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NOTES ON THE DISTRIBUTIONAL ECOLOGY OF THE CLADONIACEAE (LICHENIZED ASCOMYCETES) IN TEMPERATE AND BOREAL WESTERN NORTH AMERICA

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ABSTRACT. Based on the western North American distributions of 71 taxa and chemotypes of *Cladina* and *Cladonia* occurring at temperate and boreal latitudes, the Coast Mountains of British Columbia are shown to form a major phytogeographic barrier, dividing 21 oceanic taxa to the west from 24 continental taxa to the east. Maximum floristic diversity in these genera occurs between 52°N and 56°N, in a region occupied by glacial ice until roughly 10,000 years ago. Following deglaciation, many Cladoniaceae must have colonized this region from south of the Cordilleran Icesheet, presumably deriving from regions that no longer support them. South of 52°N, modern-day rates of decline average between three and five taxa per degree of latitude, and appear to be correlated with a southward trend from summer-moist climatic conditions to summer-dry. By contrast, the present southern limits of *Cladina stellaris*, *Cladonia macroceras* and *C. stricta* are believed to reflect historical, as opposed to strictly ecological, factors. Such species may still be extending their ranges southward.

INTRODUCTION

Phytogeographic studies in lichenology, as in other disciplines, are dependent both on sound taxonomic studies and on detailed distribution maps. Among the macrolichens of temperate and boreal western North America, few genera have been more resistant to taxonomic elucidation, and hence to accurate mapping, than *Cladisa* and *Cladosia*. Until very recently, these genera have represented one of this region's least understood macrolichen assemblages.

With the exception of Ahti (1961), the Cladoniaceae of western North America have been subjected to critical examination only within the past two decades. Since the mid 1970s, various authors have described as new to science 19 Cladoniaceae occurring in this region (Thomson 1976, Ahti 1978, 1980, Tønsberg & Ahti 1980, Ahti & Hyvönen 1985, Hammer 1989, 1991, 1993, Stenroos 1989, Hammer & Ahti 1990, Brodo & Ahti 1996). Though a majority of these taxa are endemic to western North America (Hammer 1995), at least two are circumpolar, and a few are known to occur also in western Europe.

Apparently the earliest dot maps to appear for the Cladoniaceae of western North America are those of Imshaug (1957), who mapped 6 alpine species in localities southward to New Mexico and northward to Banff, Alberta. During the 1970s, Bird & Marsh (1972) published maps for four species occurring in southwestern Alberta, while Anderegg (1977) mapped the ranges of eight species in Idaho. Thomson (1984) later published comprehen-

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sive maps for 63 species extending to arctic regions. More recently, Geiser et al. (1994) mapped the distributions of 58 taxa in coastal southeast Alaska, while Hammer (1995) produced maps for 57 Cladoniae in the American Pacific Northwest, south to central California, and east to western Montana. The following year, Brodo & Ahti (1996) published 28 maps detailing the distributions of the Cladoniaceae of the Queen Charlotte Islands, while Goward, Ahti & Brodo (in prep.) prepared maps for 84 taxa (including eight chemotypes) in British Columbia as a whole.

Notwithstanding these advances, considerable work remains to be done before it will be possible to fully document the western distributions of *Cladina* and *Cladonia*. Inventories and maps are still needed, for example, for southern California, Arizona, Mexico, New Mexico, Nevada, eastern Oregon, southern Idaho, and coastal Alaska (excluding southeast Alaska). What is more, species concepts adopted in many of the earlier maps are now badly out-of-date, and are not easily reinterpreted against modern concepts. Nevertheless, sufficient mapping has now been performed to allow at least a rough outline of the distributional ecology of a majority of the species, especially at mid temperate through boreal latitudes.

Objectives and Methods

The purpose of this paper is to offer a brief analysis of the distributional ecology of *Cladina* and *Cladonia* in North America west of the Rocky Mountains, with special emphasis on those species occurring in British Columbia. Present distributional patterns will also be correlated with presumed patterns of post-Pleistocene recolonization. Our analysis is drawn primarily from the maps and text of Goward, Ahti & Brodo (in prep.), and secondarily from those of Hammer (1995), Geiser et al. (1994) and Thomson (1984). We also draw heavily on field experience in different portions of British Columbia.

The British Columbia maps have been assembled on the basis of approximately 8200 specimens housed at CANL, H and UBC. Even so, the following rare or uncommon species are still inadequately mapped, and have thus generally been omitted from discussion: *Cladonia coccifera*. *C. grayi*, *C. homosekikaica*, *C. imbricarica*, *C. luteoalba*, *C. parasitica*, *C. subfurcata* and an undescribed taxon related to *C. fimbriata*. In a similar vein, certain taxonomically difficult species groups have had to be treated collectively, as follows: *C. cariosa* s. lat. (including *C. symphycarpia*); *C. coniocraea* s. lat. (including *C. ochrochlora*); and *C. cervicornis* s. lat. (including *C. cervicornis* subsp. *cervicornis* and *C. cervicornis* subsp. *verticillata*). Likewise, *C. dahliana* has been treated as a chemotype of *C. symphycarpia*, and *C. poroscypha* has been placed under *C. crispata* var. *cetrariiformis*. By contrast, an undescribed taxon related to *Cladonia phyllophora*, is recognized as *C. phyllophora* s. lat.. This taxon may be recognized by its pale-spotted, narrow, scarcely flaring podetia.

In total, our analysis incorporates 71 taxa, consisting of seven Cladinae, and 64 Cladoniae. These figures include five pairs of distributionally distinctive chemotypes, i.e., *C. bellidiflora* I (=squamatic) and *C. bellidiflora* II (=thamnolic); *C. crispata* I (=squamatic) and *C. crispata* II (=thamnolic, i.e. "*C. artuata*"); *C. macilenta* I (=thamnolic) and *C. macilenta* II (=barbatic, i.e. "*C. bacillaris*"); *C. squamosa* I (=squamatic) and *C.*

squamosa II (=thamnolic, i.e., "var. *subsquamosa*"); and *C. umbricola* I, II (=squamatic) and *C. umbricola* III, IV (thamnolic). Goward, Ahti & Brodo (in prep.) recognize 13 additional chemotypes, but as these fail to show distinctive distributions, they are omitted from the present discussion. A few species here denoted as having their main southern limits within the Pacific Northwest in fact extend much farther south elsewhere in North America. *Cladina arbuscula* subsp. *beringiana* and *Cladonia bacilliformis*, for example, both disappear southward of the Canadian border – only to reappear nearly 10 degrees farther south in Colorado (Weber & Wittmann 1992). Other species have recently been detected in the mountains of Mexico (Ahti, unpublished data). Such populations, however, tend to be very localized, and are here classified as outliers of the main, more contiguous populations farther north. Similar outlying populations apparently occur also within the Pacific Northwest itself (see, for example, Hammer 1995), but as these are more closely contiguous with the main distribution area, we have made no attempt to distinguish them.

RESULTS AND DISCUSSION

Longitudinal Patterns

British Columbia comprises a succession of roughly parallel mountain ranges running southeast and northwest. These ranges are aligned perpendicular to the prevailing westerly flow of moist air from the Pacific Ocean, and thus create a steep climatic gradient from west to east (Demarchi et al. 1990). In general, regions lying adjacent to the outer coast experience a hypermaritime climate, with heavy precipitation, high humidity and comparatively small seasonal fluctuations in temperature. To the east, climatic conditions gradually and consistently become more continental, with more distinct fluctuations in seasonal temperature. Precipitation, by contrast, does not decrease uniformly with increasing thermal continentality. On the leeward sides of the mountain ranges, conditions tend to be dry, especially in the southern half of the province, where an "interior drybelt" may be recognized. The windward side of the same mountains are much wetter, and may be described as the "interior wetbelt." In the northeast corner of the province, a true boreal climate prevails, with moderate precipitation and wide seasonal fluctuations in temperature. See Tuhkanen (1984), Meidinger & Pojar (1991) and Goward & Ahti (1992) for further details.

At boreal and temperate latitudes in western North America, a very pronounced transition occurs from oceanic to rather continental conditions within 150 km to 200 km of the ocean, i.e., at the crest of the coast ranges. Hammer (1995) has already drawn attention to the "major biogeographical boundary" formed in the American Northwest by the Cascade Mountains. In British Columbia, the Coast Mountains represent a no less striking boundary, dividing the ranges of several coastal taxa from those of various inland taxa. Similar observations have been made for other cryptogamic groups, including bryophytes (Schofield 1984) and fleshy fungi (Redhead 1989). To Hammer's list of taxa restricted to coastal regions (i.e., *Cladonia crispata* II [as *C. artuata*], *C. furcata*, *C. gracilis* subsp. *vulnerata* and *C. macilenta* I), the following species may be added: *Cladina ciliata*, *C. portentosa* subsp. *pacifica*, *C. asahinae*, *C. bellidiflora* II, *C. cornuta* subsp. *groenlandica*, *C. kanewskii*, *C. novochlorophaea*, *C. schofieldii*, *C. squamosa* II, *C. transcendens*, and *C. wainioi*. By contrast, the following Cladoniae occur primarily in coastal regions, but reappear secondarily in highly humid inland regions: *Cladonia crispata* var. *cetrariiformis*, *C. ecmocyna* subsp. *occidentalis*, *C. prolifica*, *C. scabriuscula*, *C. singularis*, and *C. umbricola* III & IV. All of these taxa, not surprisingly, are characteristic of very humid climates, and virtually all are restricted to oceanic regions throughout their ranges. Most occur only at lower and middle elevations, and are absent in the alpine.

The following species are restricted more or less entirely to regions east of the coast ranges: *Cladonia amaurocraea*, *C. bacilliformis*, *C. botrytes*, *C. cenotea*, *C. cyanipes*, *C. decorticata*, *C. deformis*, *C. gracilis* subsp. *elongata*, *C. macroceras*, *C. macrophylla*, *C. multiformis*, *C. phyllophora* s. str., *C. pocillum* and *C. stricta*. To this list may be added several additional taxa present primarily in inland regions, but having at least a few outlying coastal populations, often at alpine elevations: *Cladina arbuscula* subsp. *mitis*, *Cladonia acuminata*, *C. borealis*, *C. cariosa* s. lat., *C. cornuta* subsp. *cornuta*, *C. digitata*, *C. macrophyllodes*, *C. pleurota*, *C. subulata*, and *C. sulphurina*. With the exception of *Cladonia multiformis*, which is restricted to North America, all of these taxa are essentially circumpolar in distribution, and less than half occur at alpine elevations.

The following species appear in British Columbia to be indifferent to continentality, and are present in coastal and highly continental inland regions alike: *Cladina arbuscula* subsp. *beringiana*, *C. rangiferina*, *Cladonia carneola*, *C. cervicornis* s. lat., *C. crispata* I, *C. ecmocyna* subsp. *intermedia*, *C. fimbriata*, *C. macilenta* II, *C. pyxidata*, and *C. uncialis*. All of these species (but not the subspecies!) have circumpolar distributions, and most occur upward into the alpine.

In sharp contrast to the above patterns, no Cladoniaceae at all are restricted in British Columbia to boreal regions east of the Rocky Mountains. However, much more work is needed on this component of the flora.

From the data presented in Table 1, six climatic regions may be assessed for floristic diversity based on 71 taxa: hypermaritime, maritime, interior drybelt, interior wetbelt, alpine and boreal. Forty-three of these taxa are common in hypermaritime and maritime regions, though only 34 occur regularly in hypermaritime regions, as compared with 40 in maritime regions. Inland regions, with a total of 52 taxa, are floristically somewhat richer, but vary from 50 taxa in the interior wetbelt to 29 and 30 taxa in the interior drybelt and in boreal regions, respectively. British Columbia's most diverse *Cladonia* flora thus occurs in humid inland regions, whereas the least diverse floras occur in very humid coastal localities, in semi-arid inland localities, and in boreal regions.

Continentality appears to affect distributional patterns also at the level of thallus chemistry. A strong positive correlation seems to exist, for example, between humid oceanic climates and the production of thamnolic acid – as earlier noted by Huovinen & Ahti (1982), for instance. Biosequentially, thamnolic acid represents the most highly oxidized state of the beta-orcinol depside chemistry produced by these lichens. In a perhaps similar vein, Culberson et al. (1977) reported that the northernmost chemotype of the *Ramalina siliquosa* group has the most highly oxidized chemistry, with salazinic acid, whereas the Mediterranean chemotype has the least oxidized chemistry, with 4-0-demethylbarbatic acid.

In British Columbia, the following thamnolic-producing species occur only in coastal regions: *Cladonia bellidiflora* II, *C. crispata* var. *cetrariiformis* II, *C. crispata* var. *crispata* II, *C. macilenta* I, *C. squamosa* II, *C. transcendens* and *C. umbricola* III, IV. Inland chemotypes of these species never produce this substance. East of the coast ranges, only *Cladonia digitata* and *C. parasitica* regularly produce thamnolic acid, though both are again restricted to humid regions. A third inland species, *Cladonia cenotea*, while typically containing squamatic acid, has recently been found to produce a thamnolic acid chemotype in humid portions of southern British Columbia (Goward, Ahti & Brodo, in prep.). Stenroos & Ahti (1990) earlier reported this phenomenon in Tierra del Fuego.

Also showing a rather distinct "ecology" are barbatic acid (a poorly oxidized beta-orcinol compound) and zeorin. Different from thamnolic acid, these substances are especially common in inland Cladoniae. The following species contain one or both of these substances: *C. amaurocraea*, *C. bacilliformis*, *C. botrytes*, *C. carneola*, *C. coccifera*, *C. cyanipes*, *C. deformis*, *C. luteoalba*, *C. macilenta* II. Only *C. borealis* and *C. norvegica*, both with barbatic acid, and *C. pleurota*, with zeorin, occur (secondarily) in coastal regions.

Chemical variability among the Cladoniaceae appears to be greater in oceanic regions than in continental regions. Of 18 species assigned by Goward, Ahti & Brodo (in prep.) to more than one chemotype in British Columbia, all but two (i.e., *Cladonia acuminata* and *C. cenotea*) occur at least in part in coastal regions. Moreover, the thamnolic-containing species listed above tend to produce thamnolic *and* squamatic chemotypes in coastal regions, but only squamatic chemotypes in inland regions. A similar pattern is seen in *Cladina rangiferina*, *Cladonia bellidiflora* and *C. umbricola*, in which atranorin/usnic-containing chemotypes and atranorin/usnic-deficient chemotypes occur in coastal regions, but only atranorin/usnic-containing chemotypes occur in inland regions. The strictly coastal taxa *Cladina ciliata*, *C. portentosa* subsp. *pacifica* and *Cladonia schofieldii* all likewise produce both usnic-containing and usnic-deficient chemotypes – a phenomenon unknown in inland regions, with the exception of *Cladonia cariosa* s. lat.. Such patterns possibly suggest that selective pressures are less stringent in oceanic regions than in inland regions. Even so, further work on the "distributional ecology" of lichen substances is needed before it will be possible to account in detail for the above patterns. See also Brodo (1984, p. 89) for parallel observations.

Elevational Patterns

The elevational data given in Table 1 reveal that a majority of British Columbia's Cladoniaceae are common primarily at lowland elevations. Indeed, 64 of 71 taxa regularly occur at lower elevations (below e.g., 800–1200 m), as compared with 48 taxa at middle elevations, and only 21 taxa at alpine elevations. Moreover, only two of the taxa present in the alpine are actually restricted to this zone, i.e., *Cladonia macroceras* and *C. stricta*. Alpine ecosystems also appear rarely, if ever, to support more than one chemotype of any of the Cladoniaceae. By contrast, chemical diversity among the species is greatest at lowland elevations. From these observations, it can be concluded that the vast majority of Cladoniae present in British Columbia are adapted to moderate conditions characteristic of temperate and low boreal climates. This point will be returned to in the next section.

Goward & Ahti (1992) have already briefly discussed the relation of *Cladina* and

Cladonia to winter snow cover, pointing out that even the most snow-tolerant of these lichens, e.g., *Cladonia bellidifera*, *C. carneola* and *C. ecmocyna* subsp. *intermedia*, may be classified as only moderately chionophilic. A majority of the species are probably appropriately classified as chionophobic, especially those species restricted to lowland coastal regions. In any case, there can be little doubt that many species are excluded from middle and upper elevations by the presence of prolonged winter snow packs.

Latitudinal Patterns

At the latitude of central California, a rather pronounced Mediterranean climate prevails, in which precipitation is confined largely to the winter half-year, with comparatively little moisture being received during the summer months (Trewartha 1968). Northward in the American Pacific Northwest, this pattern gradually weakens, but is still discernable in northern Washington (Highsmith & Kimerling 1979) and adjacent British Columbia (Demarchi et al. 1991). North of 52°N, however, late spring and early summer generally represent the wettest season of the year, especially in humid inland regions. Summer moisture deficits are accordingly much less severe here than at more southerly latitudes (Demarchi et al. 1991). In coastal regions, only the southeastern tip of Vancouver Island and the adjacent mainland experience significant summer moisture deficits (Demarchi et al. 1991); other portions of the coast receive rain or fog throughout the year (Meidinger & Pojar 1992).

Figure 1 summarizes the northern and southern limits of 63 and 62 Cladoniaceae, respectively, and is based on data presented in Table 1. For ease of presentation, these limits are grouped at intervals of two degrees of latitude. Figure 1 reveals striking differences between the patterning of Cladoniaceae at their southern limits and northern limits. In general, species numbers decline much more uniformly and gradually to the north (with a loss of 24 taxa over 20 degrees of latitude) than to the south (with a loss of 40 taxa over 20 degrees of latitude). Within British Columbia, only one species, *Cladonia stricta*, attains its southern limits north of 54°N, whereas south of about 52°N, a decline of approximately three to five taxa per degree of latitude occurs. South of 46°N, this decline appears to decelerate somewhat, though this may simply reflect a lack of data for southern Idaho and Nevada. In any case, only 26 of the 62 taxa in question extend southward into California. This trend toward decreasing diversity is only weakly offset by the addition of species not present in British Columbia. Hammer (1995), for example, lists five such species: *Cladonia andereggii*, *C. extracorticata*, *C. humilis* (including *C. conista*), *C. pulvinella* and *C. thiersii*. Two of these, however, are known only from single localities.

Figure 2 summarizes actual numbers of Cladoniaceae recorded at various latitudinal intervals between 36°N and 60°N. From these observations, it is evident that western North America's most diverse *Cladina* and *Cladonia* floras, with between 76 and 78 taxa, are situated in British Columbia at between 52°N and 56°N. No fewer than 50 taxa are known to occur, for example, in a 600,000 ha area centring on Wells Gray Provincial Park, at 52°N (Goward & Ahti 1992, Goward, unpublished data). Similarly, Brodo and Ahti (1996) report 44 taxa from the Queen Charlotte Islands, between 52°N and 54°N.

That western North America's richest cladoniiform flora occupies a region largely ice-covered until 10,000 to 13,000 years ago (Pielou 1991) is perhaps unexpected. However,

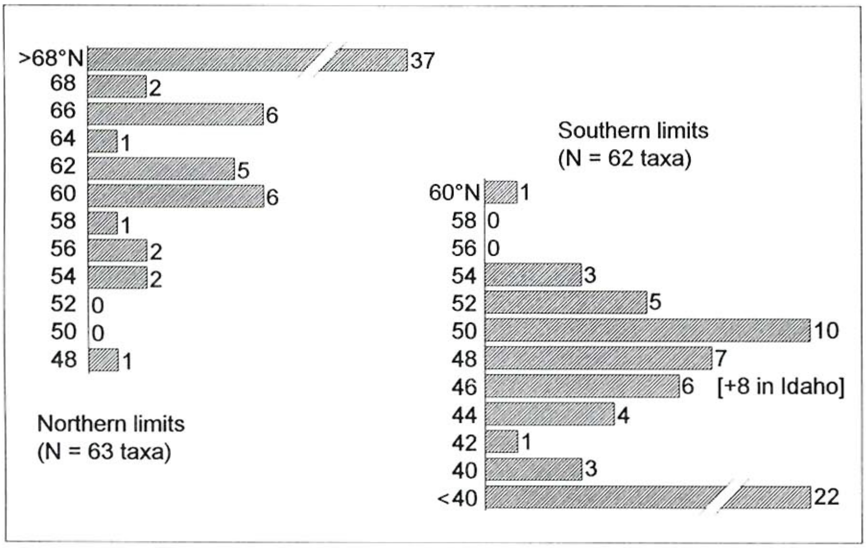

Fig. 1. Northern and southern limits of selected Cladoniaceae in temperate, boreal and arctic Western North America. Based on Goward, Ahti & Brodo (in prep.), Geiser et al. (1994), Hammer (1995) and Thomson (1984).

even at the height of the Pleistocene glaciation, 18,000 years ago, northwestern North America was by no means entirely covered by the Cordilleran Icesheet (Prest 1973). At its northern limit, the icesheet extended into southern Alaska and the adjacent Yukon, north to approximately 63°N; most of central and northern Alaska and the western Yukon therefore escaped glaciation. In the south, the ice reached only as far as northern Washington and Idaho, at roughly 47°N.

In coastal regions, moreover, numerous glacial refugia are now believed to have existed along the western shores of Vancouver Island and the Queen Charlotte Islands (Warner et al. 1982). Some authors, indeed, have suggested that some of these refugia may have supported forest ecosystems (composed e.g., of *Pinus contorta*) throughout the Pleistocene (Hebda & Whitlock 1996; see also Foster 1984). Such could have provided suitable conditions for at least some oceanic Cladinae and Cladoniae, especially those taxa currently extending into the alpine, e.g., *Cladina rangiferina*, *Cladonia bellidiflora* I, *C. crispata* var. *crispata* I, *C. gracilis* subsp. *vulnerata*, *C. kanewskii*, *C. metacorallifera*, *C. pyxidata*, and *C. uncialis*. The North Pacific endemic *Cladonia schofieldii* might also have persisted in this region. By contrast, it seems unlikely that oceanic taxa currently restricted to lowland elevations could have survived the Pleistocene Epoch in coastal British Columbia. Following deglaciation, such taxa probably entered this region from areas beyond the immediate influence of the Cordilleran Icesheet. Some species, for example, may have colonized British Columbia as a result of long-distance dispersal from Eurasia. Elsewhere in the world, long-distance dispersal has been shown to profoundly influence lichen phytogeography. The macrolichen flora of the geologically young island of Tristan da Cunha, for exam-

Table 1. (Continued)

	hyper-maritime	maritime	"wetbelt"	"drybelt"	boreal	low	mid	alpine	N to	S to
macroceras			●					●	66?	50
macrophylla			●				●	●	70	51
macrophyllodes		○	●	●		●	●	●	65	37
merochlorophaea		○	●	●		●	●		70	CA
metacorallifera	●	●	●			●	●	●	70	49
multiformis		○	●	●	●	●	●		70	ID
norvegica	●	○	●	○		●	●		58	48
novochlorophaea	●						●		AK	47
phyllophora s.s.		○	●	●	●	●	●		?	45
phyllophora s.l.		●	●	○		●	●	●	70	?
pleurota		●	●	●	●	●	●	●	?	ID
pocillum			●	●	●	●	●	●	83	ID
prolifica	●	●	○			●			54	38
pyxidata	●	●	●	●	●	●	●	●	83	ID
rei		○	●			●			61?	49
scabriuscula	●	●				●			70	ME
schofieldii	●					●	●	○?	60	53
singularis	○	●					●		55	46
squamosa I	●	●	●			●	●	○	70	39
squamosa II	●	●				●			55	37
stricta			●					●	75	59
subulata		○	●	●	●	●	●		70	37
sulphurina		○	●	●	●	○	●		70	ID
symphycarpia s.l.	○	○	●	●	●	●	●		70	40
transcendens	●	●				●			61?	CA
umbricola I, II	●	●	●			●	●		?	42
umbricola III, IV	●	●				●			?	CA?
uncialis	●	●	●	●	●	●	●	●	75	46
verruculosa	○	●	●	○		●			59	37
wainioi	●	●	●			●	●	○	66?	53

ple, shares striking floristic similarities with the lichens of southern South America, approximately 4000 km distant (Jørgensen 1977). The only plausible explanation is that lichen propagules have been transported across the vast expanse of ocean by strong west winds (the "roaring forties"). The possibility should not be overlooked that the "westerlies" may perform a similar function in western North America. Because, however, distances across the North Pacific are much greater, and wind force much weaker (Trewartha 1968), long-distance colonization from Eurasia is probably a rare event. For a few coastal species, however, colonization is expected to have proceeded stepwise along the Aleutian Archipelago (see also Schofield 1980).

A few Cladoniae have clearly entered British Columbia from north of the Cordilleran Icesheet (see below), whereas others may have persisted in nunataks rising above the ice. Conditions here, however, would have been very severe, and would have presumably favoured only those taxa well adapted to arctic-alpine conditions. Table 1 lists 21 such species. Many of these, however, can be expected to have persisted also in appropriate

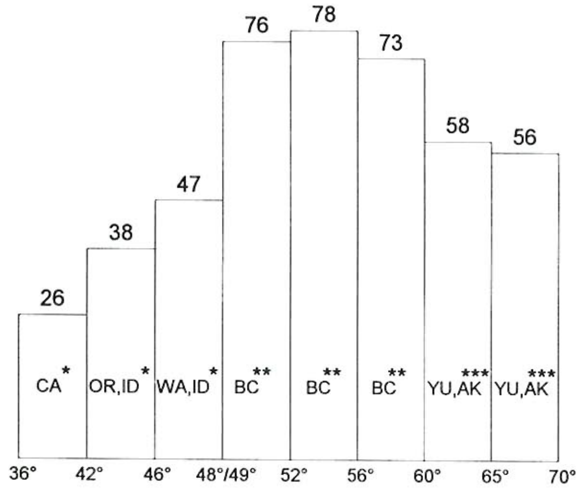

Fig. 2. Diversity among the Cladoniaceae of temperate, boreal and arctic western North America. *=Based on Hammer (1995); **=based on Goward, Ahti & Brodo (in prep.) and Geiser et al. (1994); ***=based on Thomson (1984); numbers approximate. Abbreviations: AK=Alaska, BC=British Columbia, CA=California, ID=Idaho, OR=Oregon, WA=Washington, YU=Yukon.

habitats southward of the icesheet. It thus seems likely that many of British Columbia's Cladoniaceae, especially those taxa currently restricted to lower elevations, arrived in the province from south of the Cordilleran Icesheet. If this is so, then the American Northwest must have once supported a richer cladoniiform flora than at present. The ranges of *Cladina ciliata*, *Cladonia acuminata*, *C. bacilliformis*, *C. botrytes*, *C. cornuta* var. *groenlandica*, *C. cyanipes*, *C. decorticata*, and *C. rei*, which currently have their southern limits at or near the Canadian border, probably formerly extended southward into what is now Washington, Idaho and Oregon. Many other taxa were doubtless once more broadly distributed in this region. This hypothesis appears to be supported by the existence of several outlying populations far south of the main ranges. Such populations are probably relictual, deriving from a time when *Cladina* and *Cladonia* were more widespread at temperate latitudes than at present. The outliers, of course, might equally be interpreted as resulting from recent southward colonization, though in this case it would be difficult to explain why these species should only now be colonizing regions not affected by glacial ice.

Much of this post-Pleistocene loss in species diversity is probably attributable to increasing summer moisture deficits since deglaciation. As has already been observed, humid inland portions of British Columbia support a much richer *Cladonia* flora (N=50) than do adjacent semi-arid regions (N=36). Indeed, the driest grasslands of southern inland British Columbia support only approximately a half dozen species, e.g., *C. cariosa*, *C. cervicornis* s. lat., *C. fimbriata*, *C. pocillum* and *C. pyxidata*.

This line of reasoning assumes that most western Cladoniaceae have attained their full ecological distributions. Even so, the distributions of at least some species still appear to be expanding. In inland regions, for example, *Cladina stellaris* and *Cladonia stricta* attain their southern limits north of 54°N., in portions of the province in which no obvious latitudinal climatic gradients occur. That both of these species are restricted primarily to alpine elevations (at least in the southern portions of their ranges) has presumably demanded an ability to "island-hop" from mountain to mountain. In the absence of effective vegetative diaspores, this must be a slow process in these species. A similar argument may be applied to *Cladonia macroceras*: another alpine species that reaches its southern limits just north of the British Columbia–U.S. border. These lichens may thus still be extending their ranges southward from refugia occupied during the Pleistocene.

CONCLUSIONS

Six broad conclusions may be drawn from the foregoing analysis:

1) Western North America's richest assemblage of *Cladina* and *Cladonia*, with between 76 and 78 taxa, occurs in British Columbia between 52°N and 56°N, in a region covered by glacial ice until roughly 13,000 to 10,000 years ago.

2) South of 52°N, species diversity declines dramatically, with a loss of between three and five taxa per degree of latitude.

3) With the exception of those species able to persist in nunataks at alpine elevations, or under arctic conditions to the north of the ice, or again in small, periglacial refugia along the west coast, most of the Cladoniaceae of British Columbia must have passed the Pleistocene south of the Cordilleran Icesheet.

4) Floristic and chemical diversity in the Cladoniaceae are greater in humid regions than in arid regions, and at lower, forested elevations than at upper, alpine elevations. Many species may therefore be assumed to require habitats subject to only relatively brief periods of desiccation.

5) Given that many Cladoniaceae probably passed the Pleistocene south of the Cordilleran Ice Sheet, the absence of numerous species from all or most of Washington, Oregon, and California must reflect climatic changes in this region since deglaciation. An increase in summer moisture deficits is assumed to be largely responsible for this trend.

6) Though a majority of these lichens are probably now at distributional equilibrium, a few species appear to be still extending their ranges southward from refugia north of the Cordilleran Icesheet.

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