Nephroma occultum and the Maintenance of Lichen Diversity in British Columbia

Trevor Goward

Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 2B1, Canada[1]

[1] Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0, Canada

Abstract

Based on field studies conducted in British Columbia in 145 forested sites of different ages, the distributional ecology of *Nephroma occultum* is described. Three macroclimatic "range classes" are recognized for this species: 1) a primary range, in which it is restricted to the upper and middle canopies of oldgrowth forests; 2) a secondary range, in which it colonizes the middle and lower canopies of oldgrowth and seral forests alike; and 3) a tertiary range in which it is confined to the lower canopy of oldgrowth forests. In British Columbia, *N. occultum* is judged to have its widest ecological amplitude in its secondary range, which may therefore be termed this species' "effective ecological epicentre".

Any viable conservation strategy intended to maintain *N. occultum* throughout its current distribution area must effectively treat this species as a separate ecological entity within each of its range classes. It is concluded that the range class model may prove useful for expressing the distributional ecologies – and hence the conservation requirements – of other oldgrowth-dependent lichens.

Keywords: British Columbia, Canada, lichens, ecology, oldgrowth, conservation, *Nephroma occultum*

1 Introduction

Oldgrowth dependency among lichens has been documented in the deciduous woodlands of Great Britain (ROSE 1976) and Luxembourg (DIEDERICH 1991), as well as in the coniferous forests of Sweden (TIBELL 1992), New Brunswick (SELVA 1989, 1990) and British Columbia (GOWARD 1993, 1994a). The authors of all these studies have called attention to the usefulness of lichens as indicators of environmental continuity.

GOWARD (1994a) has further discussed the phenomenon of oldgrowth dependency *per se,* suggesting that certain species are restricted to oldgrowth forests by reason of: 1) the unique microclimatic conditions associated with such forests; 2) their relative environmental stability; and/or 3) their great age. GOWARD also distinguished between "Type A" lichens, which can be defined as having a broad ecological amplitude within a given region, and "Type B" lichens – including oldgrowth-dependent species – which have a much narrower ecology within the same region. He noted that a lichen may behave as a Type A species in one portion of its range, and a Type B species in another. Finally, he proposed that old oldgrowth (= "antique") forests may have greater conservation value for Type B lichens than younger oldgrowth forests.

In British Columbia, oldgrowth-dependent lichens are highly vulnerable to habitat disruption associated with current forestry practice. They are, indeed, probably more at risk of local or regional extirpation than any other single group of organisms (GOWARD 1994b). Notwithstanding these observations, conservation strategies aimed specifically at the maintenance of lichen diversity in forested ecosystems in British Columbia have yet to be developed. In the light, however, of recent modifications to forestry practices in adjacent portions of the American Northwest (ROSENTRETER, 1995 this vol.), there is reason to believe that a Canadian conservation strategy for lichens may not be far off.

In this paper I discuss certain aspects of lichen distribution and ecology which warrant special consideration in the development of such a strategy. I base my discussion on field observations on *Nephroma occultum* Wetm.: a recently described western North American epiphyte (WETMORE 1980) that provides a rare opportunity to examine the distributional ecology of a lichen throughout its presumed historic range.

Nephroma occultum is a conspicuous and distinctive species whose main diagnostic features include the foliose habit, proportionately broad lobes (to 1.5 cm across), bluish grey colour, reticulate upper surface, sorediate ridges and glabrous lower surface. As the only North American representative of the *N. cellulosum* group – an assemblage of four species otherwise endemic to the southern hemisphere, especially southern Chile and Argentina (WHITE and JAMES 1988) – *N. occultum* is phylogenetically isolated on this continent.

2 Materials and methods

Field studies for this report were carried out in various humid regions of coastal and inland British Columbia during the summers of 1991 and 1992 (Goward, in prep.). In total, 145 localities were investigated for the presence of *N. occultum*. Approximately half of the localities supported oldgrowth forests (as defined below), whereas the other half contained younger forests types. At each locality an attempt was made to assess epiphytic macrolichen diversity as thoroughly as possible, usually by means of comprehensive collections. In total, nearly 3,000 lichen specimens were assembled in connection with these studies.

For localities found to support *N. occultum*, detailed relevés were performed. These yielded data on canopy structure, canopy closure, height of the dominant trees, spacing, and size class distribution of standing stems. In an effort to determine the relative degree of environmental continuity at these sites, I also documented the presence, size and state of decomposition of large logs, and assessed the age of representative standing trees using an increment borer.

Most observations were made within two to three metres of the ground. However, in order to assess the vertical distribution of *N. occultum* in the forest canopy, the branches of recently wind-thrown trees were also closely examined; such trees are almost invariably present along the perimeters of recent clear-cuts. With the assistance of professional climbers, I also sampled the crowns of standing trees at three localities.

In general, ecologists prefer to define oldgrowth with reference to various ecosystem attributes, including structural diversity, canopy heterogeneity, numbers of standing dead trees, and presence of large woody debris (FRANKLIN *et al.* 1981). For practical purposes,

94

however, the British Columbia 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 120 years to 200 years. In this study the term oldgrowth will be applied to forests older than about 150 years. Forests younger than 150 years will be referred to here as "seral" forests, though this is not meant to imply that forests older than 150 years are thought to represent climax forest types.

3 Study area

Within the biogeoclimatic system of the British Columbia Ministry of Forests (MEIDINGER and POJAR 1991), most of the localities visited may be classified as belonging in the Coastal Western Hemlock Zone (CWH) or the Interior Cedar-Hemlock Zone (ICH). These are the only vegetation zones in which *N. occultum* has been found to date, and the only zones in which it is expected to occur.

The CWH encompasses the most humid and highly oceanic region of North America. On the mainland this zone hugs the western edge of the continent in a broad band stretching eastward to the crest of the coast ranges. Mean annual precipitation ranges from 1000 to 4,400 mm, roughly 75% of which occurs during the winter half year, and most of which falls as rain. Mean temperatures average between 13 °C and 18.5 °C during the warmest month, and between –6.5 °C and 4.5 °C during the coldest month. Extreme maximum temperatures are between 23 °C and 40.5 °C, and extreme minimum temperatures between –10 °C and –30 °C. Continentality is between 5 and 20 according to the Conrad Index of Continentality (CONRAD 1946). By comparison, continentality in the ICH registers between 20 and 35 on the same index, and the Great Plains (east of the Rocky Mountains) register between 50 and 65.

The ICH is comprised of two geographically distinct forest regions (see MEIDINGER and POJAR 1991). The larger of these occupies 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. Precipitation varies from 500 mm to 1400 mm per annum, and is rather uniformly distributed through the year, with a slight peak, in most areas, in early summer. One-quarter to one-half of this precipitation falls as snow, and snow packs of between 0.5 m and 1.5 m are typical. Mean temperatures during the warmest month average between 16 °C and 21 °C, and during the coldest month between –3 °C and –10 °C. Extreme maximum and minimum temperatures are 43 °C and –46 °C respectively.

The second, more north-westerly portion of the ICH was earlier included in the CWH (KRAJINA 1973). Located roughly between 55° N and 57° N, this region occupies the leeward slopes and adjacent lowlands of the coast ranges, and is therefore thermally much more oceanic than its south-eastern counterpart. It is also much more continental than the CWH, and in fact combines the climatic features of both zones.

Both the CWH and the ICH are of broad climatic amplitude, and are comprised of ten and eleven subzones respectively. Within the Bioclimatic System of AHTI *et al.* (1968) and TUHKANEN (1984), they embrace the humid and perhumid expressions of four subzones, i.e., the North Temperate Subzone, the Orohemiboreal Subzone, the Lower Oroboreal Subzone, the Lower Oroboreal Subzone and the Middle Oroboreal Subzone. The com-

parative positioning of these subzones in Europe and other regions of the world is discussed by AHTI *et al.* (1968), HÄMET-AHTI *et al.* (1974), HÄMET-AHTI (1986) and TUH-KANEN (1984, 1987, 1992). See also GOWARD and AHTI (1992).

4 Results

In Washington and Oregon, *N. occultum* has been reported from a total of five localities (NEITLICH *et al.* 1994) spanning five degrees of latitude and one degree of longitude. In British Columbia, by contrast, it has been detected at 21 localities (Goward, in prep.) spanning ten degrees of latitude and eight degrees of longitude. Based on current data, therefore, British Columbia comprises roughly 75% of this species' global distribution area. Yet even here, *N. occultum* occurs in only two of 14 biogeoclimatic zones, i.e., the CWH and the ICH. Within the CWH, moreover, it is further restricted to subzones of intermediate humidity, whereas in the ICH it is confined to the wettest and/or coolest subzones.

Though *N. occultum* can be broadly characterized as oldgrowth-dependent, its ecological behaviour is by no means uniform throughout its range. In inland regions (Range III
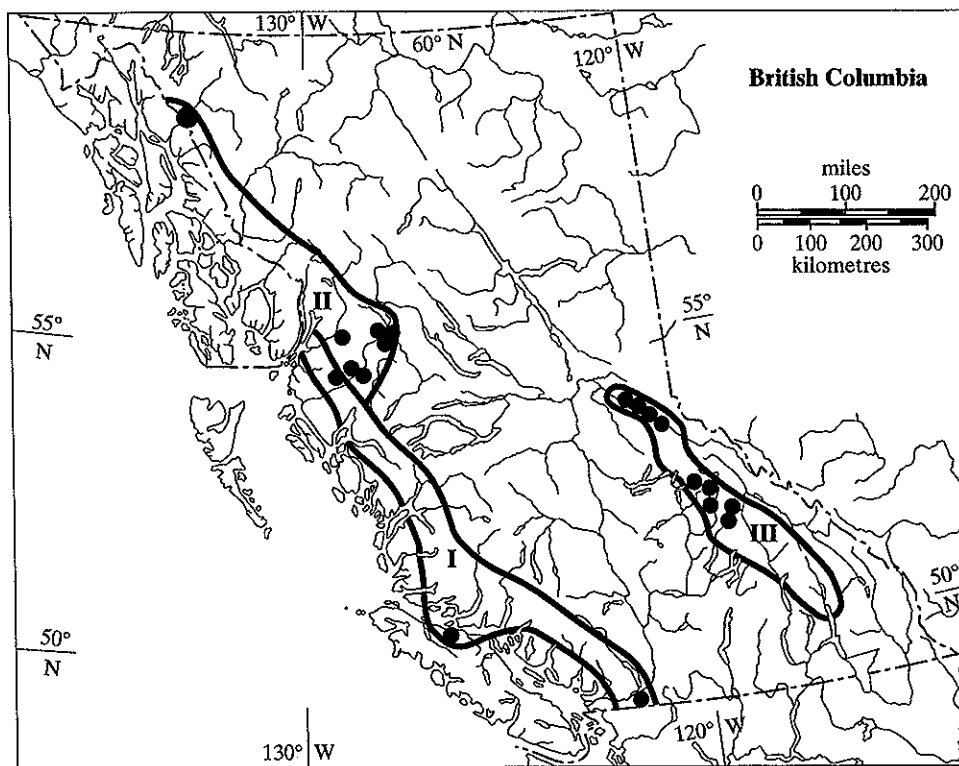

Fig. 1. The range classes of *Nephroma occultum* in British Columbia. Dots represent known localities.

of Fig. 1), for example, it is essentially restricted to oldgrowth forests in valley-bottom situations, whereas in coastal and near-coastal localities (Ranges I and II), it inhabits old-growth forests in valley bottoms and on valley slopes alike. What is more, in the north-west portion of the ICH (Range II), it appears to occupy both oldgrowth forests *and* seral forests (as young as 40 years), again in a variety of topographic positions.

These habitat differences closely parallel regional differences in *N. occultum's* vertical distribution in the forest canopy. Originally, WETMORE (1980) characterized this species as occurring "high up in old trees on moderate-sized branches, and never lower on the trunks". In fact this comment would apply in British Columbia only to coastal localities (Range I), where *N. occultum* is indeed usually located in the upper and middle portions of the canopy, often as high as 30 m above the ground. In somewhat more inland locali-ties (Range II), by contrast, it occurs in the middle and lower canopy. Farther inland again (Range III), it seems to be entirely restricted to the lower canopy, usually within two to three metres of the ground. Exceptions, however, do occur. In well-illuminated, well-ven-tilated coastal localities, for example along the margins of streams, the lower trunks and branches of trees are also on occasion colonized. Conversely, *N. occultum* has been found to occur in inland localities as high as 10 m in the spray zones of waterfalls.

5 Discussion

Based on the above regional differences in ecological expression, it is possible to distin-guish three range classes for *N. occultum* (see Fig. 2). These range classes are broadly de-fined by this species' response to regional climatic conditions. In the first category, i.e., its "primary range" (= Range I in Fig. 1), *N. occultum* appears to be well adapted to re-gional climate. This is suggested both by its occurrence in the upper forest canopy (where regional climate is presumably most fully expressed), and by its broad topographic dis-tribution in valley-bottom and valley-slope forests alike. Given that *N. occultum* is like-wise reported to be restricted to the middle and upper canopy in the holotype locality in Oregon (WETMORE 1980), this area, too, could possibly be classified as belonging within *N. occultum's* primary range.

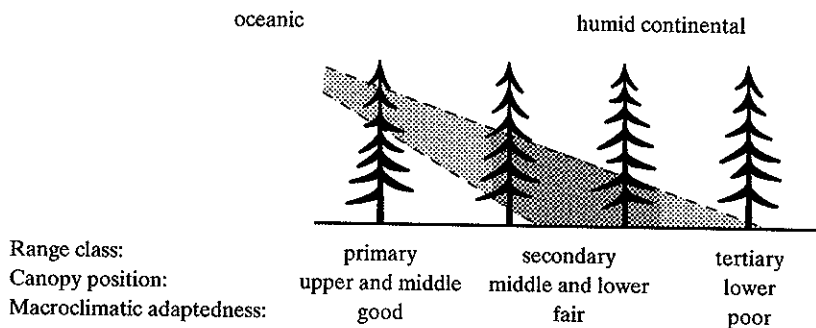| Range class: | primary | secondary | tertiary |
| Canopy position: | upper and middle | middle and lower | lower |
| Macroclimatic adaptedness: | good | fair | poor |

Fig. 2. The range class model as applied to *Nephroma occultum* in British Columbia. Darker shading indicates the effective ecological epicentre of the species (see text).

Interestingly, *N. occultum* does not achieve maximum ecological amplitude within its primary range. In the first place it appears to be essentially absent here from the lower canopy. And in the second place it usually does not occur in younger forest types. Its absence from the lower canopy can perhaps be explained by an inability: 1) to withstand the continuously high humidity associated with this portion of the forest (FRANKLIN *et al.* 1981); and/or 2) to compete for space with epiphytic bryophytes such as *Isothecium stoloniferum* Brid., which are ubiquitous in the lower canopy.

Nephroma occultum's absence from seral forests within its primary range probably reflects the relative environmental instability associated with such forests. Here vertical canopy growth rates may exceed 75 cm per year (Goward, unpublished data), resulting in rapidly changing microclimatic conditions unsuited to the physiological requirements of most lichen species. Only after growth rates decline – usually after the forests attain 100 years of age – do epiphytic lichens encounter the relative environmental stability for which many species, including *N. occultum,* appear to have evolved (see also GOWARD 1994a).

In its secondary range (Range II), *N. occultum* displays a somewhat broader ecological amplitude. Here it: 1) colonizes both oldgrowth forests and (to a lesser extent) seral forests; 2) occurs in the lower and middle canopies; and 3) occupies valley-bottom sites and valley-slope sites alike. This relative breadth of ecological tolerance can be interpreted as suggesting at least partial physiological adaptedness to macroclimatic conditions. However, *N. occultum*'s absence from the upper forest canopy indicates that it is less well macroclimatically adapted here than in its primary range.

In its tertiary range (Range III) *N. occultum* is again ecologically more restricted, and is, indeed, entirely confined to within two or three metres of the ground in oldgrowth forests in sheltered, humid, valley-bottom localities. Here this species appears to be supported entirely by the localized microclimatic conditions associated with the lower canopies of such forests (see McCUNE 1993). Certainly it could not persist in this portion of its range in the absence of oldgrowth forests.

As defined above, the primary, secondary and tertiary ranges of *N. occultum* can be viewed as nodes along an east-west macroclimatic continuum. At one end of the continuum, near the Pacific coast, conditions are thermally oceanic; and at the other end, near the British Columbia–Alberta border, conditions are thermally much more continental. It is possible to record *N. occultum*'s varying degrees of adaptedness to these regional climates by observing its vertical distribution in the forest canopy: higher in regions of greater oceanity, versus lower in regions of greater continentality.

It is intriguing that, as already mentioned, *N. occultum* displays a much broader ecological amplitude in its secondary range than in its primary range. This suggests that the primary range of a species, in which it is at macroclimatic optimum, need not always coincide with what may be termed its "effective ecological epicentre", i.e., that portion of its range in which it occupies the greatest number of ecological niches. This concept will be more fully discussed in a future paper.

98

Mitt. Eidgenöss. Forsch.anst. Wald Schnee Landsch. 70, 1 (1995)

6 Conclusions

That *N. occultum* behaves differently in different portions of its range is by no means unexpected. For those who study the distributional ecology of lichens, such behaviour is known to be the rule rather than the exception. Perhaps the best documented instance of this phenomenon is that of "substrate switches" (BRODO 1974), in which a lichen may colonize one substrate in one portion of its range, and a strikingly different substrate elsewhere. No less unusual, however, are regional discrepancies of other kinds, including zonal amplitude (e.g., AHTI 1977), microniche (e.g., KARSTRÖM and THOR 1991), frequency status, and – as documented here – oldgrowth dependency. In some instances such behavioural differences presumably reflect genetic variation within the species (e.g., CULBERSON *et al.* 1990), though in other instances genetic factors are probably less important than environmental factors.

These observations are intended to serve as a caveat for land managers charged with designing conservation strategies in which maintenance of lichen diversity has priority. As I have attempted to demonstrate, the global ecology – and therefore the global conservation requirements – of a given lichen cannot be deduced from its behaviour in any one portion of its range. In those instances in which a range class (i.e., primary or secondary or tertiary) exceeds a conservation unit (i.e., township or county or province or country) in areal extent, a single conservation strategy may perhaps suffice. But in those cases where the reverse obtains, i.e., where the political unit is larger than the functional ecological unit, two or more different strategies may be required. Indeed, the species in question must then be treated as a separate ecological entity in each of its range classes.

Island biogeography theory (MACARTHUR and WILSON 1967) suggests that any attempt to preserve species within small, isolated "islands" of appropriate habitat is doomed from the outset. If we wish to maintain *N. occultum* throughout its full historic range, we must be prepared to set aside considerable tracts of oldgrowth forest. How large, how closely spaced and how topographically specific these tracts need be must depend on the range class under consideration. Though considerable work remains to be done on these difficult questions, a few preliminary recommendations can be given.

Within *N. occultum*'s primary range (Range I), oldgrowth forests in valley bottom localities and on the adjacent valley walls are probably of equal value for conservation purposes. Set-asides need not be extensive. In the secondary range (Range II), by contrast, valley bottom forests, especially oldgrowth forests, should probably be selected over hillside forests. Again the set-asides need not be extensive; and there is evidence that some level of selective logging may be tolerated within them (Goward, unpublished). In the tertiary range (Range III), the set-asides should be much larger and much more intimately connected, and should also be confined to valley bottom localities.

It is of course unlikely that any broad-scale conservation plan will be designed specifically around the ecological requirements of a single lichen species. However, on the basis of the field studies on which this report is based, there are strong indications that the distributional ecologies of most, if not all, oldgrowth-dependent lichens may be reducible to three or four general patterns of the kind observed for *N. occultum*. There is also reason to believe that the range class model outlined above will be useful not only in articulating these patterns, but also in helping to formulate the most effective lichen conservation strategies possible.

7 Summary

1) Though *N. occultum* is typically described as oldgrowth-dependent, this characterization is less apt in some portions of its range than in others. In a small portion of its distribution area, *N. occultum* may occur in oldgrowth forests and seral forests alike.

2) A close examination of the distributional ecology of this species permits recognition of three range classes: 1) a primary range, in which it is well adapted to regional climatic conditions, but in which, in British Columbia at least, it is essentially restricted to the upper canopy of oldgrowth forests; 2) a secondary range, in which it is moderately adapted to regional climate, and in which it colonizes oldgrowth and seral forests alike; and 3) a tertiary range, in which it is supported entirely by special microclimatic conditions associated with the lower canopy of oldgrowth forests.

3) The existence of oldgrowth forests has enabled *N. occultum* to occupy a distribution area much larger than it would otherwise occupy in the absence of such forests. From the perspective of the macrodistribution of this species, oldgrowth forests may be viewed as an important vehicle of range extension.

4) For the purposes of lichen conservation, *N. occultum* must be treated as a different ecological entity in different portions of its range. No single management strategy is likely to allow it to persist throughout its current range. Conservation efforts must be tailored to the differing ecological requirements of this lichen in its primary, secondary and tertiary ranges.

8 References

AHTI, T., 1977: Lichens of the boreal coniferous zone. In: SEAWARD, M.R.D. (ed): Lichen ecology. New York, Academic Press. 145–181.

AHTI, T.; HÄMET-AHTI, Leena; JALAS, J., 1968: Vegetation zones and their sections in northwestern Europe. Ann. bot. fenn. 5: 169–211.

BRODO, I.M., 1974 ('1973'): Substrate ecology. In: AHMADJIAN, V.; HALE, M.E. (eds): The lichens. New York, Academic Press. 401–441.

CONRAD, V., 1946: Usual formulas of continentality and their limits of validity. Trans. Am. Geophys. Union 27: 663–664.

CULBERSON, Chicita F.; CULBERSON, W.L.; JOHNSON, Anita, 1990: The *Ramalina americana* complex (Ascomycotina, Ramalinaceae): chemical and geographic correlation. Bryologist 93: 167–186.

DIEDERICH, P., 1991: Les forêts luxembourgeoises à longue continuité historique. Bull. Soc. Nat. luxemb. 92: 31–39.

FRANKLIN, J.F.; CROMAK, K.; DENISON, W.; McKEE, A.; MASER, C.; SEDELL, J.; SWANSON, F.; JUDAY, G., 1981: Ecological characteristics of old-growth Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-118. 48 pp.

GOWARD, T., 1993 ('1991'): Epiphytic lichens: going down with the trees. In: RAUTIO, S. (ed): Community action for endangered species: a public symposium on B.C's threatened and endangered species and their habitat. Vancouver, Federation of British Columbia Naturalists. 153–158.

GOWARD, T., 1994a: Notes on oldgrowth-dependent epiphytic macrolichens in inland British Columbia, Canada. Acta bot. fenn. 150: 31–38.

GOWARD, T., 1994b: Rare and endangered lichens in British Columbia. In: HARDING, L.E.; MCCULLUM, E. (eds): Biodiversity in British Columbia: our changing environment. Vancouver, Environment Canada. 77–80.

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.

HÄMET-AHTI, Leena, 1986: The zonal position of *Nothofagus* forests. Veröff. Geobot. Inst. Eidgenöss. Tech. Hochsch., Stift. Rübel Zür. 91: 217–227.

HÄMET-AHTI, Leena; AHTI, T.; KOPONEN, T., 1974: A scheme of vegetation zones for Japan and adjacent regions. Ann. bot. fenn. 11: 59–88.

KARSTRÖM, M.; THOR, G., 1991: Field meeting in Vuollerim, Lule Lappmark by Swedish lichenologists. Graph. scr. 3: 84–93.

KRAJINA, V., 1973: Biogeoclimatic zones of British Columbia. (Map). Victoria, Dept. Lands, Forests and Water Research.

MACARTHUR, R.H.; WILSON, E.O., 1967: The theory of island biogeography. Princeton, Princeton Univ. Press. 203 pp.

MCCUNE, B., 1993: Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist 96: 405–411.

MEIDINGER, D.; POJAR, J., 1991: Ecosystems of British Columbia. – Victoria, B.C., Ministry Forests, Spec. Rept. Ser. 6: 1–330.

NEITLICH, P.; MCCUNE, B.; PITTAM, Sherry, 1994: Lichen species of late successional ecosystems: documented herbaria records. Unpublished report; Portland, Oregon, Interagency S.E.I.S. Team. 166 pp.

Old Growth Strategy Project, 1992: An old growth strategy for British Columbia. Victoria, B.C., Ministry Forests. 74 pp.

ROSE, F., 1976: Lichenological indicators of age and environmental continuity in woodlands. In: BROWN, D.H.; HAWKSWORTH, D.L.; BAILEY, R.H. (eds): Lichenology: progress and problems. London, Academic Press. 279–307.

ROSENTRETER, R., 1995: Lichen diversity in managed forests of the pacific northwest, USA. Mitt. Eidgenöss. Forsch.anst. Wald Schnee Landsch. 70, 1: 103–124.

SELVA, S.B., 1989: Lichens as indicators of old-growth forests. Fork Kent. Nature Conservancy. Unpublished report. 48 pp.

SELVA, S.B., 1990: The Caliciales of Mount Carleton Provincial Park, New Brunswick. St. John, New Brunswick Museum. Unpublished report. 61 pp.

TIBELL, L.: 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. Nord. J. Bot. 12: 427–450.

TUHKANEN, S., 1984: A circumboreal system of climatic-phytogeographical regions. Acta bot. fenn. 127: 1–50.

TUHKANEN, S., 1987: The phytogeographical position of the Faeroe Islands and their ecoclimatic correspondences on the other continents: Problems associated with highly oceanic regions. Ann. bot. fenn. 24: 111–135.

TUHKANEN, S., 1992: The climate of Tierra del Fuego from a vegetation geographical point of view and its ecoclimatic counterparts elsewhere. Acta bot. fenn. 145: 1–64.

WETMORE, C.M., 1980: A new species of *Nephroma* from North America. Bryologist 83: 243–247.

WHITE, F. Joy; JAMES, P.W., 1988: Studies on the genus *Nephroma* II. The southern temperate species. Lichenologist 20, 2: 103–166.