Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada

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The occurrence of 24 species of epiphytic macrolichens, many of which have previously been assumed to have strictly coastal distributions in western North America, is documented for five humid forests in inland British Columbia. These lichens were detected only in very old forests, and appear to be essentially absent from younger forest types in this region. Oldgrowth forests possibly favour such species by reason of their rather equable microclimate and relative environmental stability. The possibility is raised that some species may be relicts from the "Little Ice Age", when climatic conditions were presumably more favourable to long-distance dispersal by lichens outside their current primary ranges. Not all oldgrowth forests are equally rich in oldgrowth-dependent lichens. Diversity appears to be positively correlated with forest age or, more precisely, with environmental continuity. In support of this, it is observed that successful long-distance dispersal by oldgrowth-dependent lichens occurs only rarely; older oldgrowth forests can therefore be expected to support a fuller complement of such species than younger oldgrowth forests. The possibility is raised that oldgrowth-dependent lichens may provide a rough index of environmental continuity in the oldest of British Columbia's inland forests. The term "antique" is applied to such forests. It is concluded that old oldgrowth forests (= "antique forests") are more valuable for the purposes of lichen conservation than young oldgrowth forests.

Key words: British Columbia, Canada, flora, lichens, oldgrowth, phytogeogeography

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INTRODUCTION

The coniferous oldgrowth forests of the Pacific Northwest of North America have been the focus of considerable public debate in recent years (Harris 1984). At issue is the appropriate management of these forests: how much to preserve, and how much to dedicate to forestry interests. This controversy has stimulated and to some extent been stimulated by ecological research in several fields, with the result that a large body of scientific literature pertaining

to the structure and functioning of oldgrowth ecosystems now exists. For a recent bibliography pertaining to the forests of British Columbia (B.C.), see Cadrin et al. (1991).

Unfortunately, the lichens of the Pacific Northwest do not figure very prominently in this literature. For example, of a total 879 references cited in Cadrin et al. (1991), only 13 are dedicated specifically to lichenological research. What is more, none of these papers discuss the fundamental question of the relation of lichens to forest age, though in fact at least two papers addressing this topic have recently been published: Goward (1993a) for coastal British Columbia; and Lesica et al. (1991) for northern Montana. Both of these studies concluded that oldgrowth forests are of critical importance to many species of lichens.

The purpose of the present paper is to document and discuss the occurrence of various oldgrowth-dependent lichens in inland B.C., with special reference to their relation to forest age. Although I will restrict my remarks primarily to the epiphytic macrolichens of humid lowland forest types east of the coast ranges, my comments are also in part based on comparative studies in coastal areas (see Goward 1993a).

METHODS

The observations reported here derive from field studies conducted during 1991 and 1992 at a total of 135 localities in inland and coastal B.C. Field work was restricted to the southern half of the province, south of approximately 55°20'N, and was conducted primarily in humid lowland forests of the Interior Cedar-Hemlock (ICH) and the Coastal Western Hemlock (CWH) Zones. Approximately half of the localities supported oldgrowth forests, whereas the other half were characterized by younger forest types. At each locality an attempt was made to assess epiphytic macrolichen diversity as completely as possible — usually by means of comprehensive collections, but also, on occasion, by detailed relevés (see below).

In total, nearly 3 000 lichen specimens were assembled in connection with these studies; these are now housed at UBC. The specimens have been identified with the aid of dissecting and light microscopes, as required. In some cases, identification was further assisted by use of chemical spot tests. The taxonomy and nomenclature adopted in this paper follow Egan (1987, 1989, 1990, 1991).

For 40 localities found to have unusually rich epiphytic floras, detailed relevés were performed. As data from these are only indirectly incorporated in the present report, I have refrained from giving a complete account of my methods at this time. For each reléve, however, I did record canopy structure, canopy closure, height of the dominant trees, spacing, and size class distribution of standing stems. I also documented the presence, size and state of decomposition of large logs, and assessed the age of representative standing trees by use of an increment bore. These observations were intended to provide insights into the relative degree of environmental continuity at these sites.

Data were taken primarily within two to three metres of the ground. However, in an effort to detect additional species that might be restricted to the middle or upper crowns of the forest canopy, the branches of recently downed trees were also examined where available. With the assistance of professional climbers, I also sampled the crowns of standing trees at three localities.

A clear, inclusive definition of "oldgrowth" has yet to be formulated. In general, ecologists prefer to define oldgrowth with reference to various ecosystem attributes, e.g., structural diversity, canopy heterogeneity, numbers of standing dead trees, presence of large woody debris (Franklin et al. 1981). For practical purposes, however, the B.C. Ministry of Forests has recently proposed minimum age criteria for the recognition of oldgrowth in British Columbia (Old Growth Strategy Project, 1992). The ages recommended vary from ecosystem to ecosystem, but range in inland forests from 120 years to 200 years. In this study the term oldgrowth will be applied to forests older than about 150 years.

STUDY AREA

In B.C., the ICH is comprised of two forest regions that are distinct from one another both geographically and, to some extent, ecologically (see Meidinger & Pojar 1991). The larger of these occupies much of the south-east corner of the province, extending north in a 200 km-wide band from the Canada-U.S.A. border (at 49°N) to roughly 54°N. Physiographically, this portion of the ICH zone is restricted to the western, windward slopes of the Columbia Mountains and, to a lesser extent, the Rocky Mountains. Topographically, it forms an intersecting reticulum of more or less linear lowland forests separated by extensive tracts of upland forest and oroarctic vegetation.

The climate of this portion of the ICH is controlled primarily by topographic position relative to the Rocky Mountains and the Coast Ranges. The former mountains tend to protect the ICH from extensive outbreaks of polar and arctic air masses originating from central Canada, whereas the latter offset, but do not entirely negate, the prevailing onshore flow of mild, moist maritime air from the Pacific Ocean. Winters are therefore cold, but not extreme, with average nighttime temperatures of roughly –10°C to –15°C, though temperatures as low as –40°C are occasionally recorded. In summer, typical daytime high temperatures are in the range 22°C to 25°C. Precipitation is rather uniformly distributed through the year, with a slight peak, in most areas, in early summer. Amounts vary from 500 mm to roughly 1200 mm per annum, depending on locality. One-quarter to one-half of this precipitation falls as snow (Meidinger & Pojar, 1991), and snow packs of between 0.5 m and 1.5 m are typical.

The climate of the ICH has been described by Meidinger & Pojar (1991) as "continental", though for comparative purposes, and adopting the terminology of the bioclimatic system of Ahti et al. (1968) and Tuhkanen (1984), this portion of B.C. is more appropriately characterized as of intermediate continentality (see also Goward & Ahti 1992). Continentality ratings of between 30 and 35 are typical according to the Conrad Index of Continentality (Conrad 1946). By comparison, coastal areas average between 5 and 20 on the same index, and the Great Plains (east of the Rocky Mountains) average between 50 and 65. These values, it should be noted, are based entirely on thermal considerations.

The dominant trees of mature and climax ICH ecosystems include especially *Thuja plicata* and *Tsuga heterophylla,* with an understory of *Cornus, Menziesia, Oplopanax, Paxistima, Taxus* and various species of *Vaccinium.* In most regards the ICH is vegetationally somewhat similar to the CWH from which it differs primarily in being thermally much more continental, as noted above. See Meidinger & Pojar (1991) for further details.

The second, more northwesterly portion of the ICH was earlier included in the CWH (Krajina 1973). Located between roughly 55°N and 57°N, this forest region essentially occupies the leeward slopes and adjacent lowlands of the Coast Ranges; it is therefore thermally much more oceanic than the main portion of the zone. Transitional between the ICH and the CWH, this region is both climatically and vegetationally atypical of either zone. A locality representative of this region will be included among the data given below.

The ICH is of broad ecological amplitude, and is comprised of eleven subzones within the Biogeoclimatic System (Meidinger & Pojar 1991). Within the Bioclimatic System of Ahti et al. (1968) and Tuhkanen (1984), it embraces the humid and perhumid expressions of four subzones, namely the North Temperate Subzone, the Orohemiboreal Subzone, the Lower Oroboreal Subzone and the Middle Oroboreal Subzone. In order to keep climatic variables to a minimum, the present study will focus primarily on the ICHvk subzone, which in the Bioclimatic System is equivalent to the perhumid province of the Lower Oroboreal and Middle Oroboreal Subzones (see Goward & Ahti 1992).

RESULTS AND DISCUSSION

Floristic Patterns

Within the humid portions of the ICH, three assemblages of epiphytic macrolichens may be distinguished. The first of these consists of approximately 40 species common to forests throughout the study area, i.e. regardless of forest age. These species typically occur in relative abundance throughout the ICH, and are often also widespread, though not always abundant, in other forested zones. A similar epiphytic flora was recorded by Lesica et al. (1991), who provided a detailed list of species. The most conspicuous genera represented here include *Alectoria, Bryoria, Cetraria, Hypogymnia, Lobaria, Nephroma, Parmelia, Parmeliopsis, Platismatia* and *Usnea.* These lichens are well adapted to the broad ecological conditions within ICH forest ecosystems, and constitute what may be considered the primary epiphytic macrolichen flora of this zone. Goward (1993a) referred to such species as "Type A" lichens, though they can also be more specifically classified as "Type A-1".

A second, smaller cluster of approximately 15 epiphytes is restricted primarily, or in some cases perhaps exclusively, to younger forest ecosystems. Many of these species are favoured in seral forests by the presence of *Pinus contorta, Populus balsamifera, Pseudotsuga menziesii,* and other phorophytes in which the bark has distinctive textural or chemical properties (Gough 1975). Such trees are usually absent in oldgrowth forests, in which, in the ICH at least, total phorophyte diversity is comparatively restricted (Meidinger & Pojar 1991). Some of these lichens are probably also intolerant of the increased environmental acidity apparently characteristic of oldgrowth ICH ecosystems (Goward, unpublished data). Species belonging here include *Cetraria pallidula, Esslingeriana idahoensis, Leptogium saturninum,* and various species of *Melanelia, Ramalina, Usnea* and *Xanthoria.* Most of these lichens are widespread within the ICH. Though they are not as ecologically ubiquitous as the lichens of the previous category, they may nevertheless be classified with them as "Type A-2" lichens.

The third assemblage of lichens is much more restricted in distribution, and is essentially confined in the ICH to oldgrowth forest ecosystems. The species belonging here are clearly dependent on various special attributes of oldgrowth forests (see below); lacking such forests, most of them would certainly not occur in inland B.C. at all. Following the terminology of Goward (1993a), these species can be described as "Type B" lichens. In total, at least 24 species belong in this category. Table 1 documents the occurrence of these at five localities typical of the oldgrowth forests of the humid ICH.

Table 1. Observed occurrence of oldgrowth-dependent epiphytic macrolichens in selected localities of the Interior Cedar-Hemlock Zone of British Columbia.

Species	Localities*				
	1	2	3	4	5**
Cetrelia cetrarioides	–	–	+		–
Cavernularia hultenii	–	+	+	–	+
Collema auriforme	–	–	+	–	–
Dendriscocaulon intricatulum	+	+	+	–	+
Hypocenomyce friesii	+	+	+	+	–
Hypogymnia enteromorpha	–	–	–	–	+
Hypogymnia oceanica	+	+	+	+	+
Hypogymnia rugosa	+	+	+	+	+
Hypogymnia vittata	+	+	+	+	+
Lichinodium canadense	–	–	+	–	+
Lobaria oregana	–	+	–	+	+
Lobaria retigera	+	+	+	–	+
Melanelia glabratula	+	–	–	–	–
Nephroma occultum	+	+	+	+	+
Pannaria mediterranea	+	+	–	–	+
Parmelia pseudosulcata	–	–	+	–	+
Platismatia herrei	–	–	–	–	+
Platismatia norvegica	+	+	+	–	+
Polychidium dendriscum	+	+	+	–	+
Pseudocyphellaria crocata	+	–	–	–	–
Sphaerophorus globosus	+	+	+	+	–
Sphaerophorus tuckermannii	+	+	+	+	–
Sticta fuliginosa	+	+	+	+	+
Sticta wrightii	–	–	+	–	–

*All but one of these localities occur within the Very Wet Cool subzone of the ICH: Loc 1 = Clearwater River drainage, Azure Lake, Rainbow Falls, 650 m, 52°23'N, 119°58'W. 5 August 1992. Loc 2 = Adams River drainage, approximately 15 km N Tumtum Lake, 750 m, 51°58'N, 119°06'W. 23 September 1992. Loc 3 = Fraser River drainage, Slim Creek area, 80 km NW McBride, 800 m, 53°39'N, 121°12'W. 16, 17 August 1992. Loc 4 = Murtle River drainage, Murtle Lake area, 1 100 m, 52°08'N, 119°40'W. 9, 10 September 1992. **This locality occurs in the Moist Cool ICH, but is considerably less continental than the previous localities: Loc 5 = Skeena River drainage, 9 km NNW of Kispiox, 510 m, 55°25'N, 127°48'W. 11 July 1992.

Oldgrowth-dependent epiphytic macrolichens

It is possible to recognize several salient features of the ecology, composition and distribution of the lichens presented in Table 1. For example, virtually all of them with the possible exception of *Hypogymnia rugosa* are distinctly hygrophytic in ecology. This observation is supported by the fact, confirmed at several localities, that a majority of these species are restricted in the ICH to the lowermost portion of the forest canopy, where humidity is expected to be greatest and most equable (Geiger 1965). In this connection, it may be noteworthy that nearly half of these lichens (11 of 24) are partly or wholly cyanophilic.

A related characteristic is that most of these lichens with the exception of *Hypocenomyce* *friesii*, *Hypogymnia rugosa*, *Lichinodium canadense* and possibly *Sticta wrightii* are more common and widespread in oceanic localities, for example the CWH, than they are in the ICH. Indeed, many of them have only recently been documented from inland western North America by Goward & Ahti (1992), whereas several others have not previously been documented here at all: *Cetrelia cetrarioides*, *Collema auriforme*, *Lobaria oregana*, *L. retigera*, *Polychidium dendriscum*, *Pseudocyphellaria crocata*, and *Sticta wrightii*.

It is interesting in this connection that Locality 3, with 18 of 24 species, is located within 60 km of the British Columbia–Alberta border — in a region of pronounced continentality. Clearly the macrodistribution of most of these lichens is

controlled primarily by hygric considerations rather than by any pronounced sensitivity to extremes of temperature. Such lichens may therefore be considered oceanic in the hygric sense, but not in the thermal sense. On the other hand, *Hypogymnia enteromorpha* and *Platismatia herrei* are common only in Locality 5, which is thermally much less continental than the other localities. Both these species, it should be noted, do occur farther inland, but were not recorded in the four other localities cited in Table 1. For a recent map of *Hypogymnia enteromorpha*, see Goward & McCune (1993).

The exclusive occurrence of numerous hygrically oceanic lichens in the oldgrowth forests of the ICH supports the recognition of oldgrowth as ecologically distinct from younger forest ecosystems. Franklin et al. (1981), for example, stress that temperature and humidity relations within oldgrowth forests are considerably less extreme than in seral forests. Related to this, McCune & Antos (1982) and others have shown that oldgrowth ecosystems are also much more hygrophytic than seral forests. In these characteristics, the oldgrowth forests of the ICH can be said to more closely resemble coastal forest ecosystems than they do seral ICH ecosystems.

Another point of distinction is environmental stability. On the whole, young forest ecosystems are much more dynamic, and hence much less environmentally stable, than oldgrowth forests. Though Type A lichens are obviously well adapted to withstand fluctuations in microclimatic conditions of the kind typical of maturing forests, Type B lichens are much less fit in this regard. This may partly reflect differing levels of inherent ecological sensitivity, or it may be related to the fact that Type B lichens occur, by definition, outside their primary range: such species are usually much more adaptable within their main distribution areas, where most of them would in fact be described as Type A lichens. Whatever the explanation, it is difficult to avoid the speculation that oldgrowth-dependent lichens benefit from the comparative environmental stability characteristic of oldgrowth forests.

The possibility must also be raised that the oldgrowth-dependent status of at least some of the species in Table 1 may be an artifact of climatic warming over the past few hundred years. During the Little Ice Age, which spanned the period from about 1350 A.D. to 1870 A.D. (Pielou 1991), climatic conditions were cooler than at present,

and presumably also more humid. Under such conditions, successful long-distance dispersal by oceanic lichens must have been a more frequent occurrence than today. It is therefore conceivable that a number of "oceanic" epiphytic lichens arrived in the ICH at that time. Such species may no longer be capable of dispersing in the ICH, but are merely persisting in localities at which they became established hundreds of years ago. This comment is likely to apply especially to less common species such as *Collema auriforme*, *Lobaria oregana*, *Melanelia glabratula*, *Pseudocyphellaria crocata* and *Sticta wrightii*.

Lichens as potential indicators of forest age

It can be seen from Table 1 that the distribution of oldgrowth-dependent species within the ICH is more or less random; no single oldgrowth forest, or forest region, has yet been found to contain all of them. Whereas some species, e.g., *Hypogymnia vittata*, *Nephroma occultum* and *Sticta fuliginosa* occur in most or all of the localities visited, others are of more spotty occurrence. Many of the latter lichens, moreover, are rare throughout inland B.C., while at least four of them may be considered rare or infrequent in B.C. as a whole: *Collema auriforme*, *Lichinodium canadense*, *Lobaria retigera* and *Sticta wrightii* (Goward 1993b). These observations strongly suggest that dispersal by these lichens is on the whole a slow, random process in the ICH, and that the current distribution of each species directly reflects the colonizing powers of its diaspores.

Related to these observations, some oldgrowth forest stands are also obviously less rich in oldgrowth-dependent lichens than others. Locality 4, for example, was found to contain only nine species, whereas Localities 1, 2, 3 and 5 support 15 species or more. Notwithstanding that all oldgrowth forests in the ICH appear to support similar numbers of Type A lichens, species richness among Type B lichens varies from 18 species at Locality 3 to as few as two or three species at many other oldgrowth localities not documented here. It would appear in fact that a majority of oldgrowth forests contain only small numbers of oldgrowth-dependent epiphytes.

Putting aside obvious ecological differences such as aspect, exposure, elevation, phorophyte availability and parent material, these discrepancies appear to reflect differing degrees of environmental continuity within oldgrowth forests. Indeed, the

available evidence strongly supports the hypothesis that Type B lichens occur in greater numbers in older oldgrowth forests than in younger oldgrowth forests.

Indirect support for this hypothesis may be drawn from two unrelated observations. The first observation is simply that older oldgrowth forests have obviously been available for colonization over a longer period than younger oldgrowth forests. If it is true, as already suggested, that recruitment of Type B lichens occurs as a series of random hit-and-miss inoculations by lichen diaspores, then it is not unreasonable to suppose that colonization by a full suite of Type B lichens is a gradual process requiring the passage of considerable time. According to this view, different levels of species richness among oldgrowth-dependent lichens represent differing points along this process.

A second line of support can be derived from the fact that similar forest age — lichen diversity relationships are already well documented in Europe (Rose 1976, Diederich 1991) and eastern North America (Selva 1989, 1990). In Britain, for example, Rose (1976) demonstrated that deciduous woodlands known to have been undisturbed for many hundreds of years usually contain between 120 and 150 lichen species per square kilometre, whereas forests disturbed less than 200 years ago tend to contain fewer than 50 lichen species per square kilometre. These differences prompted Rose to devise a "Revised Index of Ecological Continuity", in which lichens are used as indicators of the degree of environmental continuity present in a given forest stand. Selva (1989, 1990) and Diederich (1991) have more recently adapted Rose's index to forests in other regions, though no attempt has yet been made to apply it to the forests of western North America.

It must be stressed that oldgrowth-dependent species occur not only among the macrolichens. Some crustose lichens can also be classified as Type B. Indeed, more than half of the species included in the oldgrowth indicator lists of Rose (1976), Selva (1989) and Diederich (1991) are crustose. The same comment applies to bryophytes: Norris (1987), studying the mosses and liverworts of oldgrowth and secondgrowth forest stands in northern California, concluded that several hepatic species were oldgrowth-dependent. Recent work in northern Sweden indicates that various unlichenized fungi, especially members of

the Aphyllophorales, may likewise be restricted to oldgrowth ecosystems (Karin Lindahl, pers. comm.). Identifying the oldest oldgrowth forests may therefore be an important exercise from the point of view of general biodiversity. In recognition of this, such forests were termed "antique" by Goward (1993a).

As a cautionary note, it must be stressed that the relation of oldgrowth-dependent lichen diversity to forest age is apparently not always straightforward. A few of the forest stands examined were certainly of great age, yet they contained only small numbers of oldgrowth-dependent macrolichens. It can perhaps be assumed that environmental continuity in such forests has at some point been disturbed by ground fire, defoliating insects, prolonged drought, or other disruptive agent. At any rate, forest age and forest continuity are probably not entirely synonymous: though the presence of great numbers of oldgrowth-dependent macrolichens is doubtless a reliable indicator of great forest age, low numbers of such species may be inconclusive.

CONCLUSIONS

The ecological requirements of oldgrowth-dependent lichens are incompatable with current forest management practice in B.C. When Lesica et al. (1991) commented that many lichens "will become less common as silvicultural practices continue to convert oldgrowth to younger aged forests", they were referring to species that would here be classified as Type A lichens. More devastating by far is the effect that progressive clearcut logging will have in the long term on Type B species. According to island biogeography theory (MacArthur & Wilson 1967), increasing fragmentation and isolation of oldgrowth forests can be expected to result in ever slower rates of colonization among oldgrowth-dependent epiphytes. The strong possibility exists, therefore, that colonization rates will eventually be overtaken by opposing rates of local extirpation. Although precise quantitative predictions are impossible at the present time, declines in epiphytic macrolichen diversity as high as 30% seem not unlikely in some portions of the province.

In the absence of detailed floristic studies supported by direct and indirect measurements of forest age, much of the preceding discussion must remain preliminary. Nothwithstanding this,

there is good reason to believe that oldgrowth-dependent lichens — in the Pacific Northwest as elsewhere — are valuable indicators of long-term environmental continuity. It is to be hoped they will be permitted to play a role in settling the debate over the future of B.C.'s oldgrowth. At the very least, resource managers must be made to understand that from the perspective of maintaining general floristic diversity in the ICH, oldgrowth forests are by no means all of equal value.

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