THE BIOGEOGRAPHY AND ECOLOGY OF SPECIES IN THE LICHEN GENUS CLADONIA IN THE COLUMBIA RIVER BASIN

Submitted to:
Eastside Ecosystem Management Project
10 January 1995

Addenda submitted 25 January 1995

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TABLE OF CONTENTS

I. INTRODUCTION

This study enumerates the species of the lichen genus Cladonia in sites east of the Cascade Mountains, primarily in the Columbia River Basin. The study summarizes the biogeography and ecology of wood-inhabiting and terricolous Cladonia species throughout the region. The biogeography of the region is of great interest. There are a number of rare, relictual, and endemic species, which may be indicators of the geological and climatic past of the region. The species are discussed in terms of community associations in the region, with an added focus upon allied lichen and plant species. From an ecological standpoint, the species of Cladonia in the region are diverse. They are found in a variety of microenvironments and many of the species occupy distinct habitat niches. This study outlines the ecological status of the species, including moisture, light, and substratum requirements. Of particular interest are species that grow on ecorticate or decaying wood, usually in old-growth or secondary-growth forests. Many of the species bind soil and other substrata such as rotting wood and duff, and these species and their modes of substrate binding are enumerated. Certain potentially important roles of the species are illustrated, primarily their contributions as soil and substratum binders, and their role as potential wood decomposers. Finally, the study offers recommendations for the preservation of lichen communities in the region, with a focus on potentially endangered species and species associations.

II. MATERIALS AND METHODS

Approximately 8000 specimens were studied for this project, including specimens obtained through extensive field collecting over several seasons (**Table 4**). Specimens from approximately 20 herbaria were also examined and annotated. Several of the herbaria contain voucher studies from this study. They are cited in this report and include ASU (Arizona State University), DUKE (Duke University), FH (Farlow Herbarium), H (University of Helsinki), ID (University of Idaho), OSU (Oregon State University), SFSU (San Francisco State University), SRP (Boise State University), UBC (University of British Columbia), US (Smithsonian Institution), WIS (University of Wisconsin), and WTU (University of Washington). Specimens were studied under various magnifications, and notes were taken on most specimens. Most of the specimens were assayed for secondary substances using thin layer chromatography (TLC). Statistical analyses of similarity were performed using the Jaccard Index value for selected sites and species. The Jaccard Index is an association coefficient, which is based on the presence and absence of species within a sampling unit. It is summarized by:

$$\pi = \frac{a}{a + b + c}$$

For each pair of sites, a = the number of species at both sites:
b = the number of species at site 1, but not site 2: and c = the number of species at site 2, but not site 1. In order to measure the association of pairs of species, the same equation is used, where a =

the number of sites where both species occur; b = the number of sites occupied by species 1, but not species 2; and c = the number of sites occupied by species 2, but not species 1.

III. GEOGRAPHICAL DISTRIBUTION OF THE SPECIES

The Cladonia flora of the northwestern United States can be divided into two distinct geographical elements; 1) an oceanic element that reaches from southern California northward to the Canadian border, 2) an inland element east of the Cascade mountains, extending to the Rockies. Species from both of these are represented in a rich flora in northwestern Washington state which extends southward to extreme northwestern California. It is the second of these floristic elements that is the focus of this study. The Cascade Mountains define the geographical distributions of many of the species, and can be considered a major barrier between the lichen floras of the western United States. Sixteen of the species in this study are found only east of the Cascade Mountains in the western United States **(Table 1).** Overall in the western United States, north-south differences are less important in determining geographical ranges of the species than are differences of east to west. In a cluster analysis based on Jaccard Index values **(Figure 1)** the importance of the Cascade Mountains as a distributional barrier is illustrated. In **Figure 1**A, counties from east of the Cascades (e.g. Flathead, Bonner and Ravalli) cluster together on the basis of their Cladonia flora. In **Figure** 1B, species from east of the Cascade Mountains (C. cenotea and C. cornuta, and to a lesser extent C. macrophyAodes and C. umbricola) cluster together, indicating their frequent occurrence together. closer look at selected counties within the region **(Figure 2)** shows that geographically contiguous counties from close physiographic regions cluster together on the basis of similar Cladonia floras.

The assemblage of Cladonia species within the region from the Cascades to the Rockies is rich and varied. All of the major infrageneric groups within the genus Cladonia are present. The Cascades block Pacific moisture from eastern Oregon and Washington, however there are broad gaps in the mountains, particularly the Columbia Gorge, through which moisture is carried farther inland. Generally, the number of species increases with increasing rainfall, but other factors, such as substratum and the surrounding vegetation are also important influences. As elevation increases, rainfall and species diversity increase, and elevation appears to be a greater influence on species distributions than latitude. For example, the Wallowa Mountains in northeastern Oregon support a richer flora at approximately 1500-2000 meters than the upland areas (ca. 1000 meters) of Asotin Co., Washington, 120 km to the north. Species abundance and variety decrease as treeline is approached, and the flora is extremely depauperate where the major precipitation is in the form of snow (see discussion below). Areas of moderately high elevation, such as the Priest Lake area of the Idaho panhandle (Bonner and Boundary Counties), and adjoining areas of Washington (Pend Oreille County) and Montana (Lincoln and Flathead Counties), support a high species diversity. They include species such as C. cenotea, C. coccifera, C. dahliana, C. multiformis, C. phyllophora, and C. rei that are circumboreal and present in eastern North America, but which are absent from the rest of the western United States. Cladonia macilenta s. str., which resembles specimens from eastern North America is also found at some of these sites.

Species are considered as rare in this report if they are found in approximately 10% or fewer of the counties in the region. Only seven of the 16 indicator taxa **(Table 1)** are rare in the region. **The** other 12 rare species **(Table 2)** are found on both sides of the Cascades. Of these, five are quite common west of the Cascades. They were termed "oceanic log lichens by McCune (1994). Of the additional three rare species reported by McCune, C. botrytes is unknown from west of the Cascades. Cladonia firma, which is morphologically and chemically similar to C. macrophyllodes (common in the region of study), is restricted to the coast of south-central California, and should be deleted from the list of species in the region. Cladonia norvegica was unconfirmed by me and remains doubtful; specimens that I examined from west of the Cascades which were labeled as C. norvegica were indistinguishable from C. bacillaris.

Species richness (number of species) as well as rare species, are centered in certain physiographic regions **(Table 3).** Preservation efforts should be focused on those regions. 18 of the counties hold 100% of the rare Cladonia species in the region **(Table 3).** All of the rare species occur in 10 of the 48 physiographic regions; Bitterroot, Clearwater, East Slope Cascades (Oregon and Washington), Flathead-Blackfoot, Kootenai, Northeast Oregon Mountains, Northeast Washington Mountains, Salmon, and Selkirk. The Selkirk and Washington East Slope regions have the most rare species but there is an important difference between the two: the Selkirk region has more rare species that are not found west of the Cascades. Two regions in this study (Salmon and NE Oregon Mountains), have only one rare species each.

IV. ECOLOGY OF THE SPECIES

Precipitation and Species Distributions

All factors that include potential evapotranspiration and exposure to sunlight play a role in Cladonia habitats, since the lichen thallus depends upon the photosynthetic algal biont for its source. Algal cells produce carbohydrates and release them to the fungal biont when the thallus is moistened, and there are specific ranges of exposure and moisture within which the species grow. While the species are strongly influenced by moisture availability, the region has an extended dry period during half of the year or longer, and thus the distribution of species reflects subtle changes in moisture availability in microhabitats. This is apparent even for weedy species like C. fimbriata, C. merochlorophaea, and C. verruculosa that are locally common along roadbanks, where the lichen cover is more abundant on north-facing surfaces. Moisture requirements **(Tables 5, 8)** differ for various species and therefore influence the distribution of species. Rare species have a higher moisture requirement that the species overall (**Figure 3**; $p \leq 0.0001$). Generally, species of Cladonia occur in frequently dampened habitats that experience partial sunshine. A few species, viz. C. andereggii, C. ochrochlora, and C. transcendens, and to a lesser extent C. cenotea and C. umbricola, grow in deep shade **(Tables 6, 8)**. The rare species in the region require a darker habitat that the species overall (**Figure 3**; $p \leq 0.0001$).

The Influence of Edaphic and Biotic Conditions on Species Distributions

Soil conditions play a role both in species composition and richness. For example, lava outcrops that occur where the precipitation is low (ca 1000 mm), such as in Benewah County, Idaho, support unusual species, such as C. imbricarica. The acidic, raised bog at Hanna Flats, Bonner County, Idaho, which receives less than 1000 mm of rainfall is also remarkable. The species of Cladonia growing there are mostly boreal, and the diversity of species is noteworthy in view of the relatively low amount of precipitation. Calcareous soils are not well represented in the region, but one in Latah County, Idaho, supports the only known population of C. anderegii. Few species of Cladonia have been collected on serpentine soils.

Most of the species of Cladonia require surface organic matter as a substratum **(Table 7)**, and this is linked both to rainfall and edaphic conditions **(Table 8)**. Rare species in the region require a substratum higher in organic matter than do the species overall (**Figure 3**; $p \leq 0.0001$). Moisture, light, and substratum composition are summarized in an index of equability (**Table 8**). The equability index for the rare species in the region is compared with the species overall in **Figure 4.** Rare species have a significantly higher equability index value than the species overall ($p \leq 0.0001$). Hanna Flats **(Table 4**, site 12) is an example of a locality where organic matter strongly influences edaphic conditions, particularly water retention, at the interface between the thallus and its growing surface. Water retention may play an important role in the non-lichenized stage of the life cycle, when the lichen fungal biont establishes in an organic substratum such as wood **(Figure 5).** For many species, organic matter such as decaying wood also anchors the mature thallus to the substratum, and may provide nutrients for the prothallus **(Figure 5)**.

Phanerogamic vegetation also influences species distributions. Coniferous forest floors, even if they are very damp, support few species of Cladonia, because they are permanently shady. Cladonia species thrive in an environment of alternating sun and shade, and forest margins are particularly good habitats. Duff from the fallen leaves of Arctostaphylos and other taxa supports Cladonia species where the underlying soil is poor in organic matter, such as over sand dunes or on hardpan soils. Conifers increase moisture availability by providing shade, and conifer needles increase the acidity of the substratum, supporting species of Cladonia in otherwise marginal habitats. In the region, Cladonia species are most common in association with western red cedar and western hemlock. Cladonia species may also be found near stands of Douglas fir. In general, the pine forests east of the Cascade Mountains are too dry to support most of the species, but some of the species with drier habitat requirements may be found there. Deciduous forests, which are uncommon in the region, support few Cladonia species.

Lichens are poikilohydric (blotter-like) organisms with no roots or vascular system. They thus depend on relatively high ambient moisture levels to survive. These conditions can be predicted at a glance (for example, from a moving vehicle!) by the presence of certain indicator taxa such as the pendulous tree-inhabiting lichens Alectoria and Bryoria. Cladonia species require periodic wetting and drying, so that they are not to be expected at the wettest sites, such as near permanently standing water. Rather, they benefit from fog drip or substrata such as rotting wood, which retain moisture for a period after rainy conditions.

Because they require light for photosynthesis, most Cladonia lichens are not to be expected in the deepest shade nor in snowbank areas. Areas that receive most of their moisture as snow usually support a very limited Cladonia flora. Cladonia species do not compete successfully for light with thick vegetation such as grass, nor are they to be expected in alpine meadows. Rather, they thrive among mosses or in situations where mosses might be expected to occur. Most species thrive at trailsides (and to a lesser extent at roadsides), where there is alternating light and shade, and where moisture conditions such as seepage are optimal. Cladonia species do not establish on the banks of logging roads. These roads are usually very poor in organic materials. Further, they are muddy and prone to erosion in heavy rainfall, and cannot support even weedy species such as C. verruculosa. In situations where phanerogamic vegetation (for example ferns) dominates trailside sites, Cladonia species are infrequent. The least productive habitats are exposed hillsides and mountain sides that have been clearcut. Lichen establishment is restricted by severe soil erosion, a dry season unameliorated by shade, the lack of fog-drip, and the lack of soil and organic matter. Abiotic factors such as evapotranspiration are influenced by the lack of forest cover and microenvironmental conditions are also altered. This results in the absence of Cladonia species in logged areas.

Cladonia Species as Part of a Community

Lichens, and Cladonia species in particular, grow within a living matrix of interrelated species, a community. As part of a community they fulfill a variety of roles, particularly as substratum binders **(Table 9).** The various physiognomic groups (see **Table 10)** generally bind the substratum in distinct ways. **Table 9** summarizes four categories of substratum-binding mechanisms. All Cladonias protect the soil surface by the presence of their **aboveground thalli. In** many species, the leaflike primary **squamules (see Table 10)** persist. These protect the ground surface from rain and wind erosion, and from blowing particles of sand. Cladonia species grow vertically from an apical meristem, and as the thalli grow and ramify, lower parts slowly die. Particles of soil and organic matter settle among the dying parts of the thallus. The result is a mat of old thalli and organic matter which may reach a depth of several centimeters. Old lichen thalli are brittle when dry, but they continue to absorb and retain moisture when wet, much like living thalli. **Buried thallus parts** are an important part of the surface biomass. They bind the soil surface, provide air pockets and cavities for microorganisms, and they retain moisture. Finally, many species (particularly but not exclusively red-fruited Cladonia species), develop extensive and long-lasting **hyphal networks** in the substratum. These networks ramify throughout the substratum and the mycelium is often indistinguishable from the substratum. In addition to their mechanical binding action, the hyphae exude a gelatinous substance that maximizes their surface contact with the substratum. This substance provides strong binding properties at the cellular and molecular level. It adds to the moisture retention capabilities of the species and my be involved in extracellular digestion, which is a hallmark characteristic of fungi. Thus, Cladonia species are an important factor in the overall health of ecosystems, particularly in sites that are adjacent to areas which have been compromised by logging or other human disturbance factors.

The habitat requirements of Cladonia species are strongly linked to the habitat requirements of their neighbors. This shared set of requirements can be termed an association. By analyzing community associations we gain a fuller understanding of the collective roles of the individuals in the community. More importantly, association data **(Table 11)** provides a practical basis for field identification. For example, pendulous tree lichens such as Alectoria and Bryoria spp. are conspicuous and readily identified at a distance. They are good indicators for Cladonia species and should be used to identify sites for preservation. Another good indicator is the varied thrush, a bird species that shares the range of many Cladonia species in moist forests. The distinct call of the varied thrush is easy to recognize. It should be used as an indicator for Cladonia species, particularly those species with high equability indices (see **Table 8**). Biotic associations are a powerful tool for on-site conservation management. Consideration of these associations takes into account the broad ecological requirements of the taxa being studied, as well as their particular habitat needs.

TABLE 1. LIST OF THE CLADONIA SPECIES IN THE INTERIOR NORTHWEST

Species in **bold type are** found only east of the Cascade Mountains in the western United States. All of the **bold type** species can be considered indicator species for the region.

1. **Cladonia andereggii** Hammer
2. Cladonia asahinae J.W. Thomson
3. Cladonia bacillaris Genth
4. Cladonia bellidiflora (Ach.) Schaerer
5. Cladonia borealis Stenroos
6. Cladonia cariosa (Ach.) Sprengel
7. Cladonia carneola (Fries) Fries
8. **Cladonia cenotea** (Ach.) Schaerer
9. Cladonia cervicornis (Ach.) Flotow subsp. cervicornis
10. Cladonia cervicornis subsp. verticillata (Hoffmann) Ahti
11. Cladonia chlorophaea (Flörke ex Sommerfelt) Sprengel
12. **Cladonia coccifera** (L.) Willdenow
13. Cladonia coniocraea (Flörke) Sprengel
14. Cladonia conista A. W. Evans
15. Cladonia cornuta (L.) Hoffmann subsp. cornuta
16. Cladonia cornuta subsp. groenlandica (E. Dahl) Ahti
17. **Cladonia crispata** (Ach.) Flotow
18. **Cladonia dahliana** Kristinsson
19. **Cladonia deformis** (L.) Hoffmann
20. Cladonia digitata (L.) Hoffmann
21. Cladonia dimorpha Hammer
22. **Cladonia ecmocyna** subsp. **intermedia** (C. Robbins) Ahti
23. Cladonia ecmocyna Leighton unnamed subspecies
24. Cladonia fimbriata (L.) Fries
25. Cladonia gracilis subsp. turbinata (Ach.) Ahti

26. **Cladonia imbricarica** Kristinsson

27. **Cladonia luteoalba** Wheldon & A. Wilson

28. Cladonia macilenta Hoffmman

29. Cladonia macrophyllodes Nylander

30. Cladonia merochlorophaea Asahina

31. **Cladonia multiformis G.** K. Merrill

32. Cladonia ochrochlora Flörke

33. **Cladonia phyllophora** Hoffmann

34. Cladonia pleurota (Flörke) Schaerer

35. **Cladonia pocillum** (Ach.) Grognot

36. Cladonia prolifica Ahti & Hammer

37. **Cladonia pyxidata** (L.) Hoffmann

38. **Cladonia rei** Schaerer

39. Cladonia scabriuscula Del.

40. Cladonia singularis Hammer

41. Cladonia squamosa Hoffmann var. squamosa

42. Cladonia squamosa var. subsquamosa (Leighton) Vainio

43. Cladonia subulata (L.) Weber ex Wiggers

44. **Cladonia sulphurina** (Michaux) Fries

45. Cladonia transcendens (Vainio) Vainio

46. **Cladonia umbricola** Tønsberg & Ahti

47. Cladonia uncialis (L.) Weber ex Wiggers

48. Cladonia verruculosa (Vainio) Ahti

TABLE 2. RARE <u>CLADONIA</u> SPECIES IN THE REGION'

Species	common elsewhere in western USA	uncommon elsewhere in western USA	Not found elsewhere in western USA	Present in ca x% of counties in the region[1]
Cladonia andereggii [2]			• ⊠⊠	3
Cladonia bellidiflora [2]		***		5
Cladonia coccifera [2]			• ⊠⊠	3
C. cornuta subsp. groenlandica [2]		• ⊠⊠		2
Cladonia crispata			***	2
Cladonia dahliana [3]		***		10
Cladonia digitata			• ⊠⊠	6
Cladonia dimorpha [2]	. • **			2
Cladonia imbricarica [2]		• ⊠⊠		8
Cladonia luteoalba			• ⊠⊠	4
Cladonia macilenta [2]	• ⊠⊠			2
Cladonia prolifica [2]		• ⊠⊠		2
Cladonia rei [2]			• ⊠⊠	4
Cladonia scabriuscula [2]	• **			4
Cladonia singularis [2]		***		2

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Species	common elsewhere in western USA	Uncommon elsewhere in western USA	Not found elsewhere in western USA	Present in ca x% of counties in the region[1]
Cladonia squamosa var. squamosa[3]	• ✉✉			🗁🗀
Cladonia squamosa var. subsquamosa	***			4
Cladonia transcendens	• ✉♍✋			5
Cladonia uncialis		• ✍✉		6

[1] Cladonia taxa were reported from 47 counties in the region.

19 (39.6%) of the taxa were present in 1-10% of the counties.
11 (22.9%) of the taxa were present in 11-20% of the counties.
6 (12.5%) of the taxa were present in 21-30% of the counties.
12 (25.0%) of the taxa were present in >30% of the counties.

[2] Not reported in McCune Eastside lichen report (1994).

McCune reported the following taxa that were not confirmed by me:

C. botrytes
C. firma
C. norvegica

[3] Not reported as rare in McCune Eastside lichen report.

TABLE 3. NUMBER OF *CLADONIA* SPECIES PER COUNTY

COUNTY	STATE	No. of taxa	No. of rare taxa	No. of uncommon taxa[1]	PHYSIOGRAPHIC REGION NAME	CODE [2]
Flathead	MT	27	3	7	Flathead-Blackfoot	3
Idaho	ID	26	3	4	Clearwater	9
Latah	ID	26	5	5	Selkirk	1
Bonner	ID	21	2	4	Selkirk	1
Ravalli	MT	20	2	4	Bitterroot Range	10
Lake	MT	19	2	2	Flathead-Blackfoot	3
Missoula	MT	19		5	Flathead-Blackfoot	3
Kittitas	WA	18	6	2	E Slope Cascades,WA	34
Wallowa	OR	18	1	2	NE Oregon Mts.	42
Benewah	ID	17	2	1	Selkirk	1
Pend Oreille	WA	17	1	1	NE Washington Mts.	35
Shoshone	ID	17	2	2	Clearwater	9
Ferry	WA	16	2	3	NE Washington Mts	35
Lemhi	ID	16		3	Salmon	16
Boundary	ID	13	1		Selkirk	1
Custer	ID	13	1	1	Salmon	16
Hood River	OR	12	3	2	E Slope Cascades	40
Stevens	WA	11	1	2	NE Washington Mts	35
Spokane	WA	10		1	NE Washington Mts	35
Lincoln	MT	9	2	2	Kootenai	2
Yakima	WA	9	1		E Slope Cascades,WA	34
Lewis	ID	7	1		Clearwater	9
Mineral	MT	7		2	Bitterroot Range	10
Okanogan	WA	7			NE Washington Mts	35
Chelan	WA	7			E Slope Cascades,WA	34
Glacier	MT	6		1	Kootenai	2
Asotin	WA	4			Columbia Basin	36
Klamath	OR	4		1	E plateaus & hills	41
Kootenai	ID	4		1	Selkirk	1
Nez Perce	ID	4			Columbia Plateau	8
Blaine	ID	3			East-central Idaho	17
Clearwater	ID	3			Clearwater	9
Grant	OR	3			NE Oregon Mts.	42

COUNTY	STATE	No. of taxa	No. of rare taxa	No. of uncommon taxa[1]	PHYSIOGRAPHIC REGION NAME	CODE[2]
Sanders	MT	3		1	Kootenai	2
Union	OR	3			NE Oregon Mts.	42
Valley	ID	3			Payette	16
Whitman	WA	3			Columbia Basin	36
Adams	WA	2			Columbia Basin	36
Garfield	OR	2			NE Oregon Mts.	42
Klickitat	WA	2			Columbia Basin	36
Baker	OR	1			NE Oregon Mts.	42
Deschutes	OR	1			E slope Cascades	40
Jefferson	OR	1			E slope Cascades	40
Walla Walla	WA	1			Columbia Basin	36
Wasco	OR	1			E slope Cascades	40
Washington	ID	1			Seven Devils	15
Wheeler	OR	1			E plateaus & hills	41

1 Taxa found in 11-20% of the counties in the region

2 After McCune Eastside lichen report (1994).

TABLE 4. LOCALITIES VISITED FOR THIS STUDY [1]

1. WA. Yakima Co., Little Naches Road
2. ID. Latah Co., Moose Creek Divide, Laird Park, St. Joe NF
3. ID. Latah Co., Milepost 16, Hwy. 6
4. ID. Benewah Co., Basalt Outcrop, Santa Creek Bridge, Emida
5. ID. Shoshone Co., Emerald Ck. Rec. Area Road
6. ID. Idaho Co., Major Fenn Trail, Clearwater NF nr. Lowell
7. ID. Idaho Co., Split Ck Trail, Rd. 133, Clearwater NF
8. MT. Missoula Co., Seeley Lake and Lake Alva Rec. Areas
9. MT. Flathead Co., Numa Ridge Trail, Glacier Natl Park
10. MT. Lincoln Co., Yook River Cpgrd.
11. ID. Boundary Co., Smith Lk. Cpgrd.
12. ID. Bonner Co., Hanna Flat Nature Trail nr. Nordman
13. WA. Pend Oreille Co, Granite Creek-Roosevelt Cedars, Stagger Inn Cpgrd.
14. WA. Stevens Co., Flowery Trail, 10 mi. E. of Chelewah
15. WA. Ferry Co., Log Flume Trail, 20 mi. W. of Kettle Falls
16. WA. Ferry Co., Sherman Pass Natl Rec. Area, Colville NF
17. WA. Chelan Co., Rainy Pass, Hwy. 20
18. WA. Yakima Co., Clear Ck. Falls, 1 mi. E. of White Pass, 1500 m
19. OR. Hood River Co., Government Camp, 1300 m
20. OR. Wallowa Co., Minam State Rec. Area off Hwy. 86
21. OR. Wallowa Co., Lostine River Valley S. of Lostine, 1000-1700 m elev.
22. OR. Wallowa Co., Road to Hat Point, 2 mi. E. of Imnaha
23. OR. Wallowa Co., Trail above Wallowa Lake
24. WA. Asotin Co., Field's Springs State Park
25. ID. Idaho Co., Roadside nr. Harpster
26. ID. Idaho Co., Btwn Red River Hot Springs and Ditch Creek Cpgrd, near Elk City
27. ID. Idaho Co., Beaver Ridge Rd, Hwy. 12 btwn Powell and Lolo Pass
28. ID. Idaho Co., Lolo Pass
29. MT. Mineral Co., Rest Area, Tarkio
30. ID. Bonner Co., Nature trail near Nordman
31. WA. Stevens Co., Tacoma Divide, Hwy. 20
32. WA. Okanogan Co., Cedar Creek Trail, ca. 1000 m
33. WA. Chelan Co., Rainy Pass, Hwy. 20

[1] Many of the localities cited represent two or more nearby collecting sites.

TABLE 5. MICROHABITAT MOISTURE REQUIREMENTS

No.	Species	1 (Dry)	2	3 (Intermediate)	4	5 (Wet)
1.	C. andereggii					. . . . .
2.	C. asahinae		. . . . .			
3.	C. bacillaris			. . . . .		
4.	C. bellidiflora			. . . . .		
5.	C. borealis	. . . . .				
6.	C. cariosa		. . . . .			
7.	C. carneola		. . . . .			
8.	C. cenotea					. . . . .
9.	C. cervicornis subsp. cervicornis	. . . . .				
10.	C. cervicornis subsp. verticillata	. . . . .				
11.	C. chlorophaea	. . . . .				
12.	C. coccifera			. . . . .		
13.	C. coniocraea			. . . . .		
14.	C. conista	. . . . .				
15.	C. cornuta subsp. cornuta			. . . . .		
16.	C. cornuta subsp. groenlandica			. . . . .		
17.	C. crispata			. . . . .		
18.	C. dahliana				. . . . .	
19.	C. deformis				. . . . .	
20.	C. digitata			. . . . .		
21.	C. dimorpha				. . . . .	
22.	C. ecmocyna subsp. intermedia		. . . . .			
23.	C. ecmocyna unnamed subspecies		. . . . .			
24.	C. fimbriata	. . . . .				
25.	C. gracilis subsp. turbinata			. . . . .		
26.	C. imbricarica		. . . . .			
27.	C. luteoalba			?		

Dry Intermediate Wet

2 3 4 5

28. C. macilenta • • • • •
29. C. macrophyllodes • • • • •
30. C. merochlorophaea • • • • •
31. C. multiformis • • • • •
32. C. ochrochlora • • • • •
33. C. phyllophora • • • • •
34. C. pleurota • • • • •
35. C. pocillum • • • • •
36. C. prolifica • • • • •
37. C. pyxidata • • • • • •
38. C. rei • • • • •
39. C. scabriuscula • • • • •
40. C. singularis • • • • •
41. C. squamosa var. sq-uamosa • • • • •
42. C. squamosa var. subsquamosa • • • • •
43. C. subulata • • • • •
44. C. sulphurina • • • • •
45. C. transcendens • • • • •
46. C. umbricola • • • • •
47. C. uncialis • • • • •
48. C. verruculosa • • • • •

TABLE 6. MICROHABITAT LIGHT REQUIREMENTS

	Light 1	2	Intermediate 3	4	Dark 5
1. C. anderggii					. . . . .
2. C. asahinae		. . . . .			
3. C. bacillaris					. . . . .
4. C. bellidiflora			• • • • •		
5. C. borealis	• • • • •				
6. C. cariosa		• • • • •			
7. C. carneola		• • • • •			
8. C. cenotea					• • • • •
9. C. cervicornis subsp. cervicornis		• • • • •			
10. C. cervicornis subsp.. verticillata	• • • • •				
11. C. chlorophaea	• • • • •				
12. C. coccifera			• • • • •		
13. C. coniocraea		• • • • •			
14. C. conista	• • • • •				
15. C. cornuta subsp. cornuta			• • • • •		
16. C. cornuta subsp. groenlandica			• • • • •		
17. C. crispata			• • • • •		
18. C. dahliana				• • • • •	
19. C. deformis				• • • • •	
20. C. digitata			• • • • •		
21. C. dimorpha				• • • • •	
22. C. ecmocyna subsp. intermedia				• • • • •	
23. C. ecmocyna unnamed subspecies				• • • • •	
24. C. fimbriata		• • • • •			
25. C. gracilis subsp. turbinata			• • • • •		
26. C. imbricarica		• • • • •			

No.	Species	Light 1	2	Intermediate 3	4	Dark 5
27.	C. luteoalba				?	
28.	C. macilenta			• •	• • •	
29.	C. macrophyllodes	. . .	..			
30.	C. merochlorophaea			•	• • • •	
31.	C. multiformis			• • •	• •	
32.	C. ochrochlora			• • •	• •	
33.	C. phyllophora			• • • •	•	
34.	C. pleurota			• • • •	•	
35.	C. pocillum	• •	• • •			
36.	C. prolifica	•	• • • •			
37.	C. pyxidata'			• • •	• •	
38.	C. rei		• • • •	•		
39.	C. scabriuscula			• •	• • •	
40.	C. singularis				• • • • •	
41.	C. squamosa var. squamosa				• • • • •	
42.	C. squamosa var. subsquamosa			• • •	• •	
43.	C. subulata			• •	• • •	
44.	C. sulphurina	• •	• • •			
45.	C. transcendens				• • • • •	
46.	C. umbricola				• • •	• •
47.	C. uncialis				• • • • •	
48.'	C. verruculosa	• • • •	•			

TABLE 7.. MICROHABITAT SUBSTRATUM REQUIREMENTS

	MOST COMMON ORGANIC SUBSTRATUM	RANGE OF SUBSTRATUM TOLERANCE (Inorganic 1 2 3 4 5 Organic)
C. andereggii	muscicolous	• • • • •
C. asahinae	dead twigs	• • • • •
C. bacillaris	dead wood	• • • • •
C. bellidiflora	duff	• • • • •
C. borealis	(soil)	• • • • •
C. cariosa	(soil)	• • • • •
C. carneola	dead wood	• • • • •
C. cenotea	rptting wood	• • • • •
C. cervicornis subsp. cervicornis	duff	• • • • •
C. cervicornis subsp. verticillata	duff	• • • • •
C. chlorophaea	(soil)	• • • • •
C. coccifera	(soil)	• • • • •
C. coniocraea	rotting wood	• • • • •
C. conista	(soil)	• • • • •
C. cornuta subsp. cornuta	dead wood	• • • • •
C. cornuta subsp. groenlandica	duff	• • • • •
C. crispata	duff	• • • • •
C. dahliana	duff	• • • • •
C. deformis	rotting wood	• • • • •
C. digitata	dead wood	• • • • •
C. dimorpha	(soil)	• • • • •
C. ecmocyna subsp. intermedia	(soil)	• • • • •
C. ecmocyna unnamed subspecies	(soil)	• • • • •
C. fimbriata	varies	• • • • •
C. gracilis subsp. turbinata	dead wood	• • • • •

	MOST COMMON ORGANIC SUBSTRATUM	RANGE OF SUBSTRATUM TOLERANCE Inorganic 1	2	3	4	Organic 5
C. imbricarica	(soil, basalt)	. . . . .				
C. luteoalba	(parasitic)			n.a.		
C. macilenta	dead wood				. . . . .	
C. macrophyllodes	(soil)	. . . . .				
C. merochlorophaea	duff			. . . . .		
C. multiformis	duff			. . . . .		
C. ochrochlora	rotting wood				. . . . .	
C. phyllophora	duff				. . . . .	
C. pleurota	rotting wood		. . . . .			
C. pocillum	duff			. . . . .		
C. prolifica	duff				. . . . .	
C. pyxidata	(soil) wood			. . . . .		
C. rei	duff				. . . . .	
C. scabriuscula	(soil)		. . . . .			
C. singularis	duff				. . . . .	
C. squamosa var. squamosa	rotting wood				. . . . .	
C. squamosa var. subsquamosa	rotting wood				. . . . .	
C. subulata	(soil)		. . . . .			
C. sulphurina	rotting wood,			. . . . .		
C. transcendens	rotting wood					. . . . .
C. umbricola	rotting wood					. . . . .
C. uncialis	soil		. . . . .			
C. verruculosa	varies			. . . . .		

TABLE 8. SUMMARY OF ECOLOGICAL REQUIREMENTS OF *CLADONIA* SPECIES

	MOISTURE	LIGHT	SUBSTRATUM	EQUABILITY INDEX[1]
1. C. anderggii	5	5	5	5.0
2. C. asahinae	2	2	4	2.7
3. C. bacillaris	3	5	4	4.0
4. C. bellidiflora	3	3	3	3.0
5. C. borealis	1	2	2	1.3
6. C. cariosa	2	3	2	2.3
7. C. carneola	2	2	3	2.3
8. C. cenotea	5	5	5	5.0
9. C. cervicornis subsp. cervicornis	1	3	2	2.0
10. C. cervicornis subsp. verticillata	1	2	2	1.7
11. C. chlorophaea	1	1	2	1.3
12. C. coccifera	3	3	3	3.0
13. C. coniocraea	3	2	3	2.7
14. C. conista	1	1	1	1.0
15. C. cornuta subsp. cornuta	3	4	2	3.0
16. C. cornuta subsp'. groenlandica	3	3	3	3.0
17. C. crispata	3	3	2	2.7
18. C. dahliana	5	4	5	4.7
19. C. deformis	4	4	5	4.3
20. C. digitata	3	4	5	4.0
21. C. dimorpha	4	4-	3	3.7
22. C. ecmocyna subsp. intermedia	2	4	3	3.0
23. C. ecmocyna unnamed subspecies	2	3	3	2.3
24. C. fimbriata	1	2	2	1.7
25. C. gracilis subsp. turbinata	3	2	4	3.0
26. C. imbricarica	2	2	1	1.7
27. C. luteoalba				-
28. C. macilenta	3	4	4	3.7
29. C. macrophyllodes	1	3	1	1.7

	MOISTURE	LIGHT	SUBSTRATUM	EQUABILITY INDEX[1]
30. C. merochlorophaea	2	4	3	3.0
31. C. multiformis	3	4	3	3.3
32. C. ochrochlora	3	4	4	3.7
33. C. phyllophora	2	4	4	3.3
34. C. pleurota	1	4	2	2.3
35. C. pocillum	1	2	3	2.0
36. C. prolifica	3	1	4	2.7
37. C. pyxidata	2	5	3	3.3
38. C. rei	3	1	4	2.7
39. C. scabriuscula	3	4	2	3.0
40. C. singularis	4	4	3	3.7
41. C. squamosa var. squamosa	4	4	4	4.0
42. C. squamosa var. subsquamosa	3	2	4	3.0
43. C. subulata	4	3	1	2.7
44. C. sulphurina	2	1	3	2.0
45. C. transcendens	4	3	5	4.0
46. C. umbricola	4	4	5	4.3
47. C. uncialis	4	3	2	3.0
48. C. verruculosa	1	1	1	1.0

[1] The equability index represents the relative degree to which the species require protected, unchanging conditions which might be found, for example, in a moist forest. It is the numeric mean of the other requirements. The requirements have been summarized here by a single value, but the range of ecological tolerance of the species is shown in the preceding tables.

TABLE 9. MEANS OF SUBSTRATUM STABILIZATION

	UNDERGROUND HYPHAE	BURIED THALLUS PARTS	ABOVEGROUND SQUAMULES	ABOVEGROUND THALLUS
1. C. anderggii	• ⊠⊠			★★★
2. C. asahinae		• ♦⊠	• ⊠⊠	• ♦⊠
3. C. bacillaris	• ⊠⊠	★★★		★★★
4. C. bellidiflora	• ⊠⊠⊠	★★★		• ⊠⊠
5. C. borealis				★★★
6. C. cariosa				★★★
7. C. carneola				• ⊠♦
8. C. cenotea	★★★		★★★	• ⊠⊠
9. C. cervicornis subsp. cervicornis		• ⊠⊠	★★★	★★★
10. C. cervicornis subsp. verticillata				• ⊠⊠
11. c. chlorophaea			★★★	• ♦♦
12. c. coccifera			★★★	• ★ •
13. c. coniocraea		★★★	★★★	
14. c. conista			★★★	★★★
15. c. cornuta subsp. cornuta			★★★	★★★
16. C. cornuta subsp. groenlandica		• ⊠⊠	• ⊠⊠	★★★
17. C. crispata	★★★	★★★	• ♦♦	• ⊠⊠
18. C. dahliana		• ♦♦	• ⊠⊠	• ⊠⊠
19. C. deformis		• ⊠⊠		• ⊠⊠
20. C. digitata	★★★		⊠ • ⊠⊠	
21. C. dimorpha		★★★		★★★
22. C. ecmocyna subsp. intermedia		★★★		• ⊠⊠
23. C. ecmocyna unnamed subspecies		★★★		★★★
24. C. fimbriata		• ♦⊠	★★★	★★★
25. C. gracilis subsp. turbinata		• ⊠⊠	★★★	★★★
26. C. imbricarica				• ⊠♦
27. C. luteoalba		n.a.		
28. C. macilenta	★★★		★★★	• ⊠⊠
29. c. macrophyllodes		• ⊠⊠	★★★	• ♦⊠

	UNDERGROUND HYPHAE	BURIED THALLUS PARTS	ABOVEGROUND SQUAMULES	ABOVEGROUND THALLUS
30. C. merochlorophaea		• ✉✉	★ ★ ★	★ ★ ★
31. C. multiformis		• ✉✉	• ✉✉	★ ★ ★
32. C. ochrochlora	• ✉✉	• ✉✉	• ✉✉	• ✉📫♦
33. C. phyllophora		★ ★ ★	• ✉✉	★ ★ ★
34. C. pleurota		• ✉✉		★ ★ ★
35. C. pocillum		• ✉✉	• ✉♦	• ♦✉
36. C. prolifica			• ✉♦	• ♦✉
37. C. pyxidata		★ ★ ★		★ ★ ★
38. C. rei			★ ★ ★	★ ★ ★
39. C. scabriuscula			★ ★ ★	
40. C. singularis		• ✉📫♦		• ✉♦
41. C. squamosa var. squamosa	★ ★ ★		★ ★ ★	★ ★ ★
42. C. squamosa var. subsquamosa	★ ★ ★		★ ★ ★	★ ★ ★
43. C. subulata		• ✉✉		★ ★ ★
44. C. sulphurina	• ♦✉			★ ★ ★
45. C. transcendens	★ ★ ★	★ ★ ★		★ ★ ★
46. C. umbricola	★ ★ ★	• ✉✉		• ✉✉
47. C. uncialis		• ✉✉		★ ★ ★
48. C. verruculosa		• 📫♦♦		★ ★ ★

TABLE 10. PHYSIOGNOMIC CLASSIFICATION OF THE TAXA[1]

SPECIES	PHYSIOGNOMY	McCUNE CLASSIFICATION
1. Cladonia andereggii	leaf	[2] moss lichen
2. Cladonia asahinae	cup	[2] soil lichen
3. Cladonia bacillaris	pin	rotten log and tree base
4. Cladonia bellidiflora	pin	[2] soil lichen
5. Cladonia borealis	cup	rock mats and cushions
6. Cladonia cariosa	pin	pioneer soil stabilizers
7. Cladonia carneola	cup	rotten log and tree base
8. Cladonia cenotea	shrub	rotten log and tree base
9. Cladonia cervicornis subsp. cervicornis	pin	rock mats and cushions
10. Cladonia cervicornis subsp. verticillata	pin	rock mats and cushions
11. Cladonia chlorophaea	cup	soil lichens
12. Cladonia coccifera	cup	[2] soil lichen
13. Cladonia coniocraea	pin	rotten log and tree base
14. Cladonia conista	cup	[2] rotten log and tree base
15. Cladonia cornuta subsp. cornuta	pin	rock mats and cushions
16. Cladonia cornuta subsp. groenlandica	pin	[2] soil lichen
17. Cladonia crispata	shrub	rock mats and cushions
18. Cladonia dahliana	leaf	[2] soil lichens
19. Cladonia deformis	pin	rock mats and cushions
20. Cladonia digitata	pin	rotten log and tree base
21. Cladonia dimorpha	shrub	[2] soil lichen (oceanic)
22. Cladonia ecmocyna subsp. intermedia	pin	rock mats and cushion
23. Cladonia ecmocyna unnamed subspecies	pin	rock mats and cushion

SPECIES	PHYSIOGNOMY	McCUNE CLASSIFICATION
24. Cladonia fimbriata	cup	soil lichens
25. Cladonia gracilis subsp. turbinata	pin	rock mats and cushions
26. Cladonia imbricarica	cup	[2] rock mats and cushions
27. Cladonia luteoalba	pin	soil lichens
28. Cladonia macilenta	pin	[2] rotten log and tree
29. Cladonia macrophyllodes	leaf	soil lichens
30. Cladonia merochlorophaea	cup	oceanic log lichens
31. Cladonia multiformis	shrub	rock mats and cushions
32. Cladonia ochrochlora	pin	rotten log and tree base
33. Cladonia phyllophora	pin	rock mats and cushions
34. Cladonia pleurota	cup	rock mats and cushions
35. Cladonia pocillum	cup	soil lichens
36. Cladonia prolifica	pin	[2] soil lichen (oceanic)
37. Cladonia pyxidata	cup	soil lichens
38. Cladonia rei	pin	[2] soil lichen
39. Cladonia scabriuscula	shrub	[2] soil lichen (oceanic)
40. Cladonia singularis	pin	[2] soil lichen
41. Cladonia squamosa var. squamosa	shrub	oceanic log lichens
42. Cladonia squamosa var. subsquamosa	shrub	oceanic log lichens
43. Cladonia subulata	pin	rotten log and tree base
44. Cladonia sulphurina	cup	rotten log and tree base
45. Cladonia transcendens	pin	oceanic log lichen
46. Cladonia umbricola	pin	oceanic log lichen
47. Cladonia uncialis	shrub	rock mats and cushions
48. Cladonia verruculosa	pin	soil lichens

[1] The Cladonia thallus is divided into two parts, a prostrate, leaflike squamule, and an erect, tubular podetium, which may be branched or unbranched. For the purposes of this study, "leaf" lichens are those with large, persistent squamules and inconspicuous or missing podetia. "Pin" lichens are those with podetia (usually unbranched) and squamules in the mature thallus. "Cup" lichens are characterized by stout, cup-shaped podetia, often without accompanying squamules. "Shrub" lichens have much-branched podetia and usually lack squamules at maturity. The above classifications do not reflect the taxonomy of the genus.

[2] These taxa were not reported by McCune (1994) and therefore did not carry a McCune classification in that report. I have attempted to circumscribe these taxa according to McCune's system.

TABLE 11. SUMMARY OF OPTIMAL SITES FOR *CLADONIA* SPECIES

North facing (low evapotranspiration)

Alternating sun-shade

Organic matter

- snags
- decaying wood
- conifer needles
- fallen evergreen leaves (i.e. ericaceous plants)

Associated phanerogams

- western red cedar
- western hemlock
- Douglas fir
- ericaceous (or other acid-loving) shrubs

Associated cryptogama

- *Bryoria* and *Alectoria* spp.[1]
- mosses

Other associated organisms

- Varied thrush[1]

Soil condition;

Increased acidity + low soil production = low competition from phanerogams

These conditions may be expected on:

- basalt, particularly when underconifers
- granite or other rock outcrops under conifers
- sand
- forest margins
- roadsides, trailsides

Moisture conditions

- some standing water or spray
- organic matter also ameliorates evapotranspiration
- moss cushions also maintain microhabitat moisture levels

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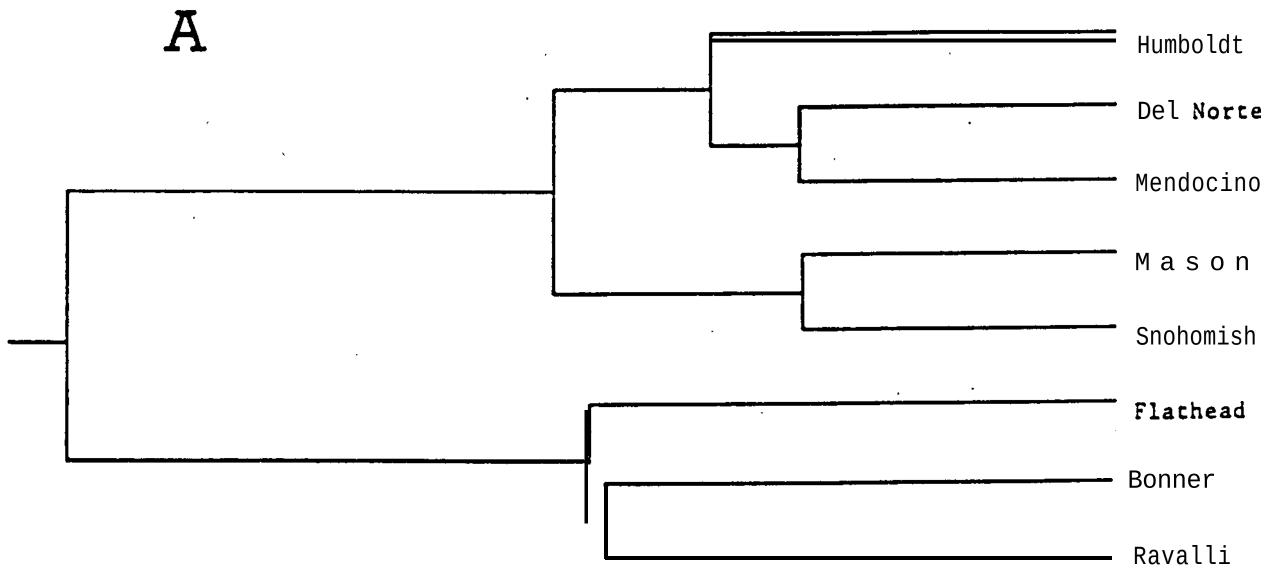
[1] These are good indicator organisms, frequently associated with *Cladonia*

FIGURE 1. Cluster analyses of selected county and species associations in the western United States

A. Selected counties B. Selected species



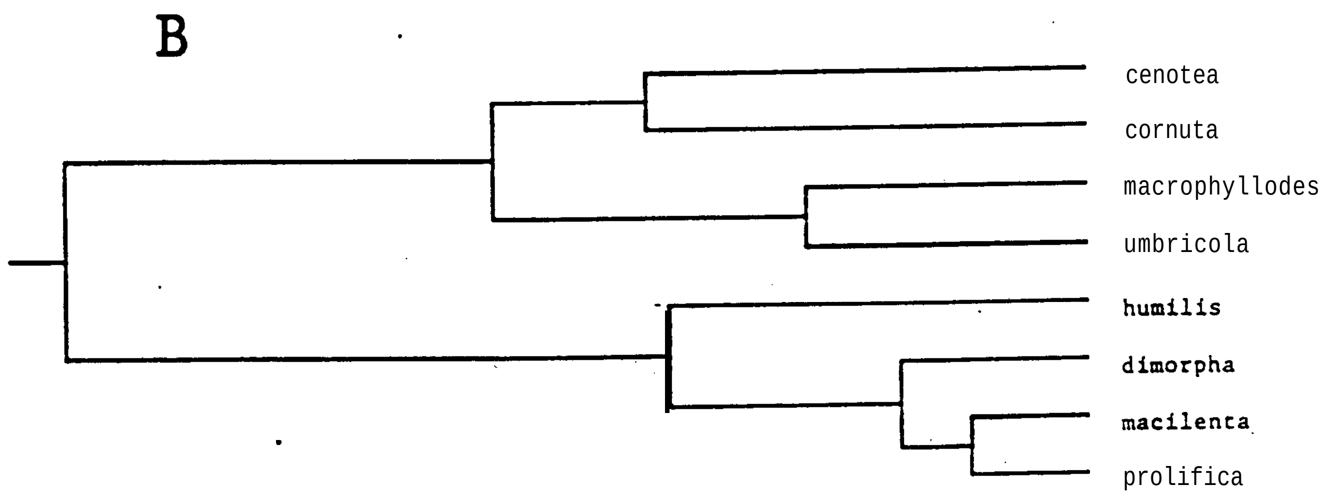


FIGURE 2. Cluster analysis of selected county associations in the Interior Northwest

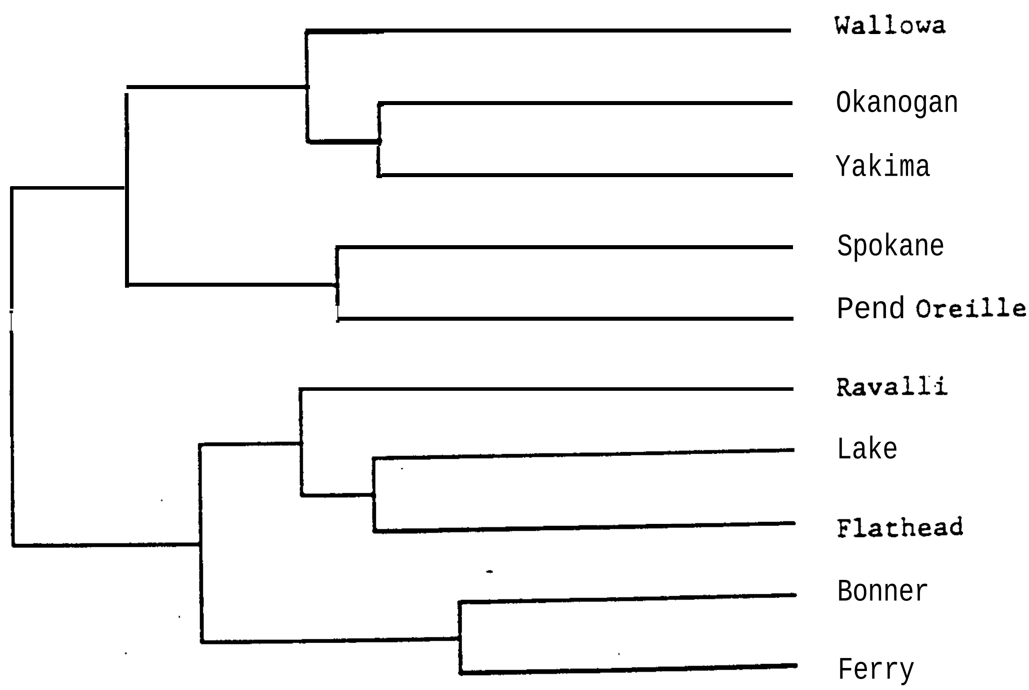
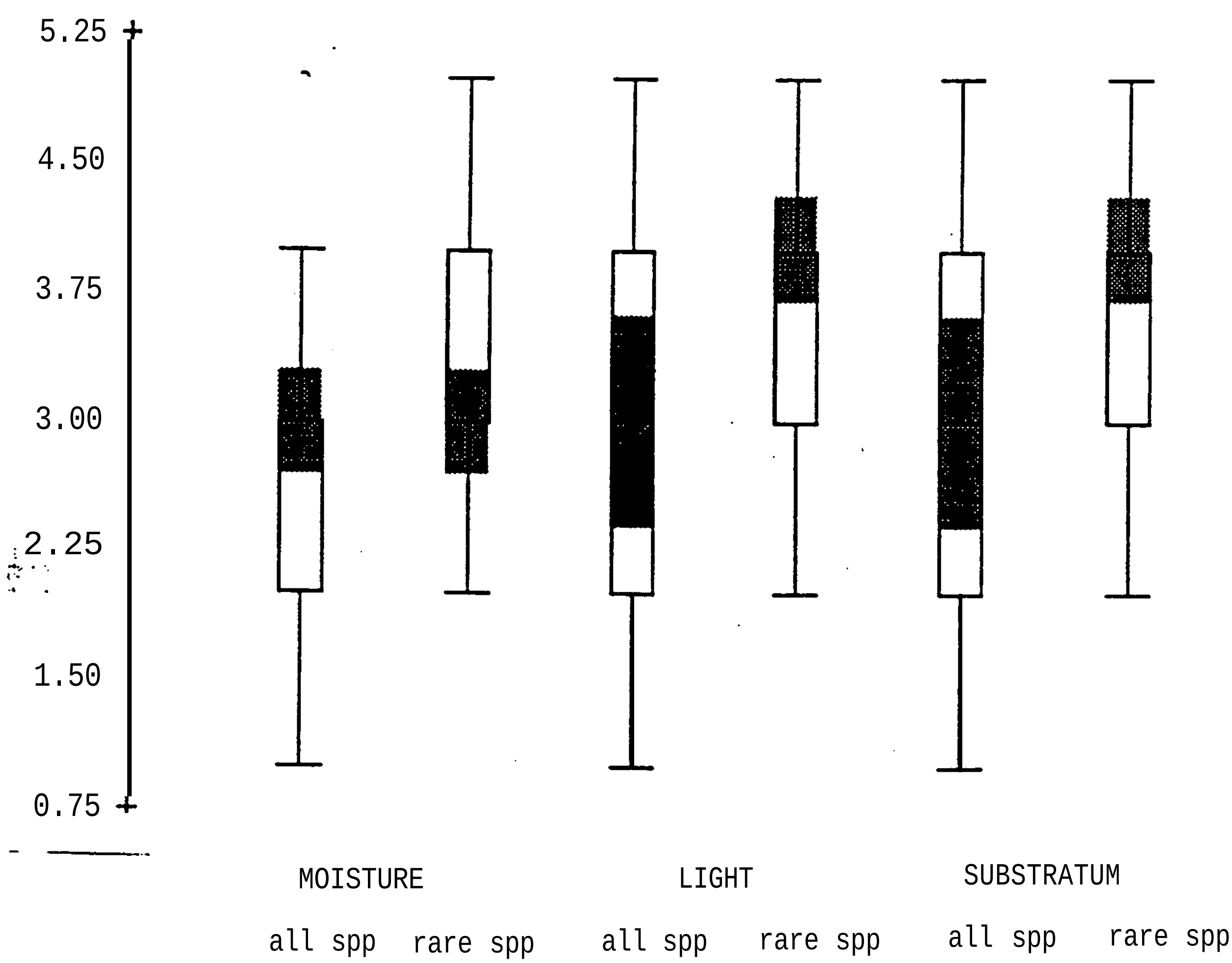


FIGURE 3. Comparison of ecological requirements of Cladonia species



t-Test of Individual μ's

No Selector

Individual Alpha Level 0.05

Ho: $\mu = 0$ Ha: $\mu \neq 0$

moisture:

Test Ho: μ(moisture) = 0 vs Ha: μ(moisture) ≠ 0
Sample Mean = 2.6595745 t-Statistic = 15.392 w/46 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

rare moisture

Test Ho: μ(rare moisture) = 0 vs Ha: μ(rare moisture) ≠ 0
Sample Mean = 3.2222222 t-Statistic = 16.533 w/26 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

light:

Test Ho: μ(light) = 0 vs Ha: μ(light) ≠ 0
Sample Mean = 3.0851064 t-Statistic = 17.187 w/46 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

rare light

Test Ho: μ(rare light) = 0 vs Ha: μ(rare light) ≠ 0
Sample Mean = 3.3703704 t-Statistic = 14.430 w/26 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

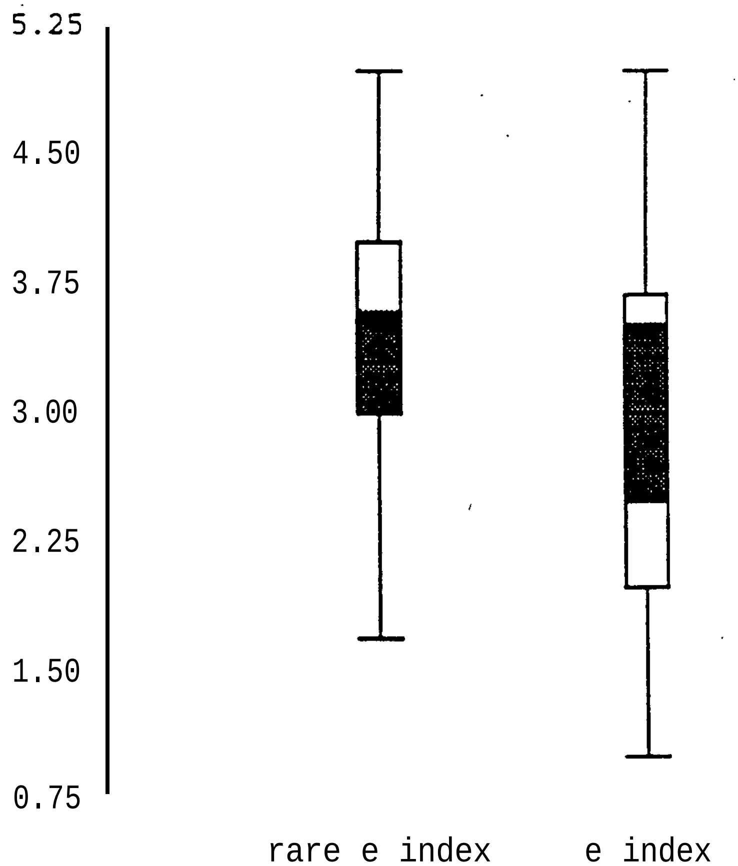
substrate:

Test Ho: μ(substrate) = 0 vs Ha: μ(substrate) ≠ 0
Sample Mean = 3.0425532 t-Statistic = 17.425 w/46 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

rare substrate

Test Ho: μ(rare substrate) = 0 vs Ha: μ(rare substrate) ≠ 0
Sample Mean = 3.6538462 t-Statistic'= 17.641 w/25 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

FIGURE 4. Comparison of equability indices of the species



rare e index:

Test Ho: μ(rare e index) = 0 vs Ha: μ(rare e index) ≠ 0
Sample Mean = 3.4111111 t-Statistic = 21.077 w/26 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

e index:

Test Ho: μ(e index) = 0 vs Ha: μ(e index) ≠ 0
Sample Mean = 2.9319149 t-Statistic = 20.117 w/46 df
Reject Ho at Alpha = 0.05
$p \leq 0.0001$

FIGURE 5. Substratum-binding activities of *Cladonia* species (Micrographs on following page)

A. *Cladonia* squamules provide spatiai variety and microhabitats. When buried, old thallus parts retain mositure and prevent compacting of the soil layer. Scale bar = 1 mm.

B. *Cladonia* squamules provide protection at the substratum surface. They may also be tightly attached to the substratum by their basal hyphae (lower left). Scale bar = 1 mm.

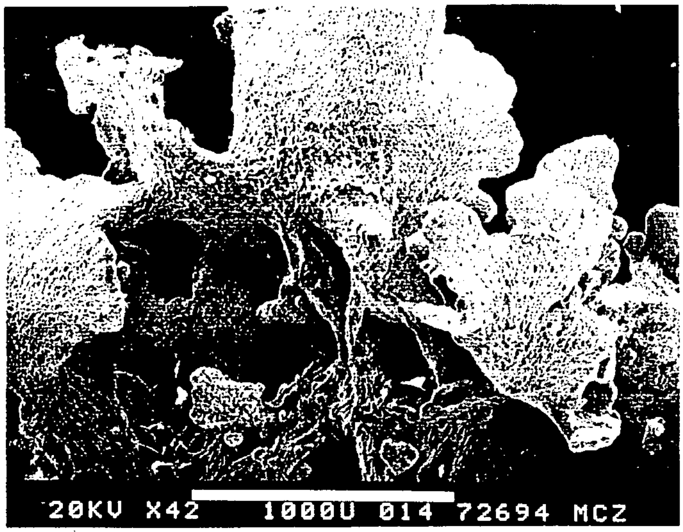
C. At the interface between substratum and thallus (arrows) the lichen is indistinguishable from its substratum. Scale bar = 100 µm.

D. Rhizoids (bundles of fungal hyphae) from many species, particularly red-fruited Cladonias (*C. macilenta* shown here) ramify through the interior surface of rotting wood. Scale bar = 1 mm.

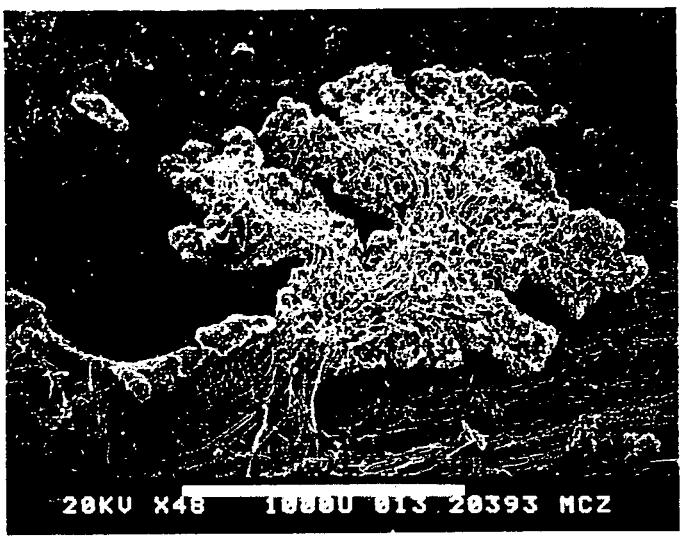
E. Hyphae of *C. transcendens* ramifying through the interior of rotting wood. Scale bar = 100 µm.

F. *Cladonia* hyphae surround inorganic particles such as this grain of sand, and prevent erosion. 'Scale bar = 100 µm.

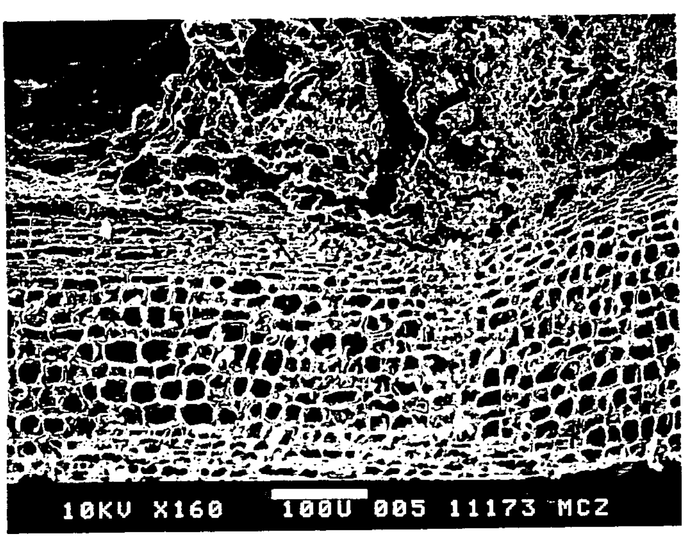
a


20KV X42 1000U 014 72694 MCZ

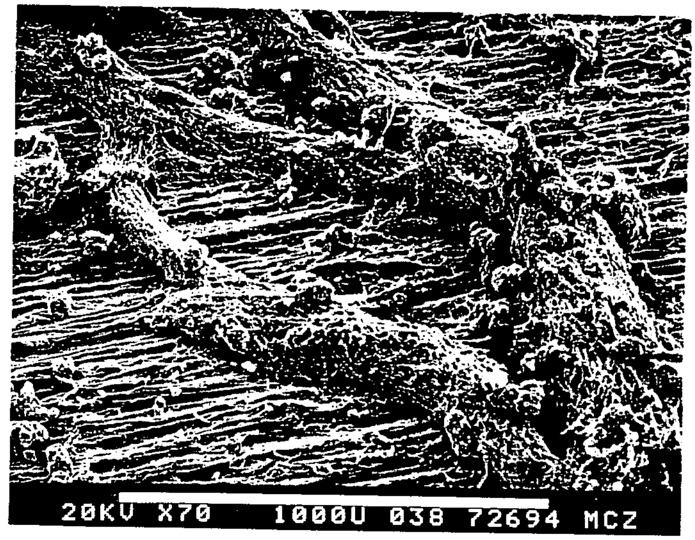
b


20KV X48 1000U 013 20393 MCZ

c


10KV X160 100U 005 11173 MCZ

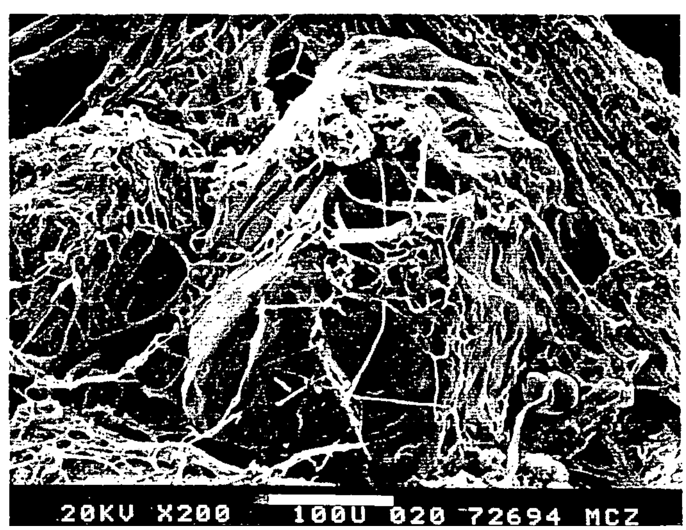
d


20KV X70 1000U 038 72694 MCZ

e


20KV X320 100U 017 20393 MCZ

f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ENUMERATION OF THE TAXA

1. CLADONIA ANDEREGGII

Type specimen: U.S.A., Idaho, St. Joe National Forest, Latah Co., Laird Park, Moose Creek Divide, June, 1989. Hammer 3798 (FH).

In deep shade in damp area with bryophytes.

Chemistry: K+ yellow, KC+ yellow, P+ orange, UV-, atranorin, stictic acid, norstictic acid.

This is the only species that appears to be narrowly endemic to the region. In my examination of approximately 8000 specimens for this projet, both in herbaria and in collections that I made, the specimens cited here are the only ones known to me.

2. CLADONIA ASAHINAE

On twigs, rotting stumps, and thin soil. Sometimes over sand, generally at lower elevations.

Chemistry: K- or K+ dingy yellowish, changing to brownish, KC-, P+ red, UV-; 1) fumarprotocetraric acid with rangiformic and/or norrangiformic acid (and accessory protocetraric acid), 2) fumarprotocetraric acid with lichesterinic and/or protolichesterinic acid and accessory protocetraric acid.

Representative specimens from the region: IDAHO. Custer Co.: Anderegg 2018 (ID); Idaho Co.: Hammer 3885 (FH, ID); Latah Co.: Anderegg 66 (ID); Shoshone Co.: Hammer 3857 (FH); Valley Co.: Anderegg 1997 (ID); MONTANA. Flathead Co.: Marianai 38 (SRP); Missoula Co.: Hammer 3919 (FH); OREGON. Wallowa Co.: Hammer 5275 (FH); WASHINGTON. Asotin Co.: Hammer 5304 (FH); Hammer 5600 (FH, ID); Chelan Co.: Hennings 1215 (DUKE); Klickitat Co.: Foster 1083 (FH); Okanogan Co.: Hammer 5503 (FH, ID), Hammer 5505 (ID); Pend Oreille Co.: Hammer 5458 (FH, ID).

The two chemical strains of C. asahinae contain different fatty acids. One strain contains lichesterinic acid and/or protolichesterinic acid, and another strain has rangiformic and/or norrangiformic acid. Specimens with the rangiformic-norrangiformic acid complex are more common in the region, with the lichesterinic-protolichesterinic strain more common west of the Cascade Mountains.

3. CLADONIA BACILLARIS

On rotting wood or thin soil, usually in shady areas.

Chemistry: K-, KC-, P-, UV-; barbatic acid.

Representative specimens from the region: IDAHO. Latah Co.: Anderegg 2568 (ID, SFSU), Shoshone Co.: Rosentreter 5057 (SRP); MONTANA. Flathead Co.: McCune 9312 (OSU); Lake Co.: McCune 8875 (OSU); Ravalli Co.: McCune 10815 (OSU).

This species is morphologically similar to three other sorediate, red-fruited species of section Cocciferae in western North America. It may be confused with C. macilenta, C. transcendens, or with C. umbricola. This species also resembles C. coniocraea, which, however, bears brown apothecia and is P+ red. Cladonia bacillaris has farinose soredia and is never corticate, while most specimens of C. macilenta have larger soredia that intergrade with patches of cortex and which also give rise to isidioid squamules. Cladonia bacillaris is found in interior Thuja forests, whereas C. macilenta is coastal and often in exposed localities. Except in the region of study, this species is quite rare. It has been compared to C. norvegica, but I have not seen that species in North American collections.

4. CLADONIA BELLIDIFLORA

Terricolous and usually exposed on bare acidic soil and on stabilized sand dunes, on rotting wood or duff, sometimes in deep shade, locally common on lava beds and volcanically derived rock at interior sites.

Chemistry: K-, KC+ bright yellow, P-, UV+ ice blue; usnic acid, squamatic acid, bellidiflorin.

Representative specimens from the region: WASHINGTON. Ferry Co.: Hammer 4050 (FH); Kittitas Co.: Hammer 4794 (FH); Pend Oreille Co.: Hammer 4011 (FH).

5. CLADONIA BOREALIS

On thin soil.

Chemistry: K-, KC+, P-, UV-; barbatic acid and usnic acid.

Representative specimens from the region: IDAHO. Bonner Co.: McCune 7740 (OSU); Boundary Co.: Anderegg 774 (ID, WIS); Custer Co.: Rosentreter 2491 (WIS); Idaho Co.: Hammer 5362 (FH); Kootenai Co.: Anderegg 804 (ID), Rust 553 (US); Shoshone Co.: Rosentreter 5043 (SRP). MONTANA. Flathead Co.: McCune 9903 (OSU); Glacier Co.: DeBolt 622 (OSU); Lake Co.:

McCune 9707 (OSU); Mineral Co.: Hammer 5416 (FH, ID); Missoula Co.: McCune L-172 (OSU); Ravalli Co.: McCune 10515 (OSU); OREGON. Wallowa Co.: Hammer 5241 (FH); WASHINGTON. Okanogan Co.: Howard 5606 (WTU); Spokane Co.: Esslinger 2449 (ASU).

Some specimens with the chemistry of C. borealis (barbatic and usnic acids) approach C. coccifera, which is very rare in the region. The podetia of C. borealis are esorediate, unbranched, scyphus-forming, with scarlet apothecia on the margins of the scyphi. Partially corticate specimens of C. pleurota may be confused with C. borealis, but C. pleurota is always sorediate.

6. CLADONIA CARIOSA

On thin soil and roadcuts, usually in damp microhabitats.

Chemistry: K+ yellowish changing to dingy brown, KC-, P+ deep yellow changing to red, UV- (fumarprotocetraric acid and atranorin), K+ persistent yellow, KC-, P-, UV- (atranorin only).

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3816 (ID); Bonner Co.: Hammer 5437 (FH, ID); Boundary Co.: Hammer 3962 (FH, ID); Custer Co.: Anderegg 2033 (WIS); Idaho Co.: Anderegg 1669 (ID); Kootenai Co.: Jong s.n. (WSP); Latah Co.: Hammer 3756 (ID); Lemhi Co.: Anderegg 1671 (ID); Lewis Co.: Cooke 24970 (WIS); Shoshone Co.: Hammer 3849 (ID); Valley Co.: Rosentreter 1098 (SRP); MONTANA. Flathead Co.: DeBolt 330 (WIS); Lake Co.: McCune 9138 (OSU); Lincoln Co.: Hammer 3949 (ID); Missoula Co.: Hammer 3923 (ID); OREGON. Baker Co.: Hale 49752 (US); Hood River Co.: Suksdorf 242 (WTU); Klamath Co.: Ryan 28261 (ASU); Wallowa Co.: Hammer 5253 (FH, ID); WASHINGTON. Chelan Co.: Howard 1291 (FH, WTU) Ferry Co.: Hammer 4051 (FH, ID); Garfield Co.: Hammer 3717 (ID); Kittitas Co.: Howard 849 (WTU); Klickitat Co.: Faxon s.n. (FH); Okanogan Co.: Hammer 5507 (FH); Pend Oreille Co.: Cooke 26545 (WIS); Spokane Co.: Essliner 2374 (ASU); Stevens Co.: Hammer 4023 (FH); Whitman Co.: Howard 1596 (WTU); Yakima Co.: Hammer 3706 (ID).

Cladonia cariosa is widely distributed, but it is more common at interior localities than at oceanic sites. It is conspicuous in lower elevations of the Cascade Range, where mats of it cover north-facing roadsides.

7. CLADONIA CARNEOLA

Terricolous on acidic soils, on rotten wood, and on stabilized sand dunes.

Chemistry: K-, KC+, P-, UV-; usnic acid with accessory barbatic acid, isousnic acid and zeorin.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3832 (FH, ID), Bonner Co.: Esslinger 2192b; (WIS); Boundary Co.: Anderegg 786 (ID, WIS); Custer Co.: Rosentreter

2501 (OSU, WIS); Idaho Co.: Blaine & Mooers 811 (SRP); Lemhi Co.: Anderegg 608 (ID); Shoshone Co.: Hammer 3897 (FH); MONTANA. Glacier Co.: Rosentreter 2077 (SRP); Flathead Co.: Hammer 3945 (FH, ID); Lake Co.: McCune 9187 (OSU); Lincoln Co.: McCune 7767 (OSU); Missoula Co.: Hammer 3924 (ID); Ravalli Co.: McCune 10934 (OSU, WIS); OREGON. Deschutes Co.: Pike L-396 (WIS); Hood River Co.: Hammer 5195 (FH); Union Co.: Anderegg 1224 (ID); Wallowa Co.: Hammer 5242 (FH); WASHINGTON. Asotin Co.: Hammer 5308 (FH); Ferry Co.: Hammer 4047 (FH); Kittitas Co.: Hammer 4855 (FH); Okanogan Co.: Hammer 5506 (FH); Pend Oreille Co.: Hammer 5461 (ID).

This species is widespread in a variety of habitats through the region, although it is usually found in relatively dry microhabitats. At higher elevations, it occurs with other simple, usually short, scyphus-forming taxa such as C. fimbriata and C. pleurota. It is rare on soil in dry or exposed localities, but fairly common on rotting wood which remains damp longer than the bare soil.

8. CLADONIA CENOTEA

On rotting stumps or partially buried, rotting wood, usually in north-facing situations.

Chemistry: K-, KC-, P-, UV + ice blue; squamatic acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3829 (FH, ID); Bonner Co.: Hammer 5423 (FH, ID); Boundary Co.: Hammer 3953 (FH, ID); Idaho Co.: Anderegg 573 (ID); Latah Co.: Hammer 3766 (FH, ID); Lemhi Co.: Anderegg 2085 (ID); Lewis Co.: Anderegg 416 (ASU, WIS); Shoshone Co.: Rosentreter 5048 (SRP); MONTANA. Flathead Co.: DeBolt 584 (WIS); Lake Co.: McCune 9849 (OSU); Lincoln Co.: McCune 7763 (OSU); Missoula Co.: McCune 8565 (OSU); Ravalli Co.: McCune 12008 (OSU); OREGON. Union Co.: Sheldon 9011 (US); Wallowa Co.: Hammer 5202 (FH, ID), Hammer 5249 (FH); WASHINGTON. Ferry Co.: Hammer 4033 (ID); Pend Oreille Co.: Hammer 4015 (ID); Spokane Co.: Bonser 10 (FH); Stevens Co.: Cooke 23339 (WIS).

9. CLADONIA CERVICORNIS subsp. CERVICORNIS

Terricolous or over duff; coastal and inland areas.

Chemistry: K- or K+ dingy yellow changing to brownish, KC-, P+ brick red, UV-; fumarprotocetraric acid with occasional atranorin.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3840 (ID); Blaine Co.: Anderegg 153 (ID); Custer Co.: Anderegg 1239 (ID); Idaho Co.: Anderegg 624 (ID); Lemhi Co.: Anderegg 654 (ID, WIS); MONTANA. Flathead Co.: Rosentreter 2075 (SRP); Glacier Co.: DeBolt 645 (OSU); OREGON. Grant Co.: Anderegg 877 (ID); Hood River Co.: Hammer 5193 (FH);

Wallowa Co.: Hammer 5264 (FH); WASHINGTON. Pend Oreille Co.: Hammer 4012 (FH, ID); Stevens Co.: Hammer 5502 (FH).

Cladonia cervicornis s. str. is restricted to localities in the Cascade Range and in the Wallowa Mountains of northeastern Oregon. At these localities it is characterized by a thick, chinky cortex, large squamules, and short, wide podetia.

10. CLADONIA CERVICORNIS subsp. VERTICILLATA

Terricolous or over duff.

Chemistry: K- or K+ dingy yellow changing to brownish, KC-, P+ brick red, UV-; fumarprotocetraric acid with rare atranorin.

Representative specimens from the region: IDAHO. Lemhi Co.: McCune 15396 (OSU); MONTANA. Flathead Co.: McCune 7538 (OSU); Missoula Co.: Hammer 3918 (ID); Ravalli Co.: McCune 9460 (OSU); OREGON. Wallowa Co.: Esslinger 1703c (WIS).

11. CLADONIA CHLOROPHAEA

Common throughout the region on a variety of substrata.

Chemistry: K- or K+ dingy yellowish-brownish, KC-, P+ red to brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3838 (FH); Bonner Co.: Esslinger 690b (WIS); Boundary Co.: Hammer 3961b (FH); Clearwater Co.: Cooke 19269 (WIS); Custer Co.: Anderegg 2019 (ID), Morton 8577 (US), Morton 8590 (US); Idaho Co.: Hammer 3900 (ID); Latah Co.: Hammer 3745 (FH, ID); Lemhi Co.: Anderegg 2099 (ID); Nez Perce Co.: Anderegg 1229 (ASU); Shoshone Co.: McCune 16424 (OSU); MONTANA. Flathead Co.: De Bolt 334 (WIS); Lake Co.: McCune 9669 (OSU); Mineral Co.: Hammer 5420 (ID); Missoula Co.: McCune 8178 (OSU); Ravalli Co.: McCune 11998 (OSU); OREGON. Grant. Co.: Goward 90-152a (UBC); Klamath Co.: Goward 90-240 (UBC); Wallowa Co.: Hammer 5204 (FH), Hammer 5214 (FH), Hammer 5215 (FH), Hammer 5265 (FH); WASHINGTON. Chelan Co.: Hammer 4054 (FH); Okanogan Co.: Hammer 5508a (FH); Pend Oreille Co.: Hammer 5454 (FH, ID); Spokane Co.: Cooke 23214 (WIS); Whitman Co.: Cooke 23292 (WIS).

Some species may be confused with C. chlorophaea, but in most cases, the species can be distinguished on the basis of morphological differences. For example, C. conista and C. humilis are stout and scyphus-bearing like the present species, but unlike C. chlorophaea, the base of the podetium is always corticate, and the cortex continues approximately halfway up the podetium, sometimes as far as the base of the scyphus. The soredia are also smaller than those of C. chlorophaea. The distinctions among the fumarprotocetraric acid- containing species C. chlorophaea, C. fimbriata, and C. pyxidata remain the most difficult to interpret. Cladonia pyxidata is corticate and esorediate, with C. fimbriata usually being ecorticate and farinose-sorediate. Specimens with characteristics of both may be placed under C. chlorophaea. There are some podetia that cannot be placed under one name or another because of their mix of characters.

12. CLADONIA COCCIFERA

On thin soil.

Chemistry: K-, KC-, P-, UV-; zeorin and usnic acid.
Representative specimen: **WASHINGTON.** Ferry **Co.:** Hammer 4029a (FH).

The specimen of C. coccifera cited above is the only one I found.

13. CLADONIA CONIOCFUEA

On rotting wood or seldom on soil.

Chemistry: K- or K+ dingy yellow to brownish, KC-, P+ orange to brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Bonner Co.: Esslinger 606 (WIS); Idaho Co.: Hammer 3905 (ID); Latah Co.: Anderegg 384 (WIS); MONTANA. Missoula Co.: McCune 7391 (OSU); OREGON. Hood River Co.: Hammer 5188 (FH); Klamath Co.: Goward 90-222a (UBC); WASHINGTON. Kittitas Co.: Hammer 4784 (FH); Spokane Co.: Bonser 1584 (FH); Stevens Co.: Cooke **23338 (FH).**

This species and C. ochrochlora are morphologically similar, but certain characteristics distinguish them. The primary squamules of C. coniocraea are always deeply incised, whereas the margins of the squamules of C. ochrochlora are nearly entire. Cladonia coniocraea never forms scyphi but C. ochrochlora rarely lacks them. The base of the podetium in C. coniocraea is only thinly corticate, while the cortex of C. ochrochlora is usually thickened and sometimes longitudinally rugose. The soredia of the present taxon are usually farinose, rarely occurring in small, diffuse soralia; soredia in C. ochrochlora are variable, but usually larger than those of C. coniocraea, and often occur in well defined, erumpent soralia. The podetia of C. coniocraea are fairly slender, usually not more than 1.5 mm diam, and are usually straight. The podetia of C. ochrochlora are generally wider, and are usually twisted.

14. CLADONIA CONISTA

On thin soil, more or less exposed localities.

Chemistry: K-, KC-, P+, UV-; fumarprotocetraric acid and bourgeanic acid.
Representative specimen: IDAHO. Latah Co.: Hammer 3787 (ID).

15. CLADONIA CORNUTA subsp. **CORNUTA**

On rotting logs, rarely terricolous

Chemistry: K-, KC-, P+ red, UV-; fumarprotocetraric acid.

Representative specimens: IDAHO. Bonner Co. Hammer 5475 (FH, ID), Kootenai Co.: Rosentreter 2325 (SRP); Shoshone Co.: McCune 16533 (OSU); MONTANA. Flathead Co.: DeBolt 565 (WIS); Lake Co.: McCune 9369 (OSU); Lincoln Co.: Rosentreter 2325 (US); Missoula Co.: McCune 8619 (OSU); Ravalli Co.: McCune 10531 (OSU); Sanders Co.: McCune 9818 (OSU); WASHINGTON. Ferry Co.: Hammer 4034 (FH).

Cladonia cornuta is uncommon in the region but it may be considered an indicator species, since it is quite rare west of the Cascade Mountains. At least in the western United States, it requires rotting logs as its substratum.

16. CLADONIA CORNUTA subsp. **GROENLANDICA**

On soil or growing over compressed duff.

Chemistry: K- or K+ dingy yellow changing to dingy brown, KC-, P+ brick red, UV-; fumarprotocetraric acid.

Representative specimen from the region: MONTANA. Ravalli Co.: McCune 10512 (OSU).

17. CLADONIA CRISPATA

Chemistry: K-, KC-, P-, UV + ice blue, squamatic acid.

Representative specimen: MONTANA. Flathead Co.: Weir 11396 (FH).

Cladonia crispata is very rare in the region, and it is absent west of the Cascade Mountains. It is presumed to be worldwide in its distribution. The cited specimen is the only one that I found.

18. CLADONIA DAHLIANA

On thin soil over duff composed of conifer needles, shady forests.

Chemistry: K+ yellowish, persistent, KC+, P+ orange, UV-; atranorin and psoromic acid.

Representative specimens from the region: IDAHO. Boundary Co.: Hammer 3958 (FH); MONTANA. Lake Co.: McCune 9182 (OSU); Ravalli Co.: McCune 11019 (SRP); OREGON. Grant Co.: Goward 90-125 (UBC).

19. CLADONIA DEFORMIS

On rotting wood and humus.

Chemistry: K-, KC+ yellow, P-, UV-; zeorin, usnic acid, isousnic acid.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 5422 (ID); Boundary Co.: Hammer 3954 (ID); MONTANA. Flathead Co.: Weir 11599 (FH); WASHINGTON. Chelan Co.: Hammer 4054; Ferry Co.: Foster 2302 (FH); Yakima Co.: Howard 1002 (FH).

Cladonia deformis is rare in the region. It grows at relatively high elevations.

20. CLADONIA DIGITATA

On dead wood.

Chemistry: K+ bright yellow, unchanging, KC+ yellow, P+ orange to red, UV-; thamnolic acid.

Representative specimens from the region: MONTANA. Flathead Co.: Rosentreter 2062 (SRP); Lincoln Co.: Rosentreter MT-286 (SRP); WASHINGTON. Kittitas Co.: Howard 850 (WTU).

This species is rare in the region of study, although C. digitata is a name that was frequently assigned to specimens of C. deformis and C. transcendens. The large, thickly corticate primary squamules and podetial base of this species resemble those on some specimens of C. macilenta, but C. digitata is scyphose and much larger.

21. CLADONIA DIMORPHA

Terricolous on roadcuts and on sandy soil, partial shade.

Chemistry: K+ dull brown to K-, KC-, P+ reddish to brick red, UV-; fumarprotocetraric acid.

Representative specimen: IDAHO. Latah Co.: Hammer 3729 (FH).

This species is quite rare in the region, although it is common west of the Cascade Mountains, primarily in oceanic habitats.

22. CLADONIA ECMOCYNA subsp. INTERMEDIA

On thin soil over rocks and roadsides, rarely on wood.

Chemistry: K+ yellowish, changing to dingy yellowish-brown after a few seconds, KC-, P+ red to brick red, UV-; fumarprotocetraric acid and atranorin.

Representative specimens from the region: IDAHO. Bonner Co.: Esslinger 2286 (ASU); Custer Co.: Anderegg 2013 (ID); Idaho Co.: Hammer 5360 (FH, ID); Latah Co.: Anderegg 1348 (ID); Lemhi Co.: Anderegg 602 (ID, WIS; Shoshone Co.: McCune 16534 (OSU); MONTANA. Flathead Co.: Hammer 3928 (FH); Lake Co.: Barkley 2202 (FH); Lincoln Co.: McCune 12547 (OSU); Missoula Co.: Rosentreter 1396 (OSU); Ravalli Co.: McCune 13020 (OSU); Sanders Co.: McCune 9819 (OSU); WASHINGTON. Kittitas Co.: Pechanec s.n. (WIS); Pend Oreille Co.: Hammer 4007 (FH); Skamania Co.: Pechanec 1030 (WIS), Pechanec 3345 (WIS); Spokane Co.: Foster 2308 (FH).

There are two subspecies of Cladonia ecmocyna in the region (one unnamed), but this one is endemic to the region, and may be considered an indicator taxon. At some localities the two subspecies occur growing together.

23. CLADONIA ECMOCYNA unnamed subspecies

Terricolous over trailcuts, roadcuts, rocks, and rotting wood. Conspicuous, well-developed, and dominant over old lava beds in some localities.

Chemistry: K+ bright yellow changing to dingy yellow and then brown, KC-, P+ red, UV-; atranorin and fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 5470 (FH); Idaho Co.: Anderegg 702 (ID); Lemhi Co.: Anderegg 2148 (ID); MONTANA. Lewis Co.: Hughes 7793 (FH); Ravalli Co.: McCune 10796 (WIS); WASHINGTON. Ferry Co.: Foster 2309 (FH); Kittitas Co.:

Hammer 4837 (FH); Okanogan Co.: Hammer 5510 (FH); Pend Oreille Co.: Hammer 4018 (FH); Yakima Co.: Howard 600 (FH).

The typically subulate podetia of this subspecies intergrade with subspecies intermedia, sometimes forming distinct scyphi and abundant podetial squamules. However, in the few localities where they grow sympatrically, the two subspecies are morphologically distinct. This morph is widespread from central Oregon north to Puget Sound and east to the Rockies. It is more common in the western United States than subspecies intermedia, which is restricted to interior localities farther east and north.

24. CLADONIA FIMBRIATA

Terricolous, muscicolous over rocks, on partially rotten or on corticate wood.

Chemistry: K- or K+ dingy yellow to dingy brown, KC-, P+ brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Adams Co.: Anderegg 518 (ID); Benewah Co.: Hammer 3819 (FH, ID); Blaine Co.: Rosentreter 3632 (SRP), Bonner Co.: Hammer 3997 (FH, ID); Clearwater Co.: Anderegg 2709 (ID); Custer Co.: Morton 8561 (US); Idaho Co.: Hammer 5345 (ID); Latah Co.: Hammer 3792 (ID); Lemhi Co.: Anderegg 2119 (ID); Lewis Co.: Anderegg 1143 (ID); Nez Perce Co.: Cooke 23009 (FH); Shoshone Co.: Hammer 3851 (ID), Valley Co.: Anderegg 1993 (ID); Washington Co.: Anderegg 25975 (ID); MONTANA. Flathead Co.: McCune 14254 (OSU); Lake Co.: McCune 8666 (OSU); Missoula Co.: McCune 8580 (OSU); Ravalli Co.: McCune 12646 (OSU); OREGON. Hood River Co.: Hammer 5194 (FH); Jefferson Co.: McCune 17411 (OSU); Union Co.: Sheldon 9003 (US); Wallowa Co.: Hammer 5280 (FH); Wheeler Co.: Goward 90-152b (UBC); WASHINGTON. Asotin Co.: Hammer 5302 (FH); Chelan Co.: Howard 5217 (WTU); Ferry Co.: Hammer 4042 (ID); Garfield Co.: Hammer 3716 (FH); Kittitas Co.: Hammer 4857 (FH); Okanogan Co.: Hammer 5508 (FH); Pend Oreille Co.: Hammer 4002 (FH, ID); Spokane Co.: Bonser 1601 (FH); Stevens Co.: Hammer 4022 (FH, ID); Walla Walla Co.: Foster 5 (FH); Whitman Co.: Cooke 25206 (WIS); Yakima Co.: Hammer 5056 (FH).

This species is abundant and widespread, growing in a variety of habitats. The size of the soredia are variable, but they are somewhat smaller (40-80 µm) than those in C. chlorophaea (80-120µm). There are three morphs of C. fimbriata in the region. Although they overlap in certain characteristics, the forms remain distinct where they grow sympatrically.

Cladonia fimbriata s. str. is the most distinctive form, with stout podetia and wide scyphi, and fimbriate to bluntly digitate proliferations from the scyphus margins. The primary squamules of this form are evanescent, breaking into masses of soredia once the podetia are mature. The podetia grow in dense, uniform clusters, and the scyphi, which are symnmetrical at maturity, open from tight globose configurations. Various stages of scyphus development can be seen in a single clump. This morph is common in microenvironments with low moisture availability during the growing season, high solar insolation, and burial under snowpack for long periods. It is the most common in the region of study. A second morph, which is somewhat taller than the others, and has corticate podetial bases, is less common here than at localities west of the Cascades. In the third morph, the podetia are shorter and narrower than those described above, usually with relatively narrow scyphi, and various states of cortication and soredia. It is less distinct than the preceding, but rather common in the region. It is this morph that most frequently intergrades with C. chlorophaea and occasionally, C. pyxidata and C. pocillum.

25. CLADONIA GRACILIS subsp. TURBINATA

On soil, stabilized sand, and on dead wood, usually in somewhat shaded localities but also in more or less exposed localities.

Chemistry: K- or K+ dingy brown, KC-, P+ brick red, UV-; fumarprotocetraric acid.

Representative specimens: IDAHO. Bonner Co.: Hammer 5484 (FH); Latah Co.: Anderegg 2779 (ASU); MONTANA. Flathead Co.: Grover s.n. (US); Lincoln Co.: Hammer 3947 (FH); OREGON. Hood River Co.: Hammer 5192 (FH); WASHINGTON. Ferry Co.: Hammer 4031a (FH); Stevens Co.: Hammer 5497 (FH).

Cladonia gracilis may be difficult to distinguish from C. ecmocyna, particularly from those specimens of the former that have abundant podetial squamules and narrow cups. Secondary substances and surface pruina can distinguish the two species; C. ecmocyna contains atranorin in addition to fumarprotocetraric acid, and it also produces pruina, whereas C. gracilis contains fumarprotocetraric acid alone and does not produce pruina. The scyphi and podetia of C. gracilis are wider than those of C. ecmocyna. The cortex of C. gracilis is greenish to brownish and somewhat shiny, while the cortex in C. ecmocyna is greyish and dull.

This species is locally abundant, but it is more common in oceanic localities. It requires some organic matter and it has a more narrow ecological range than many other Cladonia species.

26. CLADONIA IMBRICARICA

On acidic soil and over volcanically-derived rocks.

Chemistry: K-, KC-, P-, UV-; sphaerophorin.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3842 (FH); Bonner Co.: Hammer 3965 (FH); Idaho Co.: Hammer 5311 (FH).

The morphology of this species is comparable to C. borealis; both species bear broad, deep, closed scyphi on wide, sometimes stalkless podetia, but C. borealis is always esorediate, yellowish (usnic acid), and has scarlet, rather than brown apothecia. The chemical spot tests of both species are similar, and even using TLC, some confusion may occur because the Rf value of sphaerophorin is very close to that of barbatic acid, which is found in C. borealis. This species is rare in North America. It has been reported from South Dakota and Wyoming, and in Skamania County, Washington, just west of the region of study.

27. CLADONIA LUTEOALBA

On soil and organic material; sometimes on podetia of C. borealis and C. coccifera.

Chemistry: P-, KC-, K-, UV- or faintly +; barbatic acid is the only compound identified from specimens in the United States, but see Stenroos (1990) for discussion of other chemical strains.

Representative specimens from the region: IDAHO. Custer Co.: Rosentreter 4526 (OSU); MONTANA. Flathead Co.: McCune & DeBolt 14593 (OSU).

The status of this rare is uncertain and I include it here provisionally. I have not seen it in the field.

28. CLADONIA MACILENTA

On dead wood, tree bases, or sometimes over soil or rocks.

Chemistry: K+ bright yellow, persistent, KC+ canary yellow, P+ orange, UV-; thamnolic, barbatic, and didymic acids.

Representative specimen in the region: WASHINGTON. Kittitas Co.: Hammer 4788 (FH).

This species is extremely rare in the region but it is common west of the Cascades. It is often confused with C. transcendens, but unlike the latter, it does not form scyphi, and pycnidia occur on the primary squamules. This species consistently produces barbatic acid in addition to thamnolic acid, whereas C. transcendens produces thamnolic acid alone. Specimens from the region have robust podetia to 4 mm wide, and 30 mm tall. They are primarily sorediate, although some cortex may persist toward the base. The soredia are farinose and fairly uniform, covering most of the podetium. These specimens resemble C. macilenta s. str., and are similar to specimens collected in eastern North America.

29. CLADONIA MACROPHYLLODES

On soil and in rock crevices, fairly dry localities.

Chemistry: K+ yellow to dingy yellow, changing to brownish, KC-, P+ red, UV-; fumarprotocetraric acid and atranorin.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3836 (ID); Idaho Co.: McCune 11502 (OSU); Lemhi Co.: Anderegg 1732 (ID); MONTANA. Flathead Co.: Howard 74 (WTU); Glacier Co.: DeBolt 621 (OSU); Missoula Co.: Hammer 3908 (FH); Ravalli Co.: McCune 11224 (OSU, WIS); OREGON. Wallowa Co.: Hammer 5284 (FH); WASHINGTON. Kittitas Co.: Hammer 4843 (FH); Pend Oreille Co.: Hammer 4005 (FH, ID); Yakima Co.: Hammer 3708 (FH).

This species may be confused with occasional atranorin- containing specimens of C. cervicornis, or with C. firma. The distinguishing character of C. macrophyllodes is the upper sides of the primary squamules, which are covered by a thick, waxy-whitish cortex that is broken into more or less isodiametric bumps. Other similar species have a smooth cortex on the upper side of the primary squamules.

This species is locally abundant in semiarid localities at low altitudes and at a few high elevation localities.

30. CLADONIA MEROCHLOROPHAEA

On thin soil over roadcuts, on duff over rock outcrops, and on stabilized sand containing some organic matter.

Chemistry: K- or K+ dingy yellowish changing to brownish, KC-, P+ orange to red, UV-; merochlorophaeic acid and accessory 4-0 methylcryptochlorophaeic acid, with fumarprotocetraric acid, protocetraric acid, and uncharacterized fatty acids in some specimens.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 5439 (FH, ID); Boundary Co.: Hammer 3955 (FH); Idaho Co.: Hammer 5385 (FH, ID); Latah Co.: Hammer 3780 (ID); Shoshone Co.: McCune 16467 (OSU); MONTANA. Flathead Co.: McCune 8030 (OSU); Lake Co.: McCune 7484 (OSU); Ravalli Co.: McCune 11015; OREGON. Hood River Co.: Hammer 5191 (FH); Wallowa Co.: Hammer 5223; WASHINGTON. Kittitas Co.: Hammer 4852 (FH); Yakima Co.: Hammer 5061 (ID).

This species is distinguished by whitish proliferations and by its abundant, imbricating, isidioid podetial squamules. Other features are 1) blackening podetial bases, 2) numerous proliferations that arise from the interior of the scyphus and which occupy almost the entire surface of the scyphus, growing very close together and occasionally fusing, and 3) brownish to bronze verruculae on the podetia.

It is uncommon west of the Cascades.

31. CLADONIA MULTIFORMIS

Terricolous on damp roadsides and over thin soil in exposed areas that are periodically dampened.

Chemistry: K- or K+ yellowish changing to dingy brown, KC-, P+ orange to purplish, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Benewah Co.: Schroeder L779 (ID); Bonner Co.: Hammer 3967 (FH, ID); Boundary Co.: Hammer 3960 (FH); Idaho Co.: Hammer 5325 (FH, ID), Kootenai Co.: Rust 557 (US); Latah Co.: Hammer 3810 (ID); Lemhi Co.: Anderegg 653 (ID); Nez Perce Co.: Cooke 20660 (WIS); Shoshone Co.: McCune 16524 (OSU); MONTANA. Flathead Co.: Weir 11585 (FH); Lake Co.: McCune 7584 (OSU); Lincoln Co.: Hammer 3948 (FH); Missoula Co.: McCune 10861 (OSU); Ravalli Co.: McCune 9472 (OSU); WASHINGTON. Ferry Co.: Foster 2357 (FH); Pend Oreille Co.: Hammer 4010 (FH); Spokane Co.: Bonser 1578 (FH); Stevens Co.: Hammer 5499 (FH).

This species is often confused with C. furcata, and both species are similar morphologically, chemically, and ecologically. In the western United States, C. furcata is found west of the Cascades exclusively. In the region of study, this species takes the ecological place of C. furcata. It is not found west of the Cascades and can be considered an indicator species for the region.

32. CLADONIA OCHROCHLORA

On old wood or thin soil over rotting wood, also on moss covered rocks, particularly at damp sites.

Chemistry: K- or K+ dingy yellow to dingy brown, KC- P+ red to brick red; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3830 (FH, ID); Bonner Co.: Hammer 5492 (FH); Boundary Co.: Hammer 3956 (FH, ID); Custer Co.: Morton 8576 (US); Idaho Co.: Hammer 3875 (ID); Latah Co.: Hammer 5403 (FH, ID); Lewis Co.: Cooke 25087 (WIS); Shoshone Co.: Hammer 3852 (ID); MONTANA. Flathead Co.: Hammer 3946 (FH); Lake Co.: McCune 7390 (WIS); Mineral Co.: Hammer 5417 (FH, ID); Missoula Co.: Hammer 3913 (ID); OREGON. Hood River Co.: Hale 21559 (US); Wallowa Co.: Hammer 5263 (FH); WASHINGTON. Asotin Co.: Hammer 5307 (FH, ID); Chelan Co.: Heller 4316 (US); Ferry Co.: Hammer 4030 (FH, ID); Kittitas Co.: Hammer 4786 (FH); Pend Oreille Co.: Layser 1472 (US); Stevens Co.: Cooke 23338 (WIS).

This species requires some organic matter as its substrate, as well as fairly damp conditions. It is common on both sides of the Casacde **Mountains.**

33. CLADONIA PHYLLOPHORA

On soil and over duff.

Chemistry: K- or K+ dingy yellowish-brownish, KC-. P+ orange red to brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 3984 (FH); Boundary Co.: Anderegg 775 (ID); Idaho Co.: Anderegg 3002 (ID); Latah Co.: Henderson 4417 (FH); MONTANA. Flathead Co.: Standley 16345 (US); Lake Co.: McCune 9721 (OSU, US); Missoula Co.: Ahti 10539 (H), McCune 6825 (OSU); Ravalli Co.: McCune 11910 (SRP); Sanders Co.: McCune 9817 (OSU); OREGON. Wallowa Co.: Hammer 5237 (FH); WASHINGTON. Ferry Co.: Hammer 4031 (FH).

In the western United States, C. phyllophora s. str. occurs exclusively east of the Cascade Mountains. It requires some organic matter as a substratum and can be considered a good indicator species for the region.

34. CLADONIA PLEUROTA

On rotting wood or duff.

Chemistry: K-, KC- or KC+ fainly yellow, P-, UV- or faintly whitish; usnic acid, isousnic acid, zeorin (present as crystals over surface).

Representative specimens from the region: IDAHO. Idaho Co.: Hammer 5361 (ID); Latah Co.: Anderegg s.n. (ID); MONTANA. Flathead Co.: McCune 14266 (OSU); Lake Co.: McCune 9722 (OSU); Mineral Co.: Hammer 5412 (FH, ID); Ravalli Co.: McCune 11050 (WIS); WASHINGTON. Ferry Co.: Hammer 4036a (FH).

Cladonia pleurota is restricted to inland localities at relatively high elevations. It is sometimes confused with C. carneola.

35. CLADONLA POCILLUM

On thin soil or duff, sometimes over pebbles, rarely muscicolous, calciphilous.

Chemistry: K- or K+ dingy yellowish, changing to brownish, KC-, P+ brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: 'DAHO. Custer Co.: Anderegg 1782 (ID); Idaho Co.: Hammer 5216 (FH), McCune 11500 (OSU); Lemhi Co.: Anderegg 1691 (ID); MONTANA. Flathead Co.: McCune 12451 (OSU); Glacier Co.: McCune 15932 (OSU); Mineral Co.: Hammer 5409 (FH, ID); Missoula Co.: McCune 10593 (OSU); OREGON. Wallowa Co.: Hammer 5297 (FH); WASHINGTON. Kittitas Co.: Hammer 4853a (FH).

This species is distinguished by its thick, brown, primary squamules, which are fused together and which resemble a foliose lichen. The lower surface of the squamules is cottony. The short (< 1 cm) podetia, with numerous peltate squamules on the insides of the scyphi, also distinguish this species. It is difficult to distinguish C. pocillum from depauperate collections of C. pyxidata, C. chlorophaea, or C. fimbriata. In specimens from montane localities, C. fimbriata may develop characters that resemble C. pocillum, particularly where the soredia have become corticate or where they have been shed. Specimens of C. fimbriata and C. chlorophaea from montane localities often consist of squamules only, which further confuses their identity. This species is an indicator species for the region, although its habitat requirements are somewhat specialized.

36. CLADONIA PROLIFICA

On duff of ericaceous shrubs, over acidic soil, on thin soil over stabilized sand dunes, under Pinus contorta, and on siliceous outcrops.

Chemistry: K- yellowish to dingy brown, KC-, P+ brick red; fumarprotocetraric acid with accessory protocetraric acid.

Representative specimen from the region: IDAHO. Latah Co.: Hammer 3772 (FH).

Cladonia prolifica is variable. It uncommon west of the Cascade Mountains, and is quite rare in the region. It grows on acidic soil over roadcuts or lava.

37. CLADONIA PYXIDATA

On soil, rarely over wood.

Chemistry: K- or K+ dingy yellowish changing to dingy brown, KC-, P+ red; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Adams Co.: Anderegg 1242 (ID); Benewah Co.: Hammer 3842 (FH); Boundary Co.: Anderegg 771 (WIS); Custer Co.: Naskali s.n. (ID); Idaho Co.: Hammer 5318 (FH, ID); Latah Co.: Anderegg 68 (ID, WIS); Lemhi Co.: Steele 2057 (ID); MONTANA. Lake Co.: McCune 9750 (OSU); Mineral Co.: Hammer 5414 (FH); Ravalli Co.: McCune 11998 (OSU); OREGON. Wallowa Co.: Hammer 5290 (FH); WASHINGTON. Pend Oreille Co.: Hammer 5451 (FH, ID); Spokane Co.: Bonser 11 (FH).

This species is distinguished by broad, deep scyphi, a persistent, longitudinally rugose outer cortex, and a short stipe. It is comparable to C. pocillum, but the primary squamules in the latter are distinctive. The peltate squamules, which occur in young specimens of C. pyxidata are occasionally seen in mature C. chlorophaea, C. dimorpha, and C. pulvinella, and C. fimbriata. This poorly understood species has been considered to be quite widespread in western North America. However, it is restricted to the region of study, being absent from areas west of the Cascade Mountains. It is a good indicator species for the region.

38. CLADONIA REI

On thin soil or terricolous over compressed duff.

Chemistry: K- or K+ dingy yellowish changing to brownish, KC-, P+ red, UV-; sekikaic and homosekikaic acids with fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 5485 (FH); WASHINGTON. Stevens Co.: Hammer 5500 (FH).

Cladonia rei is geographically restricted to the region, and has not been collected west of the Cascades. Although it is quite rare, it may be considered a good indicator species for the region.

39. CLADONIA SCABRIUSCULA

Collected on thin soil on road cuts and among mosses, usually terricolous, not collected on wood.

Chemistry: K- or K+ dingy yellow to dingy brown, KC-, P+ brick red.; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3833 (FH); WASHINGTON. Kittitas Co.: Schallert C-49 (US).

Cladonia scabriuscula is morphologically close to C. furcata. The podetia are characterized by sorediate tips, but intermediate forms may have scurfy to verruculose tips, and these conditions may intergrade. The species is rare in the region but more common west of the Cascade Mountains.

40. CLADONLA SINGULARIS

On volcanic rock and on compressed duff.

Chemistry: K-, KC-, P-, UV+ ice blue (squamatic acid).

Representative specimen from the region: WASHINGTON. Kittitas Co.: Hammer 4848 (FH).

This species resembles C. squamosa, but the podetia have subulate apices. Although it is in section Perviae, the axial and apical openings are very small and not visible at a glance.

41. CLADONIA SQUAMOSA var. SQUAMOSA

Terricolous or over duff, often on rotting, ecorticate wood. Moist forests, but the related C. cenotea is more common in the wetter forests.

Chemistry: K-, KC-, P-, UV+ ice blue; squamatic acid.

Representative specimens from the region: IDAHO. Idaho Co.: McCune 10190 (SRP); Shoshone Co.: McCune 16535 (OSU); MONTANA. Lake Co.: Rosentreter MT-293 (SRP); Lincoln Co.: McCune 16232 (OSU); OREGON Hood River Co.: Hammer 5184 (FH); WASHINGTON. Kittitas Co.: Hammer 4796 (FH).

This variety is more common in the region than the morphologically identical, thamnolic acid-containing var. subsquamosa, which is more common west of the Cascades.

42. CLADONIA SQUAMOSA var. SUBSQUAMOSA

On rotten, ecorticate wood, or terricolous.

Chemistry: K+ bright yellow, KC-, P+ yellow, changing to orange; thamnolic acid.

Representative specimens in the region: IDAHO. Latah Co.: Anderegg 2782 (ID); OREGON. Hood River Co.: Hammer 5183 (FH, ID).

43. CLADONIA SUBULATA

Terricolous over roadcuts or on bare earth, usually in shady areas.

Chemistry: K- or K+ dingy yellow to dingy brownish, KC-, P+ brick red, UV-; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3831 (FH); Bonner Co.: Hammer 5489 (FH, ID); Idaho Co.: Hammer 5363 (FH); Latah Co.: Hammer 3894 (FH, ID); Lemhi Co.: Anderegg 2117 (ID); MONTANA. Flathead Co.: Hammer 3945 (FH); Missoula Co.: Hammer 3927 (FH); WASHINGTON. Pend Oreille Co.: Hammer 5456 (FH).

This species and C. fimbriata may be difficult to distinguish, but C. fimbriata forms shallower scyphi than C. subulata. The scyphi of C. fimbriata are never perforated, but radiate perforations may form in C. subulata. Finally, C. subulata may bear central proliferations, which are not seen in C. fimbriata.

44. CLADONIA SULPHURINA

On rotting wood or compressed duff, rarely terricolous

Chemistry: K-, KC- or yellowish, P-, *W+;* usnic acid, squamatic acid, accessory bellidiflorin.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 3992 (FH, ID); Custer Co.: Anderegg 2043 (ID); Idaho Co.: Anderegg 627 (ID); Latah Co.: Anderegg 860 (ID); Lemhi Co.: Anderegg 2058 (ID); MONTANA. Flathead Co.: Williams s.n. (US); Lake Co.: McCune 7415 (OSU); Ravalli Co.: McCune 7218 (OSU); OREGON. Wallowa Co.: Hammer 5244 (FH); WASHINGTON. Chelan Co.: Hammer 4053 (FH); Ferry Co.: Hammer 4049 (FH); Kittitas Co.: Hammer 4839 (FH); Pend Oreille Co.: Hammer 4018 (FH); Stevens Co.: Hammer 4027 (FH); Yakima Co.: Hammer 5054 (FH, ID).

In the western United States, this species is restricted almost entirely to the region. It is morphologically similar to C. carneola, with sorediate, scyphus-bearing podetia, but the apothecia in C. sulphurina are scarlet whereas in C. carneola, they are beige to light brown. The color of incipient apothecia in both of the species is difficult to distinguish. The scyphi of C. carneola are more symmetrical than those of the present species, and the margins consistently bear regularly arranged pycnidia, which are absent in many specimens of C. sulphurina. This is a good indicator species for the region.

45. CLADONIA TRANSCENDENS

On rotting, ecorticate wood, rarely terricolous

Chemistry: K+ yellow, persistent, KC+ yellow, P+ deep yellow to orange-red, UV-; thamnolic acid and accessory usnic acid.

Representative specimens from the region: IDAHO. Latah Co.: Anderegg 377 (ID); Lewis Co.: Anderegg & Schroeder 1152 (ASU); OREGON. Hood River Co.: Hammer 5185 (FH); WASHINGTON. Yakima Co.: Anderegg 1102 (ID, WIS).

This species is morphologically and chemically variable. It contains thamnolic acid with accessory usnic acid, and resembles the squamatic acid-contining thalli of C. umbricola. The squamatic acid-containing C. umbricola is more common in the region than this species, which is found more commonly west of the Cascade Mountains.

46. CLADONIA UMBRICOLA

On rotting, ecorticate wood, on stumps and bases of living trees, rarely over soil.

Chemistry: K- yellow, reddish in some places, KC-, P-, UV ++ ice blue; squamatic acid.

Representative specimens from the region: IDAHO. Benewah Co.: Hammer 3824 (FH); Clearwater Co.: Anderegg 1617 (ID); Idaho Co.: Hammer 5386 (FH, ID); Kootenai Co.: Rosentreter 2318 (SRP); Latah Co.: Hammer 3781 (FH, ID); Lewis Co.: Anderegg 438 (ID); Shoshone Co.: Rosentreter 5055 (SRP); MONTANA. Flathead Co.: McCune 7248 (OSU); Lake Co.: Rosentreter 3221 (H); Missoula Co.: McCune 9505 (OSU); Ravalli Co.: McCune 9474 (OSU); OREGON. Klamath Co.: Goward 90-224a (UBC); Wallowa Co.: Hammer 5206 (FH, ID).

The specimens cited here as C. umbricola should be considered only provisionally as such, but whatever their taxonomic position, this species is a good indicator taxon for the region.

47. CLADONIA UNCIALIS

On thin soil over rocks, rarely over stabilized sand.

Chemistry: K-, KC+, P-; usnic acid.

Representative specimens: IDAHO. Idaho Co.: Rosentreter 2357 (SRP); Shoshone Co.: McCune 7737 (ID).

This species is rare in the region, and is restricted to relatively moist, equable localities in Washington and Idaho.

48. CLADONIA VERRUCULOSA

On thin soil on exposed roadcuts or under conifers, also found on stabilized sand dunes among short grasses.

Chemistry: K- or K+ dingy yellow changing to dingy brown,
KC-, P+ brick red; fumarprotocetraric acid.

Representative specimens from the region: IDAHO. Bonner Co.: Hammer 5482 (FH); Boundary Co.: Hammer 3951 (FH); Idaho Co.: Hammer 5375 (FH, ID); Latah Co.: Hammer 3796 (FH, ID); Nez Perce Co.: Cooke 19252 (WIS); Shoshone Co.: Hammer 3848 (FH); MONTANA. Glacier Co.: DeBolt 1406 (OSU); Mineral Co.: Hammer 5419 (ID); Missoula Co.: Hammer 3914 (FH); OREGON. Hood River Co.: Hammer 5196 (FH); Wasco Co.: Pike LL 196 (US); Wallowa Co.: Hammer 5277 (FH, ID); WASHINGTON. Ferry Co.: Hammer 4032 (FH, ID); Kittitas Co.: Hammer 4790 (FH); Pend Oreille Co.: Hammer 5445 (ID); Spokane Co.: Cooke 23177 (WIS), Cooke 23206 (WIS); Stevens Co.: Hammer 5498 (FH); Yakima Co.: Hammer 5066 (FH).

Cladonia verCculosa is frequently misidentified as . nemoxyna (= C. rei Schaerer). Cladonia verruculosa is widespread and abundant on both sides of the Cascade Mountains. It can tolerate a variety of microhabitats, including relatively dry microsites.

ANNOTATED LIST OF RELEVANT LITERATURE

This abbreviated list is intended as a guide to recent and historical literature on the species of Cladonia in the far western Uniited States, particularly the Columbia Basin. Where appropriate, other related sources have been included, especially in the areas of chemotaxonomy, nomenclature, and physiological ecology of lichens.

Ahti, T. 1978. Two new species of Cladonia from western North America. Bryologist 81: 334-338. (see reference to C. verruculosa).

_____. 1980b. Taxonomic revision of Cladonia gracilis and its allies. Ann. Bot. Fennici 17: 195-243. (important paper with references to C. gracilis and C. ecmocyna, but W. US neglected).

Anderegg, D.E. 1977. Idaho lichens. 1. The Cladonias of Idaho. J. Idaho Acad. Sci. 13: 1 1-22. (this and the following are early papers with some mistaken concepts).

_____, G.J. Schroeder, and N. E. Schroeder. 1973. Further additions to the lichen flora of Idaho. Bryologist 76: 207-208.

Bailey, R.H. 1976. Ecological aspects of dispersal and establishment in lichens. In Brown, D. H., D. L. Hawksworth, and R.H. Bailey, eds., Lichenology: progress and problems, 215-247. London and New York, Academic Press.

Christensen, S.N. 1987. Morphological and chemical variation in the Cladonia macilenta/bacillaris aggregate in Denmark. Lichenologist 19: 61-69. (Two problem taxa from the region discussed here).

Culberson, C. F. 1969. Chemical and botanical guide to the lichen products. Chapel Hill, University of North Carolina Press. 628 p. (The standard work for secondary chemistry of lichens).

_____. 1970. Supplement to "Chemical and botanical guide to the lichen products". Bryologist 70: 177-377.

_____, _____, and A. Johnson. 1977. Second supplement to "Chemical and Botanical Guide to the Lichen Products". St. Louis, The American Bryological and Lichenological Society. 400 p.

Culberson, C. F. and H. Kristinsson. 1969. Studies on the Cladonia chlorophaea group: a new species, a new metadepside, and the identity of "novochlorophaeic acid". Bryologist 72: 431-443. (Discussion of C. imbricarica here).

Culberson, W.L. 1969. The chemistry and systematics of some species of the Cladonia cariosa group in North America. Bryologist 72: 377-386.

Degelius, G. 1935. Das Ozeanische Element der Strauch-und Laubflechtenflora von Skandinavien. Acta Phytogeogr. Suec. 7:1-141. (Important early paper on lichens with oceanic affinities,including some problems encountered in our area).

Evans, A. W. 1955. Notes on the North American Cladoniae. Bryologist 58: 95-112. (Important paper with regard to species concepts in our region).

Eyerdam, W.J. 1960. Lichens new to the State of Washington. Bryologist 63: 107-110.

Foster, A. S. 1906. Lichens of the state of Washington. Manuscript in the Farlow Reference Library, not published. (Interesting historical account-the corresponding specimens are found in the Farlow Herbarium).

Hammer, S. 1991. A preliminary synopsis of the species of Cladonia in California and adjacent Oregon. Mycotaxon 40: 169-197.

_____. 1993a. A Revision of the lichen genus Cladonia in western North America. Dissertation, Harvard University.(complete descriptions, keys, maps, biogeographical discussions, and literature citations found here).

_____. 1993b. Development in Cladonia ochrochlora. Mycologia 85: 84-92. (reference to C. ochrochlora and other cup-forming lichen here).

_____. 1993c. Two new Cladonia species from western North America: C. artuata and C. poroscypha. Bryologist 96: 80-85. (This and paper below deal with endemic species).

_____. 1993d. A revision of Cladonia section Perviae in the western United States. Bryologist 96. (Reference to C. cenotea,C. crispata, C. squamosa).

. 1994. Cladoniaceae Americanae Exsiccatae. Mycotaxon 52:475-493. (Voucher specimens for many localities in this report may be found here).

_____. 1995. A synopsis of the lichen genus Cladonia in the northwestern United States. Bryologist 98: 1-29.(Complete keys, distribution maps, descriptions, and citations for the species under study can be found here).

and T. Ahti. 1990. New and interesting species of Cladonia from California. Mycotaxon 37: 335-348.

Hennings, C.J. 1983. The Cladonia chlorophaea- C. fimbriata group in Washington. Bryologist 86: 64-73. (Reference to these species as well as C. merochlorophaea, C. conista).

Holien, H. and T. Tønsberg. 1985. Notes on the Cladonia asahinae, C. conista and the C. grayi-group in Norway. Gunneria 5 1: 1-26.

Howard, G. E. 1937. Preliminary report of the lichens of the state of Washington. Bryologist 40: 91-112. (Early work on the region, specimens at WTU).

_____. 1950. Lichens of the state of Washington. Seattle, University of Washington Press. 187 p.

_____. 1955. Lichens of northwest America collected by W. N. Suksdorf. Bryologist 58: 49-64.

Huovinen, K., and T. Ahti. 1982. Biosequential patterns for the formation of depsides, depsidones, and dibenzofurans in thegenus Cladonia (lichen-forming ascomycetes). Ann. Bot. Fennici 19: 225-234. (This and the following papers treat chemosystematics of the species).

_____ and _____. 1986. The composition and contents of aromatic lichen substances in Cladonia section Unciales. Ann. Bot. Fennici 23:173-188.

_____, and _____. 1988. The composition and contents of aromatic substances in Cladonia section Perviae. Ann. Bot. Fennici 25:371-383.

_____, _____, and S. Stenroos. 1989a. The composition and contents of aromatic substances in Cladonia section Cocciferae. Ann Bot. Fennici 26: 133-148.

_____, _____, and _____. 1989b. The composition and contents of aromatic substances in Cladonia section Helopodium and subsection Foliosae. Ann Bot. Fennici 26: 297-306.

_____, _____, and _____. 1990. The composition and contents of aromatic lichen substances in Cladonia section Cladonia and group Furcatae. Bibl. Lichenol. 38:209-241.

Kärnefelt, I. 1980. Lichens of western North America with disjunctions in Macaronesia and west Mediterranean region. Bot. Not. 133: 569-577. (See reference to Cladonia macrophyllodes here).

Kershaw, K.A. 1985. Physiological Ecology of Lichens. Cambridge, Cambridge University Press. 239 p. (An overview of lichen physiological ecology, providing experimental data for some of the ecological tables in this report).

Lesica, P., B. McCune, S.V. Cooper, and W.S. Hong. 1990. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Can. J. Bot. 69: 1745-1755. (An important paper with implications for rare andendemic lichen species in the region).

Magnusson, A.H. 1932. Lichens from western North America, mainly Washington and Alaska. Ann. Crypt. Exot. 5:16-38. (This and the following paper are of historical interest)

_____. 1939. Western American lichens, mainly from Oregon. Medd. Göteborgs Bot. Tradg. 13: 237-253.

McCune, B. 1984. Lichens with oceanic affinities in the Bitterroot Mountains. Bryologist 87: 44-50. (A landmark paper with reference to species of the region).

Østhagen, H. Nomenclatural notes on Cladonia nemoxyna. Bryologist 79: 242-245. (Reference to C. rei here).

Pike, L. H., W. C. Denison, D. M. Tracy, M. A. Sherwood, and F. M. Rhodes. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. Bryologist 78: 389-402. (An important earlier paper on forest lichen communities).

Robbins, C. 1931. Cladonias collected by S.F. Blake in the western United States. Rhodora 30: 135-139. (Historical interest, see reference to C. ecmocyna subsp. intermedia).

Schroeder. G. J., D. E. Anderegg, and N. E. Schroeder. 1973. Cladonia yunnana new to North America. Bryologist 76: 199-200. (See Hammer 1993a for comments).

, T. L. Esslinger, D. E. Anderegg, and N. E. Schroeder. 1973. Seventy lichen species previously unreported from Idaho. J. Idaho Acad. Sci. 9: 1-6.

Schroeder, N. E., G. J. Schroeder, and D. E. Anderegg. 1975. A catalogue of the lichens of Idaho. Bryologist 78: 32-43.

Stenroos, S. 1989a. Taxonomic studies in Cladonia section Cocciferae, with special reference to secondary product chemistry. Publications from the Department of Botany, University of Helsinki 13: 1-15.

_____. 1989b. Taxonomy of the Cladonia coccifera group. 1. Ann. Bot. Fennici 26: 157-168.

_____. 1990. Cladonia luteoalba-an enigmatic Cladonia. Karstenia 30: 27-32.

Taylor, D. W. Floristic relationships along the Cascade-Sierran axis. Am. Midl. Nat. 97: 333-348. (A useful biogeographical analysis).

Thomson, J. W. 1968 ('1967'). The lichen genus Cladonia in North America. Toronto, University of Toronto Press. 172 p. (The most important work by the dean of American lichenologists--still a very useful guide).

_____. 1969. A catalogue of lichens of the state of Washington. XI International Botanical Congress, Processed publication, Seattle. 59 p.

. 1976. Cladonia asahinae sp. nov. from western North America. J. Jap. Bot. 5 1: 360-364.

Tønsberg, T., and T. Ahti. 1980. Cladonia umbricola, a new lichen species from NW Europe and western North America. Norw. J. Bot. 27: 307-309. (This and the following paper represent an effort to introduce NW European species into N. American taxonomic framework. Both species are doubtful in the region, however).

and T. Goward. 1992. Cladonia norvegica new to North America. Evansia 9: 56-58.

White, F. J., and P. W. James. 1985. A new guide to microchemical techniques for the identification of lichen substances. Brit. Lich. Soc. Bull. 75: 1-41. (A useful guide for certain chemical applications).

RARE TAXA AND THEIR LOCALITIES

(where **bold** locality numbers are provided these correspond to Table 4; Localities Visited For This Study).

Species	Locality or localities
1. C andereggii	2
2. C. bellidiflora	**13, 16**, and WA., Kittitas Co., FR 4930 along Canyon Creek, 1-3 mi. N of Kachess Campground, Wenatchee NF [1]
3. C. coccifera	15
4. C. cornuta subsp. groenlandica	McCune 10512 (OSU). I did not record exact locality data
5. C. crispata	Old specimen at Farlow Herb. Detailed locality data not available on packet
6. C. dahliana	**11**, also McCune 9182 (OSU), 11019 (SRP), and Goward 90-125. I did not record exact locality data.
7. C. digitata	Rosentreter 2062 (SRP); Rosentreter MT-286 (SRP); Howard 850 (WTU). I did not record exact locality data.
8. C. dimorpha	2
9. C. imbricarica	**4, 12, 25** (This locality is but a large boulder at the side of the road).
10. C. luteoalba	Rosentreter 4526 (OSU); McCune & DeBolt 14593 (OSU). I did not record exact locality data.
11. C. macilenta	WA., Kittitas Co., FR 4930 along Canyon Creek, 1-3 mi. N of Kachess Campground, Wenatchee NF [1]
12. C. prolifica	2

13. C. rei	**12, 31**
14. C. scabriuscula	**4**
15: C. singularis	WA., Kittitas Co., FR 4930 along Canyon Creek, 1-3 mi. N of Kachess Campground,Wenatchee NF [1]
16. C. squamosa var. squamosa	**19**, also WA., Kittitas Co., FR 4930 along Canyon Creek, 1-3 mi. N of Kachess Campground, Wenatchee NF [1]. Other specimens: McCune 10190 (SRP), McCune 16535 (OSU), Rosentreter MT-293 (SRP), and McCune 16232 (OSU), I did not record exact locality data on these specimens.
17. C. squamosa var. subsquamosa	**2, 19**
18. C. transcendens	**2, 19.** Other specimens: Anderegg & Schroeder 1152 (ASU), Anderegg 1102 (ID, WIS), I did not record exact locality data on these specimens.
19. C. uncialis	Rosentreter 2357 (SRP); McCune 7737 (ID). I did not record exact locality data.

[1] Logging activities near this site were intense when I visited it in 1991. Remaining natural areas in the vicinity N of Hwy 90 up to the border of the North Cascades National Park should be canvassed for rare species. This includes Snoqualmie-Baker National Forest and Wenatchee NF.

EXCLUDEDTAXA

Cladonia botrytes

This species was reported from Glacier National Park (McCune pers. comm.), but the specimen was unavailable for study. I did not collect the species, nor was it in herbaria, so I consider the single report as a doubtful record. I reported this species as doubtful in Hammer (1993a).

C. firma

This species was reported in Hammer and Ahti 1990 as new to North America. McCune (1994) based his reports of it on a comparison with a specimen from British Columbia that Ahti identified as *C. firma* (R. Rosentreter pers. comm). It is extremely rare in North America, and its unusual habitat requirements in central coastal California are unlike the conditions in Bristish Columbia. I have not seen any of the specimens in question. I consider *C. firma* as a doubtful species for the area.

C. norvegica

Specimens labeled as *C. norvegica* from northwestern Washington are indistinguishable from *C. bacillaris*. I have not seen any specimens labelled as *C. norvegica* from the region of study, so I am unable to judge their status.

Boston University
College of General Studies
871 Commonwealth Avenue
Boston, Massachusetts 02215

RECEIVED
JAN 30 1995
BLM-IDSO

Dr. Roger Rosentreter
United States Department of the Interior
Bureau of Land Management
3380 Americana Terrace
Boise, Idaho 83706-2500

22 January 1995

Dear Roger:

Please find enclosed my addenda to the report entitled, "The Biogeography and Ecology of Species in the Lichen Genus Cladonia in the Columbia River Basin." I have included the addenda as an entry in the original Table of Contents, so they can be found as a continuation of the revised report on page 61. The addenda section contains a separate Table of Contents, found on page 62 of the revised report.

Before I go on, let me address the issues you raised in your letter of 15 January, point by point (I have enclosed your letter, which I've annotated π 1, π 2, etc. so you can refer back to it if necessary).

π 1. If you have maps with Townships on them, I will be happy to mark the localities of rare species on them. As I have indicated on the new table "Rare taxa and their localities," I do not have exact locality data on specimens that I did not collect. There are precise data for specimens I did collect, and those are summarized on the new table. I hope this provides sufficient locality data, as far as what my records provide. If not, let me know what I can do.

π 2. An annotated list of relevant literature is included in the addendum. I hope this provides what you need. Sorry I neglected the literature cited section in the first copy of the report--I thought it kind of useless for a non-academic audience. I hope the annotations prove useful.

π 3. See comments on π 1 above.

π 4. I have gone ahead and fit McCune-type classifications to the taxa McCune did not include. The data are in a separate table in the addendum but, as indicated there, they can be slipped into the original report as desired. Since McCune didn't include them in the first place, I obviously couldn't have included his classification for them. Sorry!

π 5. a) Most of the species included are, alas, indicators rather than endemics. With the-exception of C. andereggii and possibly C. singularis (which is locally abundant just west of the region on the lava flows near Carson, WA (Skamania Co.), the rare species here are either circumboreal or escapees from oceanic areas just to the west.. I am happy to make any changes you need but I'm not sure of the difference between indicator and faithful.

b) I was blown away by McCune's Table 2 (and by his whole report, which was excellent!) and I told him so. I don't have any data like those he presented on indicator values of the functional groups, viz., air quality, high N, metal-rich rock, etc. If you need me to include those kinds of data I'll go ahead and try but it will be a stretch-in fact I cannot at all say how accurate I'd be at guessing about these.

π 6. Below are my references to logging and clearcutting. You know better than me the state of these roads; I' can't support my statements with anything but informal observations, from the few dozen logging roads I've been on.

But seriously---I'm back east here and you're' right there, and you know who'll be reading the report. Go ahead and edit these statements as you see fit to make them more tactful. You shouldn't have any trouble doing it right on the diskette-or if you want to send me your comments I'll be happy to put the changes in and send them along to you.

Cladonia species do not establish on the banks of logging roads. These roads are usually very'poor in organic materials. Further, they are muddy and prone to erosion in heavy rainfall,, and cannot support even weedy species such as C. verruculosa (p. 11).

In situations where phanerogamic vegetation (for example ferns) dominates trailside sites, Cladonia species are infrequent. The least productive habitats are exposed hillsides and mountain sides that have been clearcut. Lichen establishment is restricted by severe soil erosion, a dry season unameliorated by shade, the lack of fog-drip, and the lack of soil and organic matter. Abiotic factors such as evapotranspiration are influenced by the lack of forest cover and microenvironmental conditions are also altered. This results in the absence of Cladonia species in logged areas. (PP. 11-12).

Thus, Cladonia species are an important factor in the overall health of ecosystems, particularly in sites that are adjacent to areas which have been compromised by logging or other human disturbance factors. (p. 13).

π 7. Re some of your post-its:

C. pleurota	vs.	C. carneola
red **apothecia**		**beige apothecia**
mostly entire cup margins		crown-like ring of pycnidia around margins

Masses of Cladonias on clearcut stumps?

--Older clearcut areas? --Stumps at the edge of forests, or where forests have grown around 'em?--Were these quite recently cut?

Bryoria fremontii/Ponderosa Pine Cladonias?

No, but see p. 10: "In general, the pine forests east of the Cascade Mountains are too dry to support most of the species, but some of the species with drier habitat requirements may be found there."

C. firma seen by Ahti in BC? Sorry I wasn't with you guys there.

π 8. See my notes in addendum on excluded taxa. I can't vouch for specimens I haven't seen. But if you feel certain about them please include them.

π 9. Thanks for your comments. I changed the 4th sentence on' p. 10. Couldn't find the sentence with the missing verb on p. 54 or thereabouts. Changed Debolt to DeBolt!! Sorry!!

π 10. I'm happy to "default" to you as peer reviewer.

Please let me know if there are further revisions you need. The semester has cranked up again so time is scarce! Hope you enjoyed your travel time.

Sincerely yours,

Samuel Hammer Ph.D.
Assistant Professor