nutrient-rich soils and subject to a rainfall pH above about 5.0. Such stands are generally restricted to the base of hill slopes in the wettest subzones of the Interior Cedar–Hemlock zone, where they not only support one of British Columbia's richest assemblages of rare cyanolichens, but also themselves represent one of the province's rarest and most endangered forest ecosystems. Further work is urgently needed.

Key words: biodiversity, cyanolichens, epiphytes, inland rain forests, lichens.

Lichens can be described, with only slight exaggeration, as the 20% of fungi that have "discovered agriculture." Whereas most fungi satisfy their carbohydrate requirements largely through the absorption of nutrients from the same organic matter within which they pass their lives (decaying wood, humus, etc.), lichenized fungi cultivate their foodstuff internally; that is, among the tightly woven weft of fungal threads which comprise them. In effect, lichens are "living fungal greenhouses" in which tiny photosynthesizing cells, collectively referred to as photobionts, are simultaneously cultivated and assimilated. To date, approximately 100 algal and cyanobacterial species in 40 genera are known to act as lichen photobionts. In 90% of lichens, the photobiont is an alga. In other species, however, the lichen fungi associate exclusively or in part with cyanobacteria; for convenience, such species can be referred to as "cyanolichens."

Cyanolichens are nitrogen-fixers; they both absorb nitrogen from the atmosphere and, ultimately, release it into their immediate environment. This ability has stimulated considerable research on the potential of cyanolichens to contribute significantly to the nitrogen budgets of some ecosystems. Though conclusive experimental evidence is lacking (Nash 1996), there is growing consensus that at least epiphytic (tree-dwelling) cyanolichens probably do make a significant contribution under some circumstances. Indeed, such species are now generally assumed to be keystone organisms in some conifer forests in which nitrogen is limiting (Rhoades 1995).

Several lichen species considered to be rare or infrequent in British Columbia take the form of epiphytic cyanolichens. If only for this reason, it would be useful to develop a methodology for predicting their general levels of occurrence in different forest ecosystems. If founded on readily mappable environmental factors, such a methodology could provide a useful tool for resource managers charged with maintaining forest biodiversity at historic levels. In this paper, we attempt to contribute to a basic understanding of cyanolichen distributional ecology in intermontane British Columbia. Our specific objectives are: 1) to summarize the most important environmental factors promoting cyanolichen diversity in inland forests; and 2) to propose a simple method by which cyanolichen diversity can be reliably predicted at an operational scale, based on readily available information.

STUDY AREA

The study area encompasses all of intermontane British Columbia, comprising roughly 75% of the surface area of the province (Fig. 1). This is a highly heterogeneous region, in

1 Present address: Enlichened Consulting, Edgewood Blue
P.O. Box 131, Clearwater, BC V0E 1N0
tgoward@mail.wellsgray.net

which 3 broad "ecodivisions" (Demarchi et al. 1990) can be recognized, as well as 12 climatic regions (Marsh 1988) and 11 of British Columbia's 14 biogeoclimatic zones (Meidinger and Pojar 1991). Included here are some of the wettest, driest, warmest, and coldest portions of southern inland Canada (Phillips 1990). We have restricted our study to regions having an "intermediate" continentality (Tuhkanen 1984); that is, areas with continentality ratings (Conrad 1946) between about 30 and 45. The Nass and Skeena valleys (continentality <30) are therefore not considered; nor are regions lying north and east of the Rocky Mountains (continentality >45).

METHODS

The distributional patterns reported here are based largely on field studies conducted by the senior author over 20 years and summarized, in part, in Goward (1994, 1995, 1996, 1999), Goward and Ahti (1992, 1997), Goward and Arsenault (1997), Goward et al. (1994), as well as in several unpublished studies undertaken in the Kamloops, Nelson, Prince George, Prince Rupert, and Vancouver forest regions. In addition, more than 40,000 herbarium specimens housed at the Canadian Museum of Nature in Ottawa, the University of British Columbia in Vancouver, and the University of Victoria in Victoria have been examined and mapped. More recently, the authors have assembled quantitative data on 40 stands supporting epiphytic cyanolichens. For a summary of our field methods, see Goward and Arsenault (1997). The taxonomy and nomenclature adopted in this paper follow Esslinger and Egan (1995).

RESULTS AND DISCUSSION

Epiphytic cyanolichens are by no means randomly, or evenly, distributed in intermontane British Columbia. Rather, their occurrence appears to be closely associated with a finite number of environmental factors. Based on our field

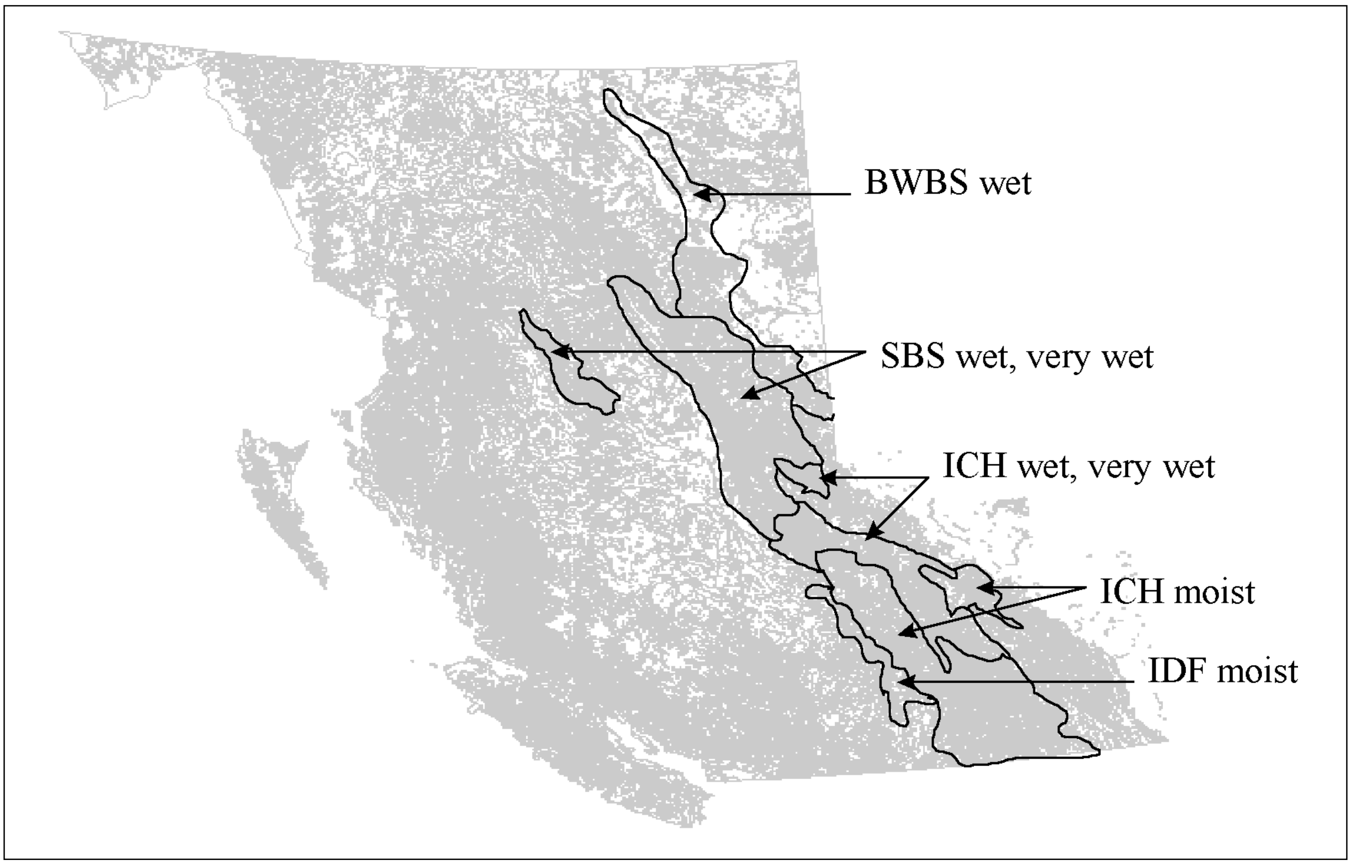

Figure 1. Occurrence of epiphytic cyanolichens on conifer branches in intermontane British Columbia. BWBS = Boreal White and Black Spruce zone (wet subzone only); IDF = Interior Douglas-fir zone (moist and wet subzones only); SBS = Sub-boreal Spruce zone (wet and very wet subzones only); ICH "inland" = Interior Cedar–Hemlock zone (moist subzones, and wet and very wet subzones only); and ICH "coast" (occurs outside study area: included for comparative purposes only).

work in the study area, as well as on research conducted in other parts of the world, at least 7 such factors can be recognized. Four of these can be considered "primary" because they appear to be prerequisite to the colonization of conifers by cyanolichens. They are: 1) air quality; 2) elevation; 3) biogeoclimatic zonation; and 4) nutrient enrichment.

Primary Cyanolichen Factors

Air Quality

Epiphytic cyanolichens are generally restricted to the bark of trees in which surface pH registers between about 5.0 and 6.0 (Gauslaa 1985). When acid rain or other factors depress bark pH below about 5.0, these species go into decline (Farmer et al. 1991, 1992). In parts of Europe in which acid rain is now prevalent, striking declines in epiphytic cyanolichen diversity have been reported in forests otherwise unaffected by human activity (e.g., Gilbert 1986, Hallingbäck and Olsson 1987, Tnsberg et al. 1996). To date, most authors have emphasized the adverse effects of acid rain on the epiphytes of deciduous trees. Yet substrate acidification is probably even more devastating to the cyanolichen floras of conifers, because of the low buffering capacity of the bark (Barkman 1958, Gauslaa and Holien 1998). Apparently reflecting this, cyanolichens have been reported from conifers only in portions of the world unaffected by acid rain, including intermontane British Columbia, where rainfall acidity is >5.0 (B.C. Ministry of Environment 1990). Elsewhere, if epiphytic cyanolichens occur at all, they are restricted primarily to the trunks and branches of deciduous trees having strongly buffered bark (Rose 1988).

Elevation

Few studies have been undertaken on lichen distribution in upper elevation forests of inland British Columbia. What little information does exist is contained incidentally in the floristic studies of Goward and Ahti (1992) and Goward and Arsenault (1997); these studies suggest that epiphytic cyanolichens are essentially absent from all upper forested zones, including the Engelmann Spruce–Subalpine Fir, the Montane Spruce, the Sub-boreal Pine–Spruce, and the Spruce–Willow–Birch zones (Meidinger and Pojar 1991). Even in sheltered, valley-bottom forests, cyanolichens tend to disappear above about 1,100 m in southern regions, and above 500–900 m farther north. Sillett and Neitlich (1996) and Neitlich and McCune (1997) report a similar phenomenon in coastal regions of the American northwest. From these observations, we conclude that epiphytic cyanolichens are optimally represented at lower elevations.

Nutrient Enrichment

There is mounting evidence that cyanolichens colonize conifer branches most abundantly in stands growing over nutrient-rich soils—presumably due to enhanced bark pH (Gauslaa 1985, Gauslaa and Holien 1998). While the precise mechanism(s) by which these 2 phenomena are linked has/have not been elucidated, Gauslaa and Holien (1998) suggest that some conifers may be capable of absorbing calcium at concentrations sufficient to promote cyanolichen growth; this hypothesis, however, requires testing. Goward and Arsenault (in press) argue that a leachate or "drip zone" effect may be involved in some cases (see also Arsenault and Goward 2000). According to this hypothesis, aspen and cottonwood (*Populus* spp.) often act as "nutrient pumps." In nutrient-rich sites, at least, the roots of these trees are capable of absorbing calcium, nitrogen, and magnesium in considerable quantities (Krajina and Klinka 1982, Peterson et al. 1996, Holien 1997). Carried into the upper canopy, these nutrients are eventually released (as leaf litter and canopy leachates) to other ecosystem components, including the branches of understory conifers. In this way the pH of conifer branches might be enhanced, and the establishment of epiphytic cyanolichens promoted. Another localized form of enrichment results from aerosols carried in the spray from waterfalls.

Biogeoclimatic Zonation

Most epiphytic cyanolichens can be characterized as hygrophytic; that is, they require prolonged wetting at rather frequent intervals. Whereas alga-containing lichens can achieve positive net gas exchange when exposed to water vapour alone, a corresponding effect in cyanolichens requires direct exposure to liquid water (Lange et al. 1986, 1993). Consistent with these observations, Figure 1 reveals that epiphytic cyanolichens are primarily restricted to the humid, windward slopes of the major mountain ranges. Similarly, Table 1 indicates a 3- to 6-fold increase in cyanolichen diversity in the wettest inland subzones of the Interior Cedar–Hemlock (ICH) zone, as compared with adjacent but slightly drier zones and subzones. This increase, moreover, continues into more "oceanic" subzones of the ICH zone located outside the study area. Thus, regions subject to humid, oceanic climates appear to be optimal for epiphytic cyanolichens.

Secondary Cyanolichen Factors

To the 4 primary cyanolichen factors discussed above, we can add 3 secondary factors: forest age; soil moisture regime; and stand spacing. While not prerequisite to cyanolichen colonization on conifer branches, these factors do promote the establishment of nodes of high cyanolichen diversity. Several rare species are restricted to such nodes.

Forest Age

Old-growth forests are important to many epiphytic cyanolichens. Not only are cyanolichens more abundant in old-growth forests than in younger forest stands (Lesica et al. 1991, McCune 1993, Esseen et al. 1996), they are also often

Table 1. Epiphytic cyanolichens of conifer branches in intermontane British Columbia. Occurrences accompanied by an asterisk are old-growth-associated in the subzones indicated. Occurrences denoted by parentheses are restricted to the spray zones of waterfalls. Zonal abbreviations as in Figure 1.

Zone and subzone(s)						
Cyanolichens [a,b]	BWBS Wet	IDF Moist Wet	SBS Wet Very Wet	ICH Moist	ICH Wet Very Wet	ICH "Oceanic"[c]
Collema auriforme					+	
Collema furfuraceum				+	+	+
Collema subflaccidum				(+)	(+)	
Fuscopannaria ahlneri						+*
Fuscopannaria leucostictoides					+*	+*
Fuscopannaria mediterranea				(+)	(+)	+*
Leptogium burnetiae				(+)	+	+
Leptogium pseudofurfuraceum		+				
Leptogium saturninum	+	+	+	+	+	+
Lichinodium canadense					+*	+*
Lobaria hallii				(+)	+*	+
Lobaria linita					+*	+*
Lobaria oregana					(+)	+*
Lobaria pulmonaria		+	+	+	+	+
Lobaria retigera					+*	+*
Lobaria scrobiculata				(+)	+	+
Lobaria silvae-veteris						+*
Nephroma bellum	+			+	+	+
Nephroma helveticum			+	+	+	+
Nephroma isidiosum				(+)	+*	+*
Nephroma occultum					+*	+*
Nephroma parile			+	+	+	+
Nephroma resupinatum	+		+	+	+	+
Parmeliella parvula				(+)	(+)	+
Parmeliella triptophylla				(+)	+	+
Peltigera collina				(+)	+	+
Polychidium contortum						+*
Polychidium dendriscum					+*	+*
Pseudocyphellaria anomala				+	+	+
Pseudocyphellaria crocata					(+)	
Spilonemella americana [d]					(+)	+*
Sticta fuliginosa			+	+	+	+
Sticta limbata				(+)	+*	+*
Sticta oroborealis					+*	+*
Sticta wrightii					+*	+*
TOTAL SPECIES	3	3	6	8(11)	25(6)	30

[a] Species in bold are considered to be rare or infrequent in intermontane regions.
[b] Underlined species are rare or infrequent in British Columbia as a whole.
[c] Located in the Skeena and Nass river valleys, and transitional to the Coastal Western Hemlock zone; included for comparative purposes only.
[d] See "Unknown 1" in Goward (1999).

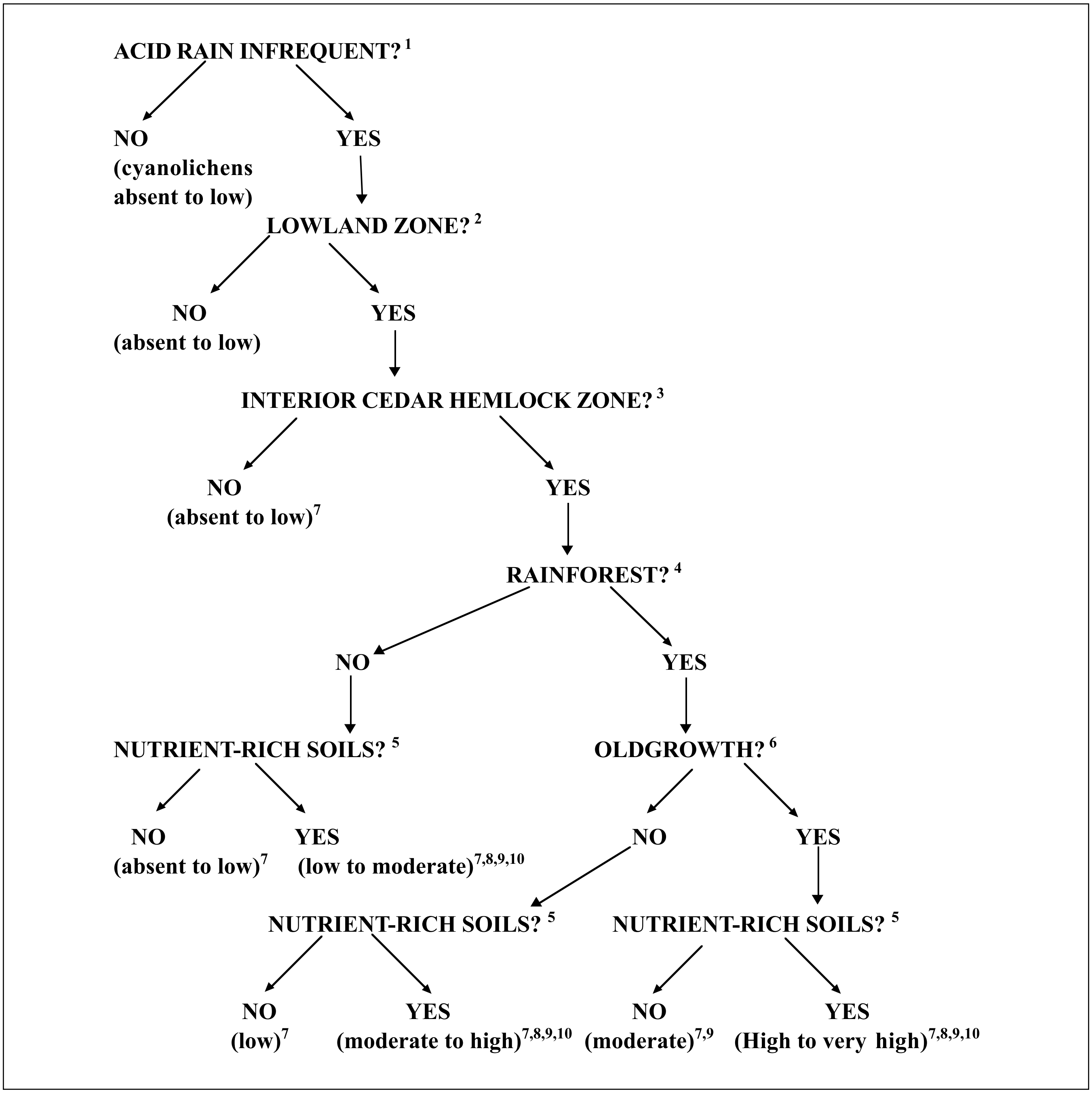

Figure 2. Provisional key to epiphytic cyanolichen diversity on conifer branches in intermontane British Columbia. Notes: [1]Rainfall pH averages >5.0; [2]Bunchgrass zone, Ponderosa Pine zone, Interior Douglas-fir zone, Interior Cedar–Hemlock zone, Sub-boreal Spruce zone, Boreal Black and White Spruce zone, and Spruce–Willow–Birch zone (Meidinger and Pojar 1991); [3]Western redcedar (*Thuja plicata*) and/or western hemlock (*Tsuga heterophylla*) present in mature stands on mesic sites; [4]Oak fern (*Gymnocarpium dryopteris*) and/or devil's club (*Oplopanax horridus*) often present in mature stands on mesic sites; [5]Aspen or cottonwood (*Populus* spp.) present, especially in the "toe" position at the base of slopes; [6]Snags and trees in all age classes present; *Populus* sparse or absent; [7]Occurrence within the spray zones of waterfalls can enhance cyanolichen diversity, assuming nutrient-rich aerosols; [8]Occurrence within the "drip zone" of *Populus* can enhance cyanolichen diversity, assuming nutrient-rich soils; [9]Hygric sites often support higher cyanolichen diversity than mesic or xeric sites; [10]Open stands support higher cyanolichen diversity than closed stands.

more diverse (Goward 1994, Goward and Pojar 1998). Goward (1994) has hypothesized that old old-growth (or "antique") forests act as "ports of entry" for rare epiphytic lichens colonizing from great distances. At least 16 cyanolichen species are essentially restricted to old-growth forests in the study area (Table 1); in the absence of old-growth, many of these species would not occur in this portion of British Columbia (Goward 1995). In coastal regions, too, many cyanolichens are restricted to older forests (Sillett and Neitlich 1996).

Soil Moisture Regime

In inland regions, mesic to hygric sites are more favourable to cyanolichen colonization than are submesic to xeric sites.

Stand Spacing

Open conifer stands are more conducive to cyanolichen development than are dense, shady stands (Neitlich and McCune 1997).

KEY TO CYANOLICHEN DIVERSITY

Our field work suggests that epiphytic cyanolichen diversity on conifers is roughly proportionate to the number of primary factors overlapping within a given forest stand. Maximum diversity is thus usually restricted to stands in which all 4 primary factors co-occur. We stress, however, that cyanolichen richness in any given stand can be further enhanced by the co-occurrence of 1 or more secondary factors. The seven cyanolichen factors discussed above can be arranged in a rough hierarchy of increasing influence, as follows: stand spacing < soil moisture regime < proximity to *Populus*/proximity to waterfalls < forest age < soil nutrient status < biogeoclimatic zonation < elevation < air quality. Guided by this schema, we have prepared a provisional "key" to epiphytic cyanolichen diversity on conifer branches in intermontane British Columbia (Fig. 2). Our key provides a simple method for the rapid assessment of cyanolichen richness. It is intended for use at an operational scale (e.g., 1:20,000–1:50,000) and should prove helpful to ecologists, forestry planners, resource managers, and others who may wish to adopt cyanolichens as surrogates for biodiversity, environmental continuity, or other ecological values.

CONCLUSIONS

The conifer forests of intermontane British Columbia support at least 31 cyanolichen species—one of the richest epiphytic cyanolichen assemblages in the world. Most of these cyanolichens are restricted in inland regions to "rain forests" located in the wet and very wet subzones of the ICH zone (Table 1). Within these subzones, moreover, the distributions of 16 species are further confined to old-growth ecosystems (Table 1). Virtually all of these species can be considered rare or infrequent in intermontane regions, while at least 12 are rare or infrequent in British Columbia as a whole: *Collema auriforme*, *Fuscopannaria leucostictoides*, *F. mediterranea*, *Lichinodium canadense*, *Lobaria retigera*, *Nephroma isidiosum*, *N. occultum*, *Parmeliella parvula*, *Polychidium dendriscum*, *Spilonemella americana*, *Sticta oroborealis*, and *S. wrightii* (Goward 1996, Goward 1999).

We conclude, then, that maximum cyanolichen diversity in inland British Columbia occurs over nutrient-rich soils in lowland old-growth rain forests subject to rainfall pH >5.0. Such stands are characteristically situated in nutrient-receiving sites, especially the "toe" position at the base of slopes. Here wildfire occurs infrequently, and stands as old as 800 years have been recorded. Reflecting their topographic position, however, such stands are highly vulnerable to road construction, timber extraction, and flooding by hydroelectric dams. Many have already disappeared and most of those that remain are now highly fragmented. Once safe havens for rare lichens, British Columbia's richest inland old-growth rain forests currently number among the most endangered of the province's endangered ecosystems. We hope the simple method advocated in this paper will assist resource managers in locating and assessing the last remaining stands, whether for designation as protected areas, old-growth management areas, or special management zones.

ACKNOWLEDGEMENTS

We are grateful to A. Roberts for data on the occurrence of epiphytic cyanolichens in the Interior Douglas-fir zone, and to E. Hamilton and L. Kowalsky for comments on an earlier draft of this paper. Funding for this project was provided by Forest Renewal British Columbia.

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