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Quantitative Relationships of Terrestrial Mosses with Some Coniferous Forests at Mt. Rainier National Park

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The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana's vegetation in past decades. Authors were Butler faculty, current and former master's degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler's first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner , included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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QUANTITATIVE RELATIONSHIPS OF TERRESTRIAL MOSSES WITH SOME CONIFEROUS FORESTS AT MT. RAINIER NATIONAL PARK

By N. HIGINBOTHAM AND BETTY WILSON HIGINBOTHAM

Relatively few studies have been made on the correlation of moss societies with tree species in climax associations in North America; this is true despite the fact that in Europe moss unions have been accorded considerable importance along with societies of larger plants in delimiting phytocoenoses. The present study is an attempt to characterize as accurately as possible the terrestrial moss communities of typical climax stands in a given area, largely in Mt. Rainier National Park, and to discover how closely related bryophyte occurrence, frequency, and coverage may be to the societies of higher plants.

The literature on bryo-sociology, as it may pertain here, has been summarized by Cain and Sharp (4) and therefore is not reviewed here. Cain and Penfound (3) included moss societies in their study of the *Acer rubrum* swamps of Long Island. In the most extensive moss ecology study in North America, Cain and Sharp (4) have described a number of moss communities found in forest types of the Great Smoky Mountains. In six forest associations 34 bryophyte communities were described on the basis of a systematic sampling method; the accuracy of the latter was tested by means of the species-area curve. They concluded that 23 of the 34 moss communities could be classified in 2 alliances comprising 10 unions and 14 (union) facies; the remaining moss communities were not so well characterized because they were less frequent or they appeared to be seral. In their study four substrate types were systematically estimated: terrestrial, epilithic, epixylic, and corticolous. It was noted that a number of species occurred in more than one habitat type and also that they ranged over two or more forest associations. Cain and Sharp emphasized species range in their discussion; however, their data show numerous correlations of the moss societies with the climax tree stands. The combinations of dominant bryophyte species seem to differ in each forest type, and some species, such as *Hylocomium splendens,* were found to be essentially restricted to as-

sociations in which *Abies fraseri* and *Picea rubens* were dominant species.

Ilvessalo (8) has attempted to give some evaluation of forest (site) types in North America by use of the ground cover as indicators. Some moss species were found to be important in a number of stands. The stands he reported on were spread over widely differing climatic areas and data were given on groups of moss species; close correlations of mosses with tree communities, therefore, were not revealed in this work.

METHODS

Selection of individual stands to be studied was based on consideration of all the various forested zones of the eastern portion of Mt. Rainier National Park and on the criteria for climax stands as subjectively judged. A tree species was considered dominant when there was good evidence that it was maintaining itself as shown by reproduction and the presence of a range of sizes from seedlings to large trees competing for the overhead canopy. Stands in which mature tree species were not reproducing themselves were considered immature or seral; such stands typically showed a multiplicity of species uncharacteristic of older stabilized forest sites.

Estimates of mosses, shrubs, and herbs were made by use of Braun-Blanquet (1) coverage scale in 0.1 square meter plots (20 cm. x 50 cm.) distributed along a straight line. With some exceptions, which are noted below, the plots were taken at each meter (0.8-meter spacing), with 25 plots examined for each stand. The exact location of the line of plots was selected as that typical of undercover areas of the stand as a whole. In particular, mesic ground surface was chosen; streams, low wet spots, rock outcrops, and chance clusters of logs were avoided. However, every substrate occurring in the plots was included in the estimates, including logs, tree bases, and rock. It should be emphasized that, in general, this method leads to a measure of relatively mature vegetational areas and minimizes seral species.

Tree coverage estimates were made in essentially the same manner, but, of course, do not represent a similar accuracy. These estimates were intended to indicate primarily the direct overhead coverage of the small plots. The species are believed to be typical of the

climax stand in each case, although the figures as given may not accurately reflect the degree of coverage of each species.

Only five coverage classes were used here in contrast with the method used by Cain and Sharp, who used a sixth, x, to indicate occurrence of a species covering 1 per cent or less (of community area). Also, in the present work, coverage and frequency data are reported in percentages, as shown in table 1.

TABLE 1

Coverage classes and percentages used in estimating area of communities.

Class	Percentage coverage range	Value (percentage used in calculating average coverage)
1	0 - 5	2.5
2	5 - 25	17.5
3	25 - 50	37.5
4	50 - 75	62.5
5	75 - 100	87.5

DESCRIPTION OF AREA

The area under study lies largely in the eastern portion of Mt. Rainier National Park and consists of the eastern slopes of Mt. Rainier (at lower elevations) and the western slopes of the Cascade Mountain Range. Eleven of the stands were within the drainage system of the Ohanapecosh River, which originates from the Ohanapecosh Glacier. Since this area is west of the divide of the Cascade Range, it receives a relatively high amount of precipitation, particularly between October and May, with much of the precipitation as snow. No records are available for precipitation in the immediate vicinity of most of the stands; however, at Longmire (2,760 ft.) about 12 miles west of Ohanapecosh Hot Springs, the mean annual precipitation is given as 78 inches, and at Paradise Park (5,557 ft.), northwest of Ohanapecosh Hot Springs, as about 100 inches (2). Since high ridges and old mountain peaks lie between these locations and the Ohanapecosh River, it is possible that a somewhat lower precipitation occurs in the region of the stands studied.

MEASURE OF ACCURACY OF THE METHOD

A common method of determining the area size required for estimating the importance of species in a community is the species-area

curve. In the present study some test of the accuracy is given by the data from stand 10 in which 50 plots were taken and calculated cumulatively in groups of five as shown in table 2. The number of species becomes nearly constant in the first 15 plots; an additional 35 plots added only one more species. Of greater significance, probably, is the estimate of percentage area covered by a species. Only 5 plots would closely reflect the relative abundance of the two more important species. The decision to use 25 plots for a stand, in most cases, seems quite adequate for the purposes of this study. It should be pointed out, however, that in regions having a lesser moss cover and/or an uneven distribution, this number might not be adequate.

TABLE 2

The relation of area to number of bryophyte species and coverage. Area by cumulative 5-plot totals, 0.1-meter plots. Data from stand 10 (*Abies amabilis-Tsuga heterophylla* community).

Plots	1-5	1-10	1-15	1-20	1-25	1-30	1-35	1-40	1-45	1-50
No. species	3	4	6	6	6	7	7	7	7	7
Per cent coverage (total bryophytes)	58	58	54	58	61	59	54	51	55	52
Species coverage										
Rhytidiopsis robusta	36	44	40	43	47	45	42	40	42	39
Dicranum fuscescens	17	13	13	14	14	13	11	10	12	12
Other species	5	1	1	1	0	1	1	1	1	1

DESCRIPTION OF THE STANDS AND RESULTS

Pseudotsuga menziesii community

Two stands of forest which apparently represent a climax of *Pseudotsuga menziesii* (Douglas-fir) were studied. Stand 1 was located on State Route 5 at Summit Creek (1.5 miles south of the park boundary) and stand 2 was 2.0 miles south of Clearfork River (4.8 miles south of the park boundary). Approximate elevations of the study sites were 1800 and 1600 feet respectively.

In these forests almost pure stands of Douglas-fir were found with all stages of reproduction and trees ranging up to more than 3 feet DBH. Although *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) occupy moister areas nearby, they did not appear to be invading the Douglas-fir stands. The more con-

spicuous plants associated with the Douglas-fir are *Acer circinatum*, the vine-maple, a shrub or small tree forming a scattered understory, and the low shrubs *Gaultheria shallon* and *Berberis nervosa*. Estimated coverage values for these and other species are given in table 3.

The mosses which were most abundant and frequent under Douglas-fir were *Eurhynchium oreganum, Hylocomium splendens,* and *Rhytidiadelphus triquetrus*. The most striking feature here, perhaps, is the high frequency of *Eurhynchium oreganum* in the Douglas-fir community and the lesser frequency of this species in other sites (table 3). The frequency of *Eurhynchium oreganum* seems directly related to the coverage value of Douglas-fir in all stands. This feature plus the coverage of *Rhytidiopsis robusta* under *Tsuga heterophylla* appears to delimit sharply the Douglas-fir stands from those of western hemlock.

Here, as in other stands, only 2 or 3 moss species contribute in a major way to the moss layer. Although other species could possibly be of value as indicators, they are not of significance in coverage or frequency.

Tsuga heterophylla-Thuja plicata community

In certain areas, at the level of the Douglas-fir stands and above, forests were observed to be predominantly of *Tsuga heterophylla* with *Thuja plicata* occupying more moist portions of lower topography (e.g., temporary stream channels). The zone of western hemlock predominance extends upward to regions occupied primarily by *Abies amabilis*, the Pacific silver fir, at elevations beginning at 2000 to 2700 feet; here *Abies amabilis* forms climax stands with western hemlock and western red cedar as lesser but codominant species. The *Tsuga heterophylla-Thuja plicata* community thus occupies much of the area between 1600 and 2500 feet in elevation and seems second in total area only to the two *Abies amabilis* zones within Mt. Rainier National Park.

The location of the six stands (3-8) of the *Tsuga heterophylla-Thuja plicata* community were as follows: stand 3, off State Route 5, 0.65 mile south of the Ohanapecosh Ranger Station; stand 4, near the Ohanapecosh Hot Springs campground, west of the Ohanapecosh River, 1/2 mile southwest of foot bridge; stand 6, same, but 1/2 mile northwest of foot bridge; stand 5, off Backbone Ridge road,

2.2 miles south from bridge over Ohanapecosh River; stand 8, same; stand 7, off State Route 5, 0.9 mile north of Ohanapecosh Ranger Station.

In the several stands of *Tsuga heterophylla-Thuja plicata* community, Douglas-fir commonly and western white pine (*Pinus monticola*) less frequently were observed as seral since they were not reproducing. As shown in table 3 these stands were predominantly of western hemlock although western red cedar could be found in lower moister spots in temporary stream channels, and on level flood plains. The area studied is characterized by relatively steep slopes and these were found to have a high proportion of western hemlock of all sizes, in some cases exceeding 4 feet DBH; young trees of western red cedar were appreciably fewer in number. Since a small hemlock 3 inches in diameter was observed to have more than 80 growth rings, a tree 2 feet in diameter could range up to several hundred years in age. In any case, these forests were judged to be quite mature and of considerable age; therefore the several stands were believed to constitute a good test of relationship of moss species to tree communities.

The undercover of these forests resembled that of Douglas-fir stands in having *Acer circinatum* and *Berberis nervosa*. However, *Gaultheria shallon* was absent or greatly reduced in coverage; and several other species appear to be common here which were not of importance under the Douglas-fir, e. g., *Vaccinium parvifolium, Cornus canadensis, Linnaea borealis* var. *americana* and *Tiarella unifoliata* (table 3). In addition some relationships appear here to the *Thuja plicata-Tsuga heterophylla* associations of the Rocky Mountains as described by Daubenmire (5).

The mosses in this community consisted primarily of *Rhytidiopsis robusta, Eurhynchium oreganum,* and *Dicranum fuscescens. Rhytidiopsis robusta* occurred largely on the ground layer—in particular on the well-littered soil characteristic of these forests—although it was found capable of growing over logs and rocks. *Dicranum fuscescens,* while common on the ground, was more frequently found on logs and tree bases. In addition to these species, *Hypnum circinale* occurred with a smaller percentage of coverage but with a high frequency; it was almost strictly confined to logs and tree bases although occasionally extending to compact litter.

A remarkable correlation appeared in coverage and frequency of *Rhytidiopsis robusta* with Tsuga in both the *Tsuga heterophylla-Thuja plicata* and *Abies amabilis-Tsuga heterophylla* communities (table 3). The reason for this is not known, but it may be surmised that in this region the litter of western hemlock provides an especially suitable substrate for *Rhytidiopsis robusta.* This seems the more plausible since a similar correlation was found with the essentially epiphytic or epixylic *Hypnum circinale.*

In contrast with the Douglas-fir community, *Hylocomium splendens* and *Rhytidiadelphus triquetrus*—though common—were found to be of little quantitative significance, relatively, in the *Tsuga heterophylla-Thuja plicata* forests. Although many other bryophyte species may be found in this zone, relatively few are of significance quantitatively within the mature stands. Most of the many species collected in the area in the several visits of the authors appeared to occur as successional types on exposed mineral soil along road cuts, on rocks, in or by streams, etc. The current report has been restricted to the relatively few in study sites within a mature area of the forest.

Abies amabilis-Tsuga heterophylla community

At an elevation of approximately 2700 feet, and extending upward to about 3800 feet, the forest was found to be dominated by *Abies amabilis* with *Tsuga heterophylla* and *Thuja plicata* as lesser codominants. *Abies amabilis* extended beyond this range but constituted at the higher levels a distinctly different community with other tree species. In the *Abies amabilis-Tsuga heterophylla* community *Abies amabilis* showed a marked vigor of reproduction exceeding that of *Tsuga heterophylla* which in turn was above that of *Thuja plicata.* The sites where plots were studied were as follows: stand 9, off State Route 5 south of Deer Creek, 0.95 mile from Deer Creek bridge; stand 10, off State Route 5, just north of Deer Creek.

At this elevation the upper limit is approached for both Douglas-fir and western white pine but both were to be found in or near the stands as seral species. Also occurring within this range were some trees of *Tsuga mertensiana,* the mountain hemlock, and *Chamaecyparis nootkatensis;* however, these species do not appear to be constituents of the *Abies amabilis-Tsuga heterophylla* forests and were not found within the stands considered here.

Judging from the diameter of trees, these stands were as old or older than several of those below, since trees were found having a DBH as follows: Douglas-fir, 5+ feet; Pacific silver fir, 2+ feet; western hemlock, 3+ feet; western red cedar, 4 feet.

As might be expected, the undercover of this community differed markedly from the previous types. *Acer circinatum, Berberis nervosa,* and *Linaea borealis* var. *americana* were absent or infrequent and other species appear, e.g., *Rubus lasiococcus, Vaccinium ovalifolium,* and *V. membranaceum.*

The predominant moss species in this community, as in the *Tsuga heterophylla-Thuja plicata* forest, was *Rhytidiopsis robusta,* with *Dicranum fuscescens* being second in abundance. A number of species of common occurrence under *Tsuga heterophylla-Thuja plicata* stands were not found in the *Abies amabilis-Tsuga heterophylla* community; these include *Hylocomium splendens, Eurhynchium oreganum, Rhytidiadelphus loreus* and *Pseudisothecium stoloniferum* (table 3). The absence of these moss species appeared to mark rather clearly the limits of these two tree communities.

Abies amabilis-Tsuga mertensiana community

Above the *Abies amabilis-Tsuga heterophylla* forest the species *Tsuga mertensiana* and *Chamaecyparis nootkatensis* assume dominance, generally at elevations between 4000 to 5000 feet. In this region evidence of the snow pack was found particularly marked by crusting of the litter and appearance of "snow mold." The stands here appeared to have a somewhat more open canopy than those of other communities below. Douglas-fir and western white pine were not observed here. There is some occurrence in the same elevation range of *Abies lasiocarpa* and of *Abies nobilis.*

The sites on which plots were located were as follows: stand 11, off State Route 5, 0.2 mile from bridge, south of Dewey Creek; stand 12, 0.55 mile north of Cayuse Pass road junction, off of U. S. Route 410.

The shrub and herb vegetation of this stand were found to be quite distinctive (table 3) with *Menziesia ferruginea* and *Xerophyllum tenax* (on well-drained soil) making an appearance.

The mosses likewise are distinctive although greatly less in cover than in lower forests. *Rhytidiopsis robusta* did not occur in any abundance in the absence of *Tsuga heterophylla*, although it was found in or near the stands. On the other hand *Dicranum fuscescens* occurred in abundance about equal to that in the *Abies amabilis-Tsuga heterophylla* forests. Although extensive data were not obtained in this community, a marked difference in the moss communities seems apparent.

Abies lasiocarpa community

Above the *Abies amabilis-Tsuga mertensiana* community the forest gradually gives way to isolated clusters of trees surrounded by subalpine meadows; the latter merge above with the alpine zone. The dominant tree in the subalpine range is *Abies lasiocarpa*, which, in the Mt. Rainier region, was observed to be associated in some places with *Tsuga mertensiana* and *Pinus albicaulis*.

Only one site was studied. This stand, no. 13, was located 1.6 miles southwest of the view point on Sunrise Ridge below Yakima Park.

The data—which conform to observations on several visits—indicate that in this community also there were distinctive features of the moss layer. Unlike the communities below, in which there was a denser forest cover with a conspicuous duff layer over which mosses grew, the subalpine mosses appeared largely to be forms characteristic of mineral soils. *Pogonatum alpinum, Polytrichum piliferum*, and *Bryum pallescens* are species characteristic of a mineral soil substrate. This observation conforms with the evidence of the high degree of rodent activity in disturbing the soil surface and the absence of a thick duff in most of the plots. Within the clumps of trees a distinct litter was found but the mosses which appeared here seemed to grow on the mineral soil and to push up through the litter rather than grow on it.

DISCUSSION

The results of the present study clearly show several features of interest with respect to both frequency and coverage of bryophytes in climax forest stands. There is a predominance of a few (2 or 3) moss species in each community. Each tree community is associated

with a characteristic bryophyte community. In general the moss species of significant frequency or coverage values are not restricted in range to a given community but rather appear to be restricted primarily in relative abundance. This is interpreted as indicating that the correlation of moss species with tree species is due to a coincidence of favorable ecologic factors and species requirements. More specifically it may be inferred that in this particular area certain bryophyte species are favored by the presence of particular tree species. Some possible factors are suggested by the influence of leaf litter of various tree species in the Pacific Northwest on soil pH and nutrient materials (5, 6).

In the present study three species of mosses seem well correlated with certain tree species. These are: *Eurhynchium oreganum* with *Pseudotsuga menziesii; Rhytidiopsis robusta* with *Tsuga heterophylla;* and *Hypnum circinale* with *Tsuga heterophylla.* The high coincidence of these species seems too great for chance. The present study serves simply to show that the relationship seems quite constant but does not reveal the cause of it.

Although some of the predominant moss species are quite restricted, others appear to be widespread and, perhaps, characteristic of coniferous forests across the continent or around the northern hemisphere. *Hylocomium splendens* and Rhytidiadelphus species are of ecologic importance in North America and in Europe (7). The following species appear to be of importance in both the Pacific Northwest (present study) and, under different dominant trees, in the Appalachians (4, 9): *Hylocomium splendens, Rhytidiadelphus triquetrus, Dicranum fuscescens,* and *Plagiothecium denticulatum.* Thus the moss communities of forest associations may have both widely ranging elements and quite restricted forms. Such combinations—together with the responsiveness of the bryophytes to various environmental factors—give considerable promise that an increasing knowledge of moss societies may be very useful in characterizing more precisely the community as a whole.

SUMMARY

1. Frequency and coverage estimates of terrestrial mosses and higher plants were made in thirteen forest stands, at different elevations, tentatively classified into five climax communities.

2. A test of the method, in which 25 one-tenth meter plots usually were estimated, revealed that (in one locality) as few as 10 plots gave number-of-species and species-coverage estimates close to those of 50 plots.

3. Each tree community appears to have a characteristic bryophyte layer with two or three moss species predominant.

4. In the *Pseudotsuga menziesii* community, lowermost altitudinally, *Eurhynchium oreganum, Hylocomium splendens,* and *Rhytidiadelphus triquetrus* were found to be predominant species of the moss layer. *Eurhynchium oreganum* was found also in the *Tsuga heterophylla-Thuja plicata* community in amounts related to the abundance of *Pseudotsuga menziesii* and *Acer circinatum.*

5. The predominant moss in five stands of the *Tsuga heterophylla-Thuja plicata* community was *Rhytidiopsis robusta* with *Eurhynchium oreganum* and *Dicranum fuscescens* occurring as less important quantitatively. Other less abundant mosses, such as *Rhytidiadelphus loreus* and *Pseudisothecium stoloniferum,* were usually present in these stands.

6. In the *Abies amabilis-Tsuga heterophylla* community, at altitudes above the *Tsuga heterophylla-Thuja plicata* community, *Rhytidiopsis robusta* was the predominant moss. This species thus seems correlated with the occurrence of *Tsuga heterophylla.* Also, in this stand, *Dicranum fuscescens* had relatively high frequency and coverage values; *Rhytidiadelphus loreus* and *Pseudisothecium stoloniferum* were absent.

7. At higher elevations, in the *Abies amabilis-Tsuga mertensiana* community, *Dicranum fuscescens* was predominant but the percentage area covered by mosses was less than that in lower forests. *Rhytidiopsis robusta,* though present, was insignificant in frequency or coverage.

8. It is suggested that the correlation of a moss species with a tree species, e.g., *Rhytidiopsis robusta* with *Tsuga heterophylla,* may be due to an effect of the tree litter on the soil pH or nutrients creating conditions favorable to the moss species.

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TABLE 3

The frequency and coverage of bryophytes in relation to other vegetation in thirteen stands of coniferous forests. The figures are from 25 1/10 meter plots except as otherwise noted.[1] Both frequency and coverage are reported as percentages, frequency being the figure to the left in each column. "C" indicates a species considered to be climax, "s" a species considered seral for the stand, "X" indicates occurrence in or near the stand. (Species occurring in only one plot, or within one stand, and not in a plot, are listed below the table.)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
TREE SPECIES													
Pseudotsuga menziesii (Mirb.) Franco	C/87	C/73	s/60	s/32	s/1	s/17	X	s/12	X	X			
Tsuga heterophylla (Raf.) Sarg.			C/80	C/39	C/87	C/52	C/87	C/75	C/15	C/–			
Thuja plicata Lamb.				C/49	X	C/14	X	C/5					
Pinus monticola Dougl.						s/12	X						
Abies amabilis (Loud.) Forbes									C/77	C/–	C/44	C/–	
Tsuga mertensiana (Boug.) Sarg.											C/33	C/–	
Chamaecyparis nootkatensis (Lamb.) Spach.											C/24	C/–	
Abies lasiocarpa (Hook.) Nutt.													C/46

[1] The number of plots for stand No. 5 was 10, for No. 10 was 50, for No. 11 was 8, and for No. 13 was 12.

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
BRYOPHYTE SPECIES													
Eurhynchium oreganum (Sulliv.) Jaeger and Sauerb.	92/8	92/33	80/8	56/7	50/0	40/8	4/0						
Hylocomium splendens (Hedw.) Bry. Eur.	84/21	12/2	24/7	X	10/0	8/0	X						
Rhytidiadelphus triquetrus (L., Hedw.) Warnst.	84/9	48/12				8/0							
Camptothecium megaptilum Sull.	12/0	X	4/0		10/0								
Rhytidiopsis robusta (Hook.) Broth.	12/1		100/52	72/10	90/33	84/28	96/57	96/28	92/33	92/39	X		
Dicranum fuscescens Turn.	4/0	20/1	36/1	8/0	20/0	44/4	36/4	28/3	56/6	68/12	38/5	56/7	
Neckera douglasii Hook.	X		X	X		X							
Antitrichia curtipendula (Hedw.) Brid.	X		X						X				
Rhytidiadelphus loreus (L., Hedw.) Warnst.	X		12/3	8/1	X	4/0	X						
Dicranum strictum Schleich.		8/0							X	6/0			
D. scoparium (L.) Hedw.		8/0	4/0										
Hypnum circinale Hook.			16/0	12/0	20/0	40/5	40/5	32/3	16/0	8/0			
Plagiothecium denticulatum (L., Hedw.) Bry. Eur.			4/0	24/1		X	4/0	8/0	32/1	6/0		16/0	

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Pseudisothecium stoloniferum (Hook.) Grout			4/0	8/0	X	X	8/0						
Heterocladium procurrens (Mitt.) Rau and Hervey			4/0	X	10/0								
Ptilidium californicum (Austin) Underwood and Cook			X		30/0		8/0	20/0	40/1	4/0		4/0	
Pseudoleskea atrovirens Dicks., Bry. Eur.			X								X		
Porella navicularis (Lehm. and Lindenb.) Lindb.				8/0									
Pseudoleskea oligoclada Kindb.				X		X							
Claopodium bolanderi Best				X							X	X	
Buxbaumia piperi Best				X					X				
Mnium spinulosum Br. and Sch. Bry. Eur.				X		X	4/0	4/0					
Brachythecium plumosum (sw.) Br. and Sch. var. *roellii* (R. and C.) Grout?				X								12/0	33/4
Scapania bolanderi Austin				X		20/0	4/0	4/0					

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Blepharostoma trichophyllum (Linne) Dumortier				X		X	X				12/0		
Lophocolea heterophylla Schrader						X			X			X	
Cephalozia pleniceps (Austin) Lindb.							X		X				
Arctoa starkei (Web. and Mohr.) Grout										X		X	
Brachythecium leibergii Grout											38/1		
Pogonatum alpinum (Hedw.) Roehl.												X	33/10
Bryum pallescens Schleich.													25/1
SHRUB AND HERB SPECIES													
Acer circinatum Pursh.	C/10	C/7	C/16	C/22	C/1	C/2	C/5						
Achlys triphylla (Smith) D.C.	76/15			32/8	10/0	24/2	32/6	X	8/1		12/0		
Gaultheria shallon Pursh.	56/15	96/47	4/0		20/0	8/0	X	4/0					
Berberis nervosa Pursh.	52/4	68/11	28/5	40/6	40/2	16/0	36/9	12/1					
Symphoricarpos mollis Nutt.	16/0	12/1				8/0							

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Rubus macropetalus Dougl.	X		8/0										
Trientalis latifolia Hook.	24/2	12/0											
Goodyera oblongifolia Raf.	8/0							X	X	–/0	12/0	–/0	
Cornus canadensis L.	8/0		16/1	8/2		4/0	24/2	X	12/1	–/0			
Chimaphila umbellata (L.) Bart. var. *occidentalis* (Ryd.) Blake		16/0			20/0	8/2	8/0		4/0				
Arenaria macrophylla Hook.		16/0											
Lactuca biennis (Moenck.) Fern.		16/0											
Collomia heterophylla Hook.		12/0											
Pteridium aquilinum (L.) Kuhn var. *lanuginosum* (Bong.) Fernald		8/2	4/0	4/0			4/0						
Vaccinium parvifolium Smith		4/0	32/3	24/8	20/0	12/0	16/0	X					
Linnaea borealis L. var. *americana* (Forbes) Rehder		4/0	X	32/8	30/2	32/1	40/10	20/2	8/0				
Tiarella unifoliata Mitt.			12/1	44/10	10/0				4/0		12/2		
Viola sempervirens Greene			8/1		30/0		8/0	4/0					
Chimaphila menziesii (R. Br.) Spreng.			4/1				X		X				
Pachistima myrsinites													

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
(Pursh.) Ref.			4/0		10/0								
Monotropa hypopitys L.			X				X						
Trillium ovatum Pursh.			X	4/0			4/0		X				
Corallorhiza mertensiana Bong.			X		X								
Listera caurina Piper			X								X		
Mitella caulescens Nutt.			4/0	28/2		12/0							
Clintonia uniflora (Schultz) Kunth.				16/2			4/0		4/0		75/7		
Gaultheria ovatifolia Gray				X						–/0			
Vaccinium ovatum Pursh.						20/2							
Oplopanax horridum (Smith) Miguel						16/0							
Rubus lasiococcus A. Gray							4/0		52/7	–/5		–/0	
Vaccinium sp.								12/1					
Rubus pedatus Smith									24/4		75/14		
Vaccinium ovalifolium Smith									20/5		75/17		
Vaccinium scoparium Leiberg									16/3	–/0	X		
Pyrola secunda L.									8/1	–/0		–/0	
Vaccinium membranaceum Doug.										–/20	38/3	–/9	
Menzeisia ferruginea Smith											88/35	–/13	

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii		Tsuga heterophylla-Thuja plicata						Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Rubus spectabilis Pursh.											12/0		
Athyrium filix-femina (L.) Roth.											12/2		
Phegopteris dryopteris (L.) Fee											12/0		
Streptopus curvipes Vail.											50/12		
Xerophyllum tenax (Pursh.) Nutt.												–/28	
Rhododendron albiflorum Hook.												–/16	

The shrub and herb species in stand No. 13 were as follows: *Valeriana sitchensis* Bong.; *Erythronium grandiflorum* Pursh. var. *pallidum* St. John; *Polemonium columbianum* Rydb.; *Viola* sp. (yellow); *Anemone occidentalis* S. Wats.; *Veratrum escholtzii* Gray; *Luzula glabrata* (Hoppe) Desf.; *Veronica cusickii* Gray; *Phlox diffusa* Benth.; *Vaccinium deliciosum* Piper; *Castilleja* sp.; *Sorbus occidentalis* (Wats.) Greene.

TABLE 3—(Continued)

The following bryophyte species occurred in only one plot or, in one stand (with insignificant frequency and coverage): *Mnium venustum* Mitt. in No. 1; *Polytrichum juniperinum* Hedw. in No. 2; *Bryum sandbergii* Holz. in No. 2 (?) and No. 8; *Dicranoweisia cirrhata* (L., Hedw.) Lindb. in No. 2; *Calliergonella schreberi* (Willd., Br. and Sch.) Grout in No. 2; *Drepanocladus uncinatus* (Hedw.) Warnst. in No. 4; *Mnium punctatum* (L.) Hedw. in No. 4; *Tetraphis geniculata* Girgens. in No. 4; *Mnium menziesii* (Hook.) C. Muell. in No. 6; *Lepidozia reptans* (L.) Dum. in No. 7; *Mnium blyttii* Br. and Sch. Bry. Eur. in No. 9; *Dicranoweisia crispula* (Hedw.) Lindb. in No. 10; *Rhacomitrium heterostichum* var. *sudeticum* (Funck) Jones in No. 11; *Andreaea rupestris* Hedw. in No. 12; *Rhacomitrium patens* (Hedw.) Huebn. in No. 12; *Polytrichum piliferum* Hedw. in No. 13; *Bryum caespiticium* (L.) Hedw. in No. 13; and *Pohlia* sp. in No. 13.

The following shrub and herb species occurred in only one plot or, in one stand (with insignificant frequency and coverage): *Rosa* sp. in No. 1; *Adenocaulon bicolor* Hook. in No. 2; *Campanula scouleri* Hook. in No. 2; *Dryopteris dilatata* (Hoffm.) A. Gray in No. 4; *Maianthemum dilatatum* (Wood) Nels. and Macbr. in No. 4; *Smilacina* sp. in No. 5; *Rubus nivalis* Dougl. in No. 6; *Viola adunca* J. E. Smith in No. 6; *Rosa gymnocarpa* Nutt. in No. 7; *Rubus* sp. in No. 7; *Allotropa virgata* T. and G. in No. 8; and *Streptopus amplexicaulis* (L.) D. C. in No. 11.