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COMPARATIVE ECOLOGY OF STRUCTURAL GROUPS:
COMPOSITIONAL PATTERNS IN THE SWAN VALLEY FORESTS, MONTANA

by

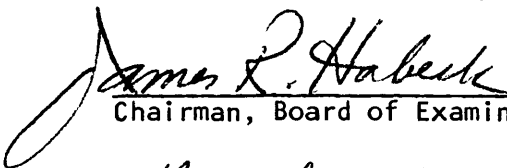
Bruce McCune

Presented in partial fulfillment of the requirements for the degree of
Master of Arts
University of Montana
1979

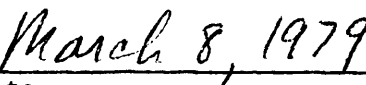
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ABSTRACT

McCune, Bruce, M.A. March, 1979
Botany

Comparative ecology of structural groups: compositional patterns in the Swan Valley forests, Montana

Director: James R. Habeck

JRH

The compositional patterns of structural groups in the Swan Valley are very weakly correlated. Evidence in support of this was derived from 1) correlations of dissimilarity matrices, 2) correlations of stand placement on ordination axes, and 3) comparison of stand groups defined by cluster analysis. While one can roughly predict the composition of one layer based upon the composition of another layer, different structural groups do not change composition across environmental gradients at the same "rate" or in the same pattern.

Several reasons for this poor correlation are suggested. The various structural groups are controlled by different sets of environmental factors. Rates of biotic response to disturbance differ between structural groups. Essentially random historical factors probably weaken compositional parallels between structural groups.

Species richness was greatest in the bryoid layer, decreasing sequentially in higher strata. Species equitability was roughly the same for all structural groups. Beta diversity paralleled species richness for all structural groups except for epiphytes. Epiphytes had a high alpha diversity but low beta diversity. Differences in species diversity between structural groups were related to differences in the degree of environmental differentiation at the levels of each structural group.

Independently defined types for structural groups were not related by either a simple hierarchy or a one-to-one correspondence. Groups defined by cluster analysis did not correspond strongly with a regional system of habitat types.

Bryophytes and lichens are of questionable utility as indicator species for purposes other than air pollution indication. The statement that bryophytes and lichens are more sensitive (narrower tolerance ranges) to their environment than vascular plants is apparently without substantial support except with respect to air pollution.

ACKNOWLEDGEMENTS

Joe Antos provided much of the foundation and inspiration for this work. The care and thought with which he built that foundation is clearly evident to me and is a model for us all. I am honored by and thankful for Joe allowing me the opportunity to build further on his work.

I would like to thank Dr. J. R. Habeck, my thesis director, for his patience and assistance, and a careful review of an early draft of this work. I commend him also for his tolerance and permissiveness of my "floating along on a theoretical level", a luxury which I appreciate. The other members of my committee, Dr. David E. Bilderback and Dr. Donald O. Loftsgaarden, both contributed valuable suggestions for improving my thesis. Dr. Bilderback has been encouraging and supportive throughout my undergraduate and graduate career at the University of Montana. Dr. Loftsgaarden teaches an excellent year-long statistics course which I had the pleasure to take.

The lichen work in this study would have suffered greatly had I not been lucky enough to have Dr. Mason E. Hale, Jr. as a teacher during my first summer of field work in the Swan. Besides helping with the names of the local lichens, his guidance and savvy in lichenological matters have proven invaluable. I am also indebted to Dr. Charles D. Bird, Dr. Theodore L. Esslinger, Dr. Irwin M. Brodo, Dr. John W. Thomson, Dr. Richard C. Harris, Dr. Lawrence Pike, Mr. Thomas Trana, Roger Rosentreter,

and Dennis Dunlap for assistance with problems in lichen identification. In addition, Dr. Robert P. Ireland was kind enough to help me with the problematic moss genus, *Scachytheceium*.

My thanks also to Patricia Muir and Roger Rosentreter for their constructive comments after reading a draft of this thesis.

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CHAPTER I

INTRODUCTION

A. The existence of compositional integrity between structural groups is an implicit assumption of many vegetation studies. Plants of one layer are generally considered to be faithfully associated with other layers. For example, we often think of douglas fir in western Montana as having certain characteristic shrub and herb associates, the assemblage of species being determined for the most part by the environmental characteristics of the site. While this is certainly true in part, I believe that this line of reasoning has been invoked to an unrealistic degree. This research was directed towards two problems that result from overextending such deterministic explanations for observed patterns in vegetation.

1. Compositions of forest layers are not necessarily correlated with each other within the hyperspace of environmental gradients.

2. A given site may be capable of supporting different communities of shade tolerant plants depending upon the history of disturbance and dispersal events.

The first problem allowed a fairly rigorous approach. However, the second problem arose in my mind as a consequence of my research on the first, and therefore, is treated here in only an intuitive manner. Hopefully the problem can be more rigorously attacked in the future.

3. The location chosen for this study was the Swan

Valley in northwestern Montana. This choice was made for two main reasons:

1. A thorough study of the upland vascular vegetation of the area by Antos (1977) laid a solid groundwork for further research. His work provided valuable insights into the important factors controlling compositional patterns and community dynamics.

2. The upland forests on the valley floor and lower slopes have a low enough beta diversity to allow meaningful approach to the objectives of this study.

C. It was also of interest to me to compare descriptive community parameters as applied to structural groups. Diversity parameters included were species richness, equitability, and beta diversity.

D. An understanding of communities is necessarily dependent upon an understanding of the ecological behavior of species. Thus, as far as was possible, I have attempted to add to our knowledge of the ecology of the macrophytic species occurring in the Swan Valley, particularly the bryophytes and lichens. At the same time, I attempt to relate the distribution of bryophytes and lichens to that of vascular plants.

E. Bryophytes and lichens are frequently considered to be sensitive indicators of environment (Lambert and Maycock, 1968; Stringer and Stringer, 1974; Shacklette, 1961; Scott, 1970; Phillips, 1951; Jesberger, 1973; Cantlon, 1953; Culberson, 1955). This has been shown

repeatedly in the numerous studies relating air pollution to the distribution of lichens and bryophytes (Ferry et al., 1973; Hawksworth and Rose, 1976). However, it is unclear whether or not species in these groups have narrower tolerances along other environmental gradients. I approached this problem by comparing estimates of beta diversity of structural groups in the Swan Valley forests.

F. Studies directed at the above objective allow the approach of another objective: evaluation of structural groups, as well as individual species, as to their usefulness in defining community types and assessment of their value as indicator species.

CHAPTER II

LITERATURE REVIEW

Comparing the ecology of structural groups has been part of quite a few vegetation studies in North America. A comparison of compositional patterns has been discussed by Phillips (1951), Whittaker (1960), Lambert and Maycock (1968), Hoffman and Kazmierski (1969), and La Roi and Stringer (1976). Although a consensus does not exist, the strength of compositional parallels between structural groups has been seriously questioned (Gams, 1918; Gleason 1926, 1939; Cain, 1936; Lippmaa, 1939; Whittaker, 1960; McIntosh and Hurley, 1964; Daubenmire, 1968; Hoffman and Kazmierski, 1969). Their doubts are opposed to the viewpoint of communities as having compositional integrity--an organismal or quasi-organismal nature of plant communities (Clements, 1936; Tansley, 1935). I attempted to approach the problem quantitatively through statistical comparisons of similarity indexes. Comparisons were made between all macrophytic groups.

Diversity relations of structural groups have been compared by Whittaker (1956, 1960, 1965, 1970), La Roi (1967), Auclair and Goff (1971), Zobel et al. (1976), and Achuff and La Roi (1977). In general, diversity of structural groups is poorly correlated between groups. Previous North American studies have included discussion of the factors controlling diversity of forest structural groups, but in none of these studies have all the

macrophyte groups been included.

Studies of interactions between structural groups are many -- too numerous to list here. Literature relevant to specific interactions will be brought out in the discussion below.

Prior to a study by Antos (1977), the vegetation in the Swan Valley had been studied only superficially. His work identifies the important environmental gradients within the tolerance range of *Abies grandis* and discusses the dynamics of the vascular vegetation, geographical relationships, and management implications. Antos concluded that site moisture is the primary physical factor controlling community composition in the Swan Valley but that temperature sets the upper elevational limit for *Abies grandis*. He also proposed that high intensity replacement burns initiate the second major compositional trend. The high frequency of burns results in a mosaic of seral communities as the natural state of the vegetation. More of Antos' conclusions concerning the Swan Valley vegetation are included in the description of the study area. The literature review in Antos (1977) should be consulted for summaries of the observations of early visitors to the Swan Valley. He also included accounts of the relevant and more recent literature from nearby areas.

Probably the most important works that allow the reader to put the Swan Valley vegetation into a regional perspective are Antos (1977), Habeck (1967), Pfister *et al.*

(1977), and Ross and Hunter (1976). This perspective is developed briefly in the description of the study area below.

Most of the studies including bryophytes in the northern Rockies do not deal extensively with ecological relationships. Reports on bryophyte ecology in this area are limited to ecologically annotated lists (Hermann, 1969; Hong, 1975, 1977), and a few ecological studies (Cooke, 1955; A. Steele, 1974, 1978; McCune, 1977), and ecological notes in a regional flora (Lawton, 1971). Some liverwort specimens from the Swan Valley are cited by Hong (1968, 1975, 1977).

The lichens of the Swan Valley are poorly known taxonomically, much less ecologically. Published floristic reports of lichens in Montana are mainly limited to scattered specimen citations in the literature. An early list of cryptogams from Montana included some lichens collected in the Swan Valley (Harris and Harris, 1904). Imshaug (1957) published keys and range maps of western alpine macrolichens, including two collecting sites in Montana. Ecological studies including lichens in the northern Rockies are few (Flint, 1932; Cooke, 1955; Habeck, 1963; Bamberg and Major, 1968; McCune, 1977).

CHAPTER III

STUDY AREA

A comprehensive description of the geography, climate, geology, and soils of the Swan Valley may be found in Antos (1977); these features of the area are briefly described below.

Geology: Figure 1 depicts the major geographic features of the Swan Valley and its surroundings. The valley was formed by high angle block faulting and was subsequently altered by continental glaciers in the valley and mountain glaciers in the Mission and Swan Ranges. The bedrock is Precambrian mudstones to sandstones showing various degrees of slight metamorphism. Much of the bedrock is calcareous although non-calcareous strata are common. Glacial till mantles the lower slopes and valley floor. A sectional view and surface geological map of the area are shown in Figure 2.

Soils: Soils in the study area were derived primarily from partially calcareous glacial till and volcanic ash. Little profile development has occurred in these immature soils. Antos (1977) reports a typical soil profile under grand fir stands as having a 2-6 cm mor humus layer on the surface, an intermittent ash-gray A2 horizon less than 1 cm thick; a loose, low-density reddish brown andic (Bir) horizon, usually 15-25 cm thick; and underlain by greyish rocky till sometimes showing some horizon development. The andic horizon is important in that it is relatively

Figure 1. Study area. Stand locations are indicated by triangles.

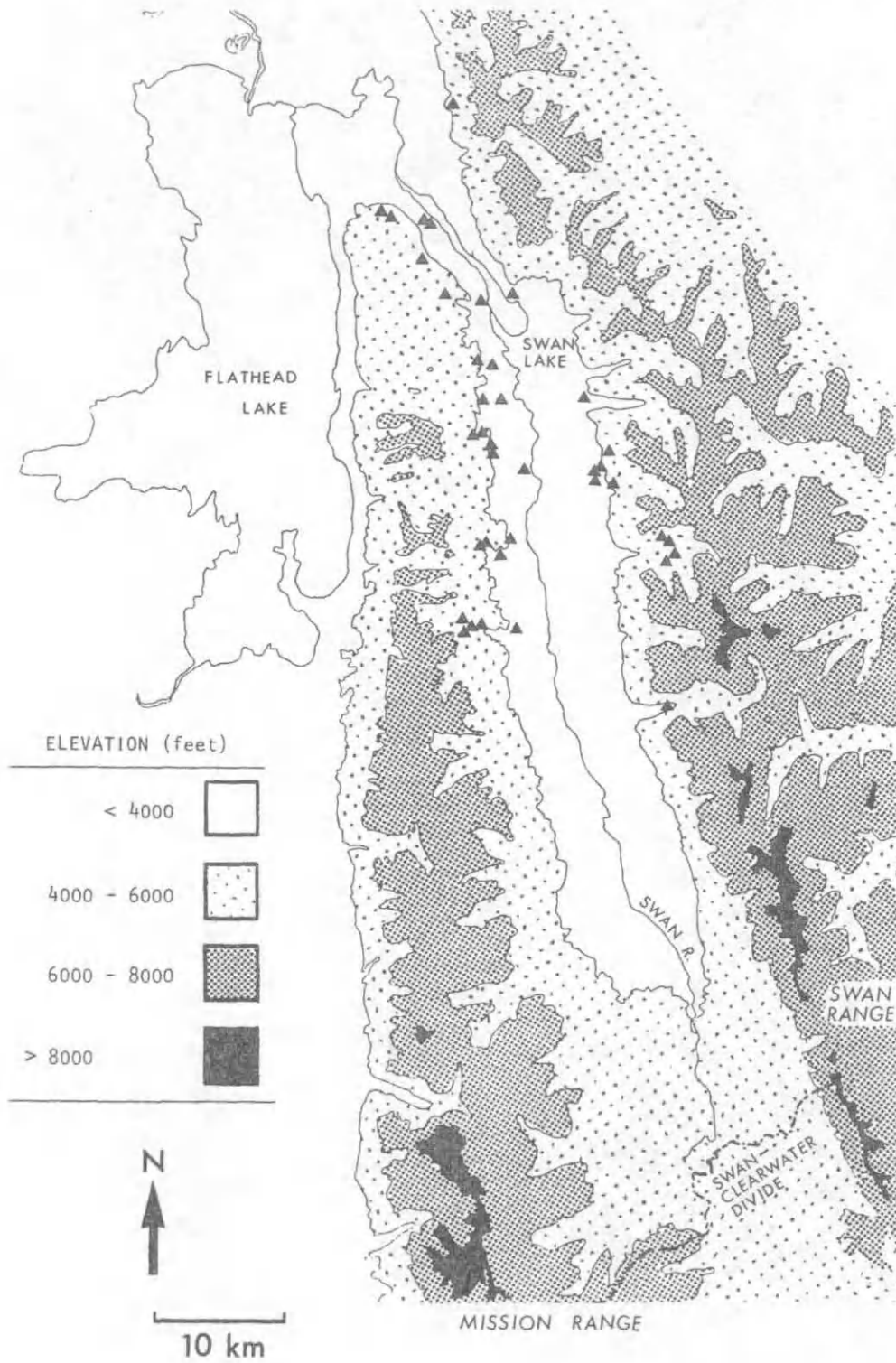


Figure 2. Geological features of the study area. (A) East-west section. (B) Surface map (after Ross, et al., 1955).

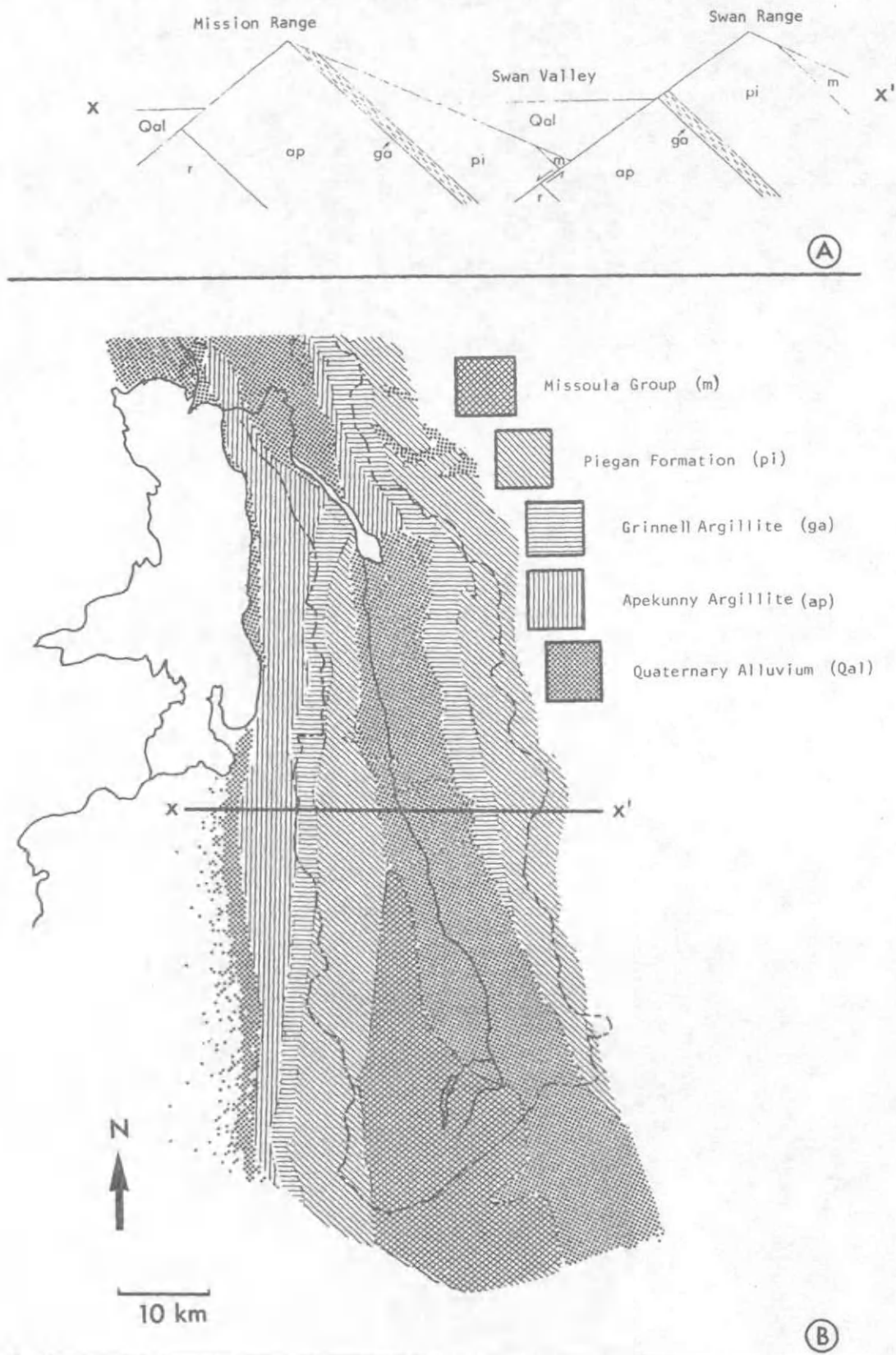
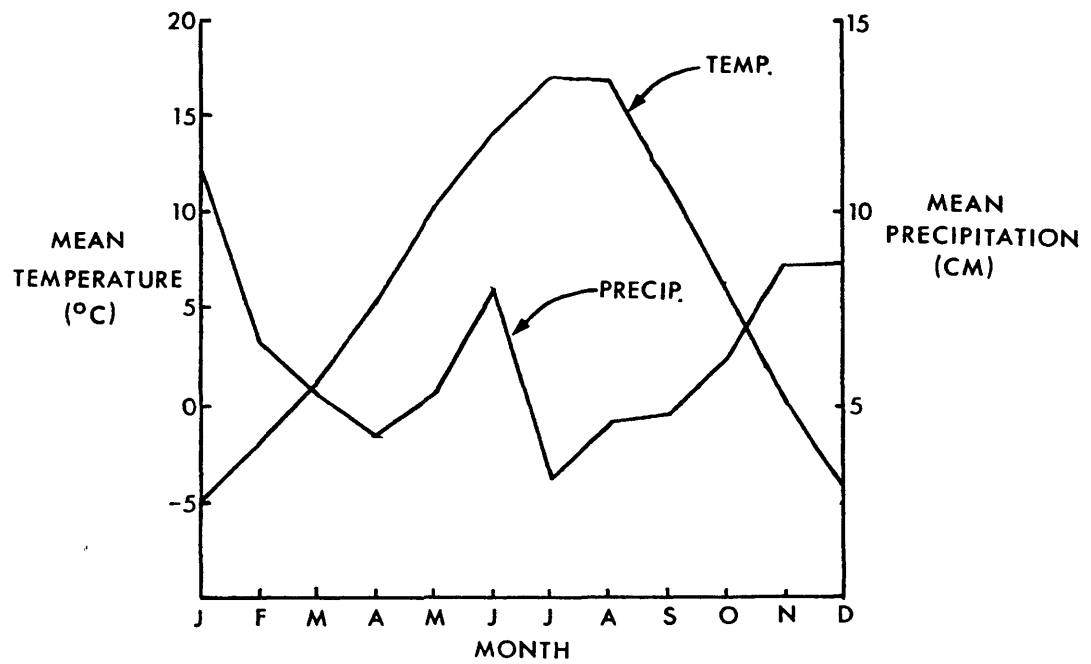


Figure 3. Monthly averages for temperature and precipitation at Swan Lake Weather Station, elevation 960 m. 20 yr means from Antos (1977).



nutrient rich, has a high water holding capacity, and a high cation exchange capacity. Antos (1977) also suggests that the soils influence the vegetation primarily through moisture effects, nutrient status being generally good as compared with many coniferous forest soils.

Climate: A north-south climatic gradient exists in the Swan Valley. The north end of the valley is relatively moist, as a result of orographic effects and the position of prevailing storm tracks. Since the Mission Range crest falls from about 2700 m at the south end of the valley to 1100 m in the north, the effectiveness of the range as a moisture barrier decreases northward. Mean annual precipitation at low elevations in the Swan Valley is roughly 75 cm, the winter months and June being relatively wet, while rain in the summer months averages only 3-5 cm per month. Snow accumulation records do not exist for the Swan Valley lowlands. However, a snowpack over 1 m deep may be typical for much of the study area (Antos, 1977). Mean January and July temperatures are approximately -5°C and 17°C respectively. Figure 3 summarizes climatic data for Swan Lake (elevation, 960 m). Antos (1977) should be consulted for further climatic information on the Swan Valley.

Vegetation: The Swan Valley is predominantly forested with the exception of wetland and aquatic habitats. In mature forests, *Abies grandis* is the most abundant tree on modal upland sites. On drier sites *Pseudotsuga menziesii*

and *Pinus ponderosa* are more prominent while moist sites frequently support *Thuja plicata* or *Larix brevifolia*. At higher elevations and in frost pockets dominance shifts to *Abies lasiocarpa* and *Picea engelmannii*. *Pinus contorta* and *Larix occidentalis* are the most important seral trees. *Populus tremuloides* and *P. trichocarpa* frequently dominate the river bottoms and other areas with easily accessible ground water. *Pinus monticola* is a frequent, although generally minor, component of moist forests at lower elevations.

Shrubs are a common understory component and occasionally reach dominance. *Salix scouleriana*, *Shepherdia canadensis*, and *Acer glabrum* are important components of young stands. *Vaccinium globulare* increases in importance in dry old stands. Old stands on moist sites are conducive to *Menziesia ferruginea*. *Rosa gymnocarpa*, *Spiraea batulifolia*, *Pachistima myrsinites*, and *Acer glabrum* occur in nearly all stands although the first two become relatively infrequent in wetter stands.

Herbs vary from nearly absent to abundant in the Swan Valley forests. Tightly closed canopies or dense shrub layers reduce herb cover greatly. Considerable diversity and variation exists in the herb layer. *Adenocaulon bicolor*, *Clintonia uniflora*, *Disporum hookeri*, *Goodyera olongifolia*, several *Pyrola* species, *Smilacina stellata*, *Viola orbiculata*, and *Xerophyllum tenax* are frequent members of the herb layer.

The moss layer is highly variable in both total cover and composition. *Brachythecium* species, *Rhytidiadelphus triquetrus*, *Rhytidiopsis robusta*, *Funaria spinulosum*, *Bryum sandbergii*, *Pleurozium schreberi*, and *Dicranum scoparium* are most frequent. The large foliose lichens *Peltigera canina* and *P. leucophlebia* are often present in this layer.

Epiphytes are typically well developed in all but the youngest stands. Lichens predominate in this structural group although the bryophytes *Dicranum tauricum* and *Phylidium pulcherrimum* are common in wetter stands. In addition, epiphytic *Orbitrichum* species are found in deciduous riparian communities. Species of *Bryoria*, *Alectoria*, *Hypogymnia*, and *Parmeliopsis* as well as *Platismatia glauca* and *Parmelia sulcata* are generally the most abundant components of this structural group.

The Swan Valley is interesting phytogeographically as many species associated with moist Pacific air approach their eastward range limit in the area (eg. *Thuja plicata*, *Apies grandis*, *Taxus brevifolia*, and *Tsuga heterophylla*). While species with west coast affinities are well represented, boreal elements also make a significant contribution to the flora (Habeck, 1967).

Anthropogenic influences: Gentle terrain in the Swan Valley and good growth of trees have promoted intensive logging of the area. Much of the old growth timber has already been removed. Other anthropogenic influences are

relatively minor except for fire suppression. Records of early visitors to the Swan Valley indicate that fire contributed significantly to the vegetation mosaic. The impact of fire suppression is not clear; loss of habitat for seral species may occur, but clearcuts may offset to a degree the loss of habitat incurred by fire suppression.

CHAPTER IV

METHODS

A. Composition sampling: From the 56 stands selected by Antos for his study (1977), I chose 42 for further work. The stands were chosen in Antos' study to represent the range of communities and environmental conditions in which *Abies grandis* is found in the Swan Valley. Only stands free from direct human influences were included. Cover data for vascular species were obtained by Antos, while I revisited his stands, sampling epiphytes and the moss layer.

Antos outlined his sampling procedure as follows:

A 375 square meter circular plot was laid out in each stand. The canopy coverages of each vascular, understory species in the plot were recorded by the following classes (Pfister *et al.* 1974, as modified after Daubenmire 1959): 1=0-1% coverage, 2=1-5%, 3=5-25%, 4=25-50%, 5=50-75%, 6=75-95%, 7=95-100%, if a species was in the stand, but not in the plot, a "+" was recorded. For tree species in the plot, canopy coverage classes were recorded separately for each of the three diameter size classes (<10 cm d.b.h., 10-30 cm d.b.h., and >30 cm d.b.h.) using the same system. In addition, all trees in the plot were tallied by 5 cm diameter intervals. Trees less than 1.4 m tall were counted in the entire 375 square meter plot.

Usually a number of trees were cored to obtain stand age as well as the ages of smaller trees in the understory. In general, at least one individual of each species in the overstory and various sized individuals of understory trees (especially grand fir) were bored. Grand firs too small to core were cut at the base to obtain age. In all cases the increment cores were taken as close to the ground level as feasible. The diameters and heights of all trees sampled for age determination were recorded.

Along with these quantitative vegetational characteristics other attributes of the stand were noted, such as the amount of insect damage and dwarf mistletoe infestation, extent of wildlife browsing and trails, evidence of past fires, and degree of windthrow. The physical parameters of the site such as elevation, slope aspect and inclination,

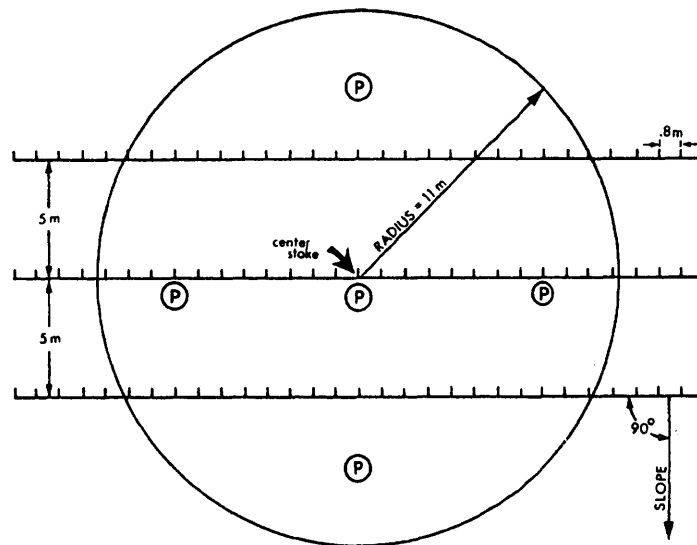
topographic position, exact location, and other physiographic information that seemed relevant were recorded. Only very cursory examination was made of the soils in the plots.

In 1977, two years after the vascular plant data was gathered, I visited the plots, sampling epiphytes and the moss layer, and measuring percent canopy cover photographically. Figure 4 shows the sampling arrangement for each plot, as explained in the text below.

The moss layer was sampled with approximately 100, 10 x 30 cm quadrats arranged at regular intervals along three transects through the original circular plot. Cover of each species in each quadrat was estimated to the nearest 0.5 dm². Occurrences with less than 0.25 dm² were assigned a cover value of 0.1 dm² or 0.2 dm². Individual values were then combined to yield a single percent cover value for each species for each plot. Quadrats falling on rotten wood or rock were excluded in order to standardize the samples as much as possible.

Accurate sampling of the moss layer was complicated by the tendency for many species to have low, patchy cover. For this reason, the sample design was that of many dispersed small quadrats within each stand. For the most part, species in the moss layer in the Swan Valley were readily distinguishable in the field with the naked eye or hand lens. The single major exception to this was in the moss genus *Brachythecium*. *B. hylotapeetum* was kept separate while all other *Brachythecium* species (*B. leibergii*, *B.*

Figure 4. Sampling arrangement used for all stands. The large circular plot was used by Antos (1977) for sampling vascular plants. Tick marks on the transects represent quadrat locations used for bryoid layer sampling. Photo points for determining canopy cover are indicated by "P". All trees within the circular plot were point-sampled for epiphytes.



salsedrasum, *B. starkei*, *B. collinum*, and *B. albicans*) were lumped in the data.

Quantification of epiphytes presents special problems. The bulk of epiphyte biomass was attached to branches, the trunk generally supporting a lichen community with lower biomass per unit area. However, only the trunk at breast height was used for epiphyte sampling in this study. The complications and inaccuracies involved in attempting to quantify epiphytes on branches were deemed to be insurmountable in the interest of reasonably rapid sampling. Thus, it should be kept in mind throughout this study that the epiphyte sample may not be representative of that structural group as a whole.

Epiphytes were point-sampled on trunks at breast height within each circular plot by wrapping a tape around each tree over 12 cm DBH. Hits were then recorded by species at 2.5 cm intervals along the tape. Most plots were sampled with at least 1000 points although individual plots ranged from 750 to 2000 points. Percent cover for each species in each stand was calculated as the proportion of hits on a given species to the total number of points for that stand. Tree species and diameters were recorded during point sampling to allow evaluation of some aspects of host-epiphyte relations.

Crustose lichens were excluded from the sampling because of difficulties in field identification and evaluation of whether or not a lichen thallus was actually

present beneath a point. This problem arises from thalli which are often barely apparent or immersed within the bark, the lichen's presence evidenced only by scattered apothecia.

A single lichen genus, *BRYORIA*, proved difficult in sampling. This large and often confusing genus was recombined into the following groups for the purposes of this study: sorediate thalli with the exception of *B. fremontii* were combined, most of the thalli being referable to *B. fuscescens*. *B. fremontii* was combined with *B. pseudofuscescens* in another group. While *B. fremontii* is readily distinguishable from all the others when it is sorediate, it usually was esorediate and often difficult to separate from *B. pseudofuscescens* in the field. *B. abbreviata* and *B. capillaris* were maintained as separate entities in the data as they are generally distinctive in appearance.

Replicate samples of the bryoid and epiphyte groups were taken for five stands, using the same plot centers, but orienting the transect axes at 45 degrees to the first sample. Replicates were made between one and two months after the first sample was taken. Dissimilarity between replicate samples was rather high, averaging 38% for epiphytes and 32% for the bryoid layer. Both within-plot inhomogeneities and sampling error contributed to this dissimilarity between replicate samples.

Canopy density was measured photographically using five photo points per stand as illustrated in Figure 4. High

speed 35 mm black and white film was used for the most part, setting the exposure to maximize depth of field. Exposures were made by holding the camera at ground level and pointing the 28 mm lens vertically. After processing, the negatives were projected by half-frames onto a 30 x 60 cm plane divided into .5 x 1 dm rectangles. The area covered by the canopy image in each rectangle was then estimated to the nearest 10%. The resulting 360 canopy cover values for each stand were then averaged to arrive at a single canopy cover value for each stand.

Nomenclature of vascular plants follows Hitchcock and Cronquist (1973). Nomenclature of mosses follows Lawton (1971) in part and Crum *et al.* (1973) in part (see Appendix A for a list of names with authorities). Nomenclature of liverworts follows Stotler and Crandall-Stotler (1977). Nomenclature of lichens follows Hale and Culberson (1970) except for the genera *Bryocia*, *Cistulaciella*, *Parmelia*, *Phaeopobyscia*, *Rhizoplaca*, and *Xanthoparmelia* which follow, respectively, Brodo and Hawksworth (1977), Bowler and Rundel (1977), Esslinger (1977), Esslinger (1978), Leuckert *et al.* (1976), and Hale (1974) (see Appendix B for a list of names with authorities).

Data analysis: Species were assigned to structural groups for the purpose of comparing the compositional patterns of those groups. Most species were easily assignable to one of the groups as defined below, with the exception of those species intermediate in form between

herbs and shrubs. Woody sub-shrubs (*Berberis repens* and *Spiraea betulifolia*) were placed with the herb group as were the smaller suffrutescent species (eg. *Chimaphila umbellata* and *Linnaea borealis*).

The term "structural groups" is frequently used in this report instead of the terms "layers" or "strata". The more general term was chosen because the epiphytic communities did not have a planar form. The host of terms coined by various authors for community fractions [eg. "microcoenoses" - Korchagin (1964), "stratocoenoses" - Ballogh (1958), and "synusia" - Braun-Blanquet (1928)] were avoided because of ambiguities (Barkman, 1973) and certain connotations associated with those terms.

Trees were defined as species over 3 m tall at maturity and usually having a single woody trunk. Species usually having multiple woody stems or shorter single woody stems over 1 m tall at maturity were classified as shrubs. Herbs included all other rooted vascular plants. The bryoid layer was defined as the non-rooted ground surface layer including bryophytes and lichens. Those non-parasitic species growing on trees or shrubs are defined here as epiphytes. In the Swan Valley the epiphytes are primarily lichens with only a few bryophytes, the reverse being true for the bryoid layer. Further restrictions on these groups were imposed by the sampling methods (see above).

A stand dissimilarity matrix based on species cover was constructed for each structural group using the

dissimilarity index of Bray and Curtis (1957). These matrices were then used to compare compositional patterns of the structural groups by 1) correlating elements of all matrix pairs, 2) correlating stand placement on polar ordinations (Bray and Curtis, 1957) for each structural group, and 3) by comparing stand groups defined for each layer by agglomerative cluster analysis using the algorithm outlined in Mueller-Dombois (1974).

The Bray-Curtis ordination technique using percent dissimilarity as the distance measure was chosen in preference to other ordination techniques. It has been consistently found to be the best ordination technique in comparative studies using simulated coenoclines (Kessell and Whittaker, 1976; Gauch and Whittaker, 1972; Whittaker and Gauch, 1973).

The degree of internal association was calculated for the bryoid and epiphyte groups. Unfortunately, similar data was not available for the other groups. The average percent similarity between replicate samples was used as a measure of internal association.

A Pearson product-moment correlation matrix was constructed for all scalar environmental variables measured and for cover of all species occurring in five or more stands. This matrix proved valuable as an aid to the interpretation of the distributional patterns of individual species and structural groups. In addition, constellation diagrams for each layer were constructed from the

correlation matrix to indicate species groups.

Alpha and beta diversities were calculated for each structural group. Alpha diversity was derived in two ways: the first using the Shannon index (Shannon and Weaver, 1949) which combines species richness with an equitability component; the second, simply by averaging species counts as estimates of species richness. Species counts are emphasized in the results and discussion in preference to the Shannon index. Species counts are more readily interpretable; the Shannon index confounds species richness and equitability, and information theoretical indices are of questionable biological significance (Hurlbert, 1971). The equitability component (Pielou, 1966) was also computed separately to allow comparison of the overall distribution of dominance in each structural group. Beta diversities were estimated for each group by dividing the total number of species encountered in all stands by the average number of species per stand. This is the simplest and a generally appropriate measure of beta diversity (Whittaker, 1960, 1970). However, Bratton (1975) points out that beta diversity may be viewed as a function rather than as a single value. Her work indicates that beta diversity is not necessarily constant along environmental gradients. As calculated in this study, beta diversity values indicate only the average rate of change across environmental gradients.

CHAPTER V

RESULTS AND DISCUSSION

A. Compositional Correlations Between Layers.

Compositional patterns of structural groups were found to be very weakly correlated with each other. Several lines of evidence derived from species' cover values support this conclusion: poor correlation of dissimilarity matrices, weak correlation of stand placement on ordination axes, and widely divergent stand clusterings based on similarity matrices.

Correlation of dissimilarity matrices: Table 1 presents r^2 and significance values for correlations of dissimilarity matrices for all group pairs. In most cases the r^2 values range between .03 and .14 with $p < .00001$. A scatter diagram and simple regression line are shown for a typical group pair in Figure 5. It can be seen from this graph that a stand pair that is 90% dissimilar in one layer could be less than 15% dissimilar in the other layer and vice-versa. Thus, knowing the similarity between two stands for one layer would allow one to predictively say little about the similarity between the two stands for any other layer.

The assumption of independent pairs of values required for Pearson correlations was violated to a degree. However, I do not believe that the degree of dependence is large enough to significantly affect my results. Each pair of values is partially dependent on only about 10% of the other

pairs. Furthermore, the effect of that dependence on the correlation would probably be to increase the r-squared values. Thus, my conclusion that the correlation is remarkably poor is probably valid.

Heterogeneity within each plot and sampling error weaken the correlation between dissimilarity values of structural groups. However, these sources of variability were not strong enough in themselves to account for the observed independence of layers. The importance of this effect was investigated by correlating dissimilarity values based on replicate samples with dissimilarity values based on averaged cover values from the original and replicate samples. This correlation was strong for the bryoid layer ($r^2 = .70$, $p < .005$). Similar analyses were not performed for the vascular groups because replicate samples were not obtained for those groups. However, if we assume that the above coefficient of determination is typical for all the structural groups, and that it roughly represents the minimum strength correlation possible given only sampling error and within-stand heterogeneity, my conclusion as stated above stands: compositional patterns of structural groups are very weakly correlated.

Correlation of stand placement on ordination axes: The weak correlation between compositional shifts of structural groups is further supported by correlations of stand placement along ordination axes (Bray and Curtis (1957) polar ordination). A stand dissimilarity matrix,

Table 1. Coefficients of determination (r^2) for correlations between dissimilarity values of structural groups. In all cases except the one marked (*), $p < 10^{-5}$.

	Epi- phyte	Bryoid	Herb	Shrub
Tree	.14	.03	.08	.11
Shrub	.04	.00*	.08	
Herb	.09	.06		
Bryoid	.04			

Figure 5. Scatter diagram with simple regression line for correlation between stand dissimilarity values based on the herb layer and stand dissimilarity values based on the tree layer. Numbers are substituted where more than one point share a position.

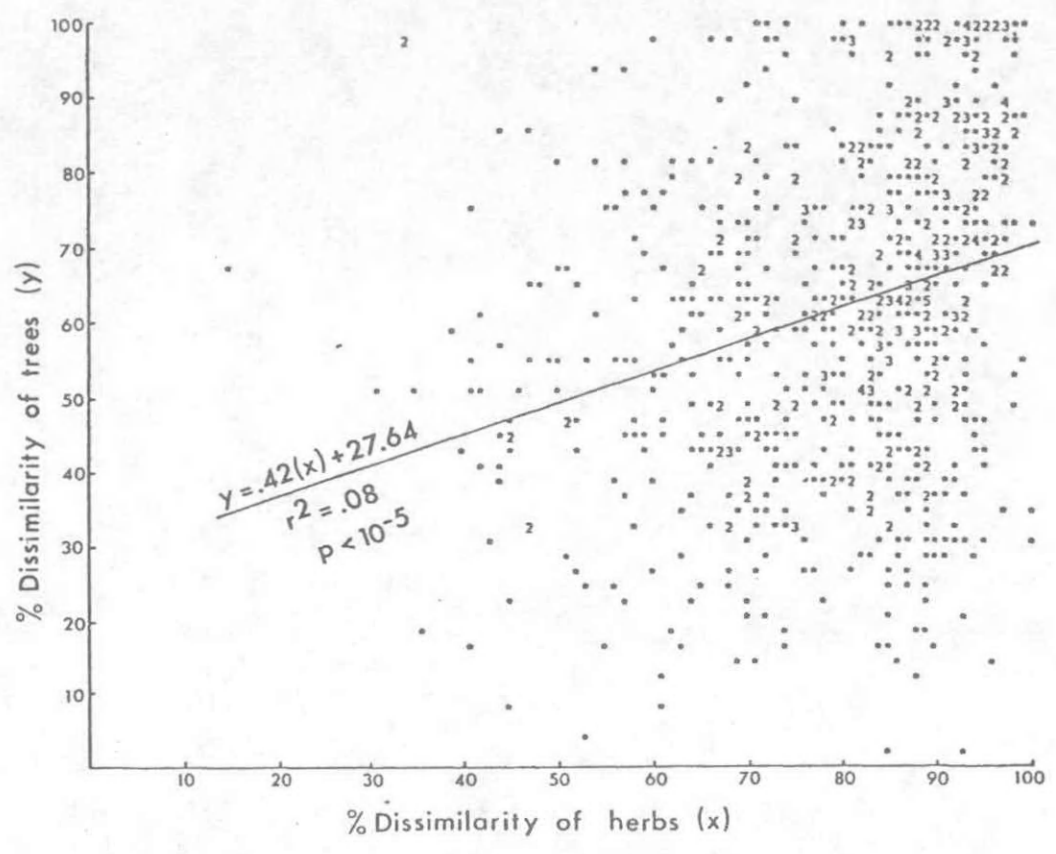


Table 2. Coefficients of determination (r^2) for correlations between stand placement on an ordinal axis (moisture). Significance at the .05 and .005 levels is indicated by (*) and (**).

	Epi- phyte	Bryoid	Herb	Shrub
Tree	.01	.05	.15**	.35**
Shrub	.06*	.26**	.39**	
Herb	.03	.17**		
Bryoid	.30**			

Table 3. Coefficients of determination (r^2) for correlations between stand placement on an ordinal axis (stand age). Significance at the .05 and .005 levels is indicated by (*) and (**).

	Epi- phyte	Bryoid	Herb	Shrub
Tree	.28**	.09*	.20**	.35**
Shrub	.51**	.10*	.26**	
Herb	.14*	.15**		
Bryoid	.01			

prepared from cover data of all vascular species, was used as the basis for endstand selection. Endstand pairs were selected that provided a readily interpretable 2-dimensional ordination, roughly orthogonal gradient axes, and a high correlation between stand dissimilarity and distance on the ordination ($r^2=.62$, $p<.01$). Moisture and stand age gradients are the primary factors corresponding to the two ordination axes, as deduced from plots of species and environmental factors on the ordination (Antos, 1977). The same endstands were then used for stand ordinations based on each structural group. Stand positions along a given ordination axis were compared for each pair of structural groups by Pearson product-moment correlations of stand distances on the axes.

Tables 2 and 3 show r^2 and significance values for correlations between structural groups on the moisture and stand age axes. In both cases, r^2 values are low for most pairs. Correlation of stand rankings on ordination axes had even lower r^2 values. It is important to realize that the results from these correlations are probably highly dependent upon choice of endstands. I do not think that the r^2 values for structural group pairs are worthy of comparison with each other. The important point is that they are generally low, indicating weak compositional parallels between structural groups.

It is notable that a pair of groups that is well correlated on one axis is not necessarily well correlated on

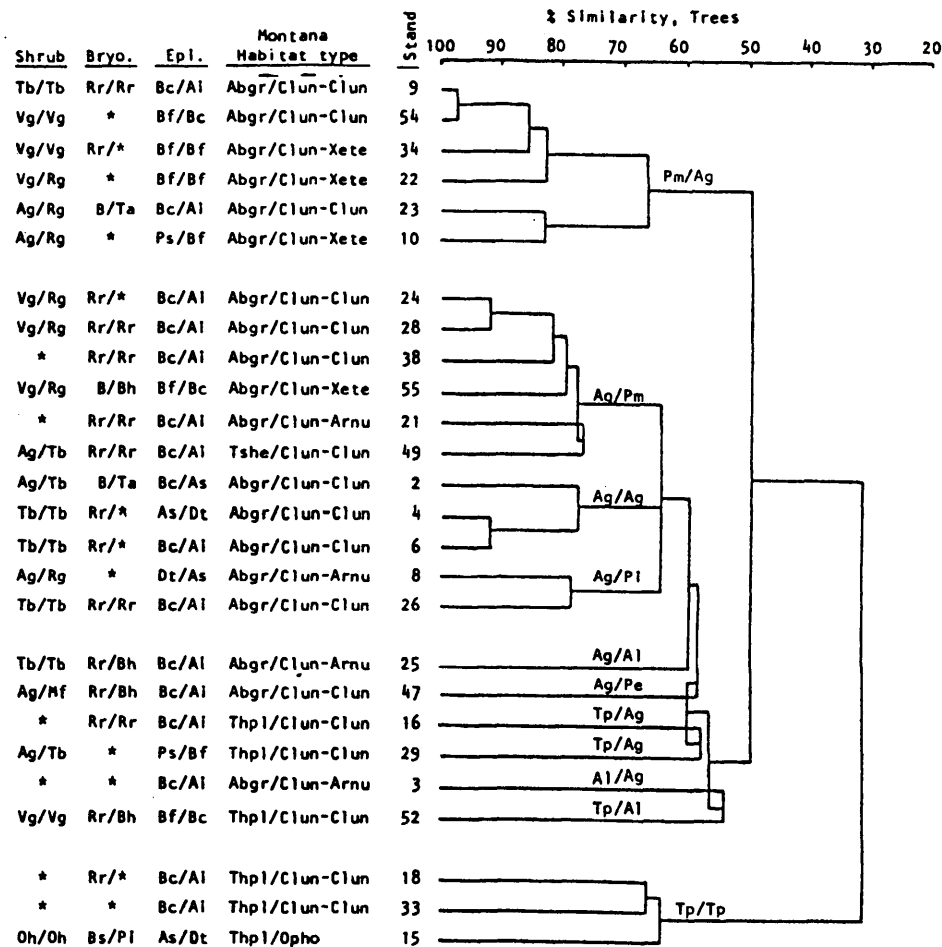
another axis. For example, trees and epiphytes had a relatively high correlation on the age axis but none at all on the moisture axis. This implies that the moisture gradient controlling tree distribution has relatively little direct control over epiphyte distribution. The pattern of epiphyte distribution is not, therefore, simply related to the moisture gradient that in part controls tree distribution. I do not think that the cause for the difference can be extracted from these results: I merely wish to point out that distributional patterns of different structural groups are evidently not controlled directly by the same factors.

Cluster analysis: Agglomerative cluster analysis of old stands (>150 yr since the last burn) was used as a comparative tool with only moderate success. In general, group separation was only fair. Group separation might have been improved by using a different computational algorithm (Robertson, 1978). Nevertheless, those stand groups that were well defined in one layer showed little resemblance to discernible groups in other layers (Figures 6 through 9). Clusters were defined at the 60-70% similarity level in most cases. The dendrogram for the herb layer is not included because clusters were formed predominantly at low levels of similarity.

Correlations of structural groups in the literature: The correlation between structural groups has rarely been

Figure 6. Cluster analysis of the tree layer compared with the Montana Habitat Types (Pfister, et al.; 1977) and stand clusters based on other structural groups. Stand groups for the tree layer are indicated within the dendrogram; classifications based on other structural groups are shown at left.

ABBREVIATIONS



Tree

- Ag = Abies grandis
- Al = Abies lasiocarpa
- Pe = Picea engelmannii
- Pl = Pinus monticola
- Pm = Pseudotsuga menziesii
- Tp = Thuja plicata

Shrub

- Ag = Acer glabrum
- Mf = Menziesia ferruginea
- Oh = Opiopanax horridum
- Rg = Rosa gymnocarpa
- Tb = Taxus brevifolia
- Vg = Vaccinium globulare

Bryoid

- B = Brachythecium spp.
- Bh = Brachythecium hylotapetum
- Bs = Bryum sandbergii
- Pl = Plagiomnium insigne
- Rr = Rhytidopsis robusta
- Ta = Timmia austriaca

Epiphyte

- Al = Alectoria imshaugii
- As = Alectoria sarmentosa
- Bc = Bryoria capillaris
- Bf = Bryoria fuscescens
- Dt = Dicranum tauricum
- Ps = Parmelia sulcata

* = group not defined

Figure 7. Cluster analysis of the shrub layer compared with the Montana Habitat Types (Pfister, et al., 1977) and stand clusters based on other structural groups. Stand groups for the tree layer are indicated within the dendrogram; classifications based on other structural groups are shown at left.

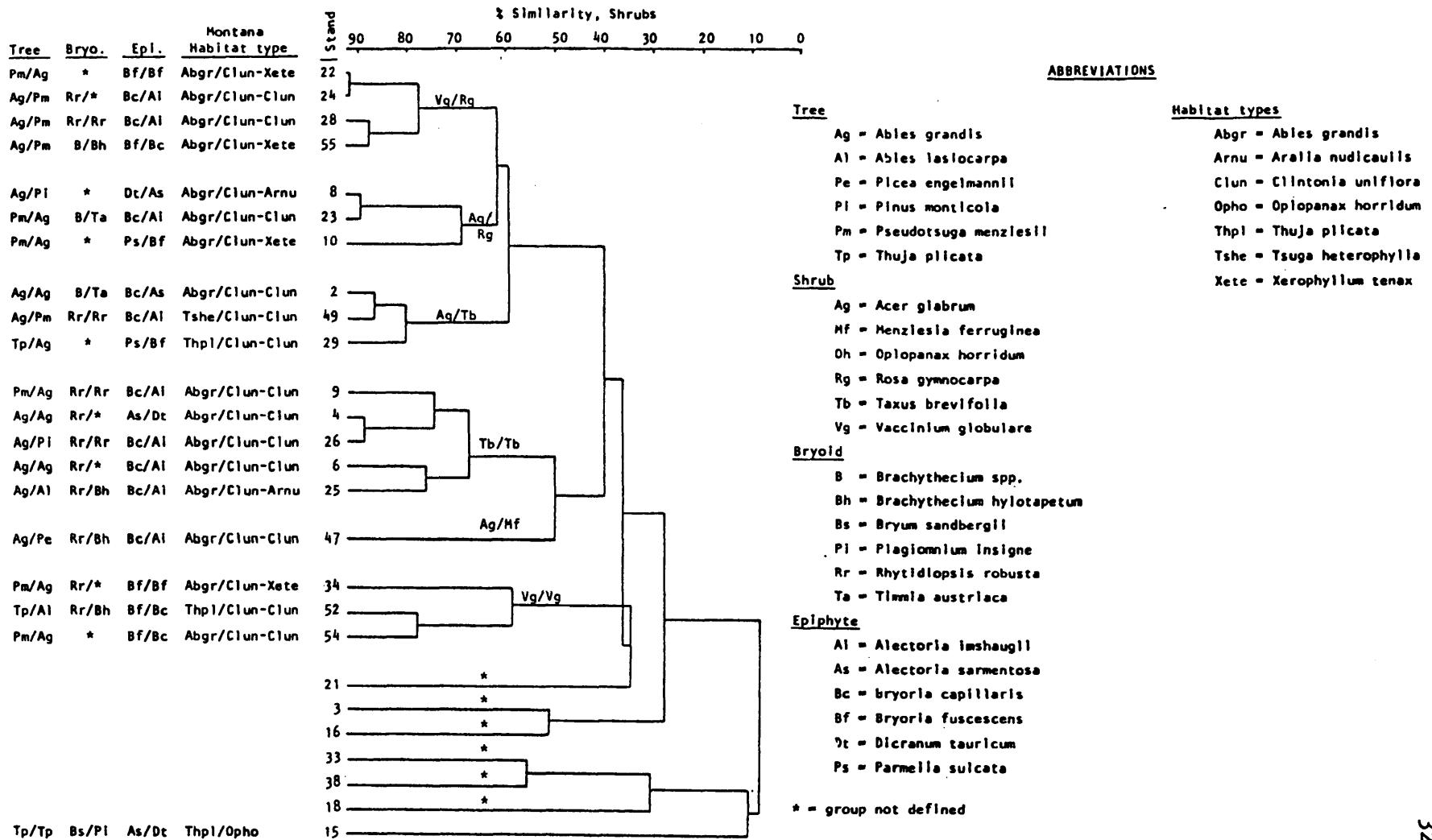


Figure 8. Cluster analysis of the bryoid layer compared with the Montana Habitat Types (Pfister, et al., 1977) and stand clusters based on other structural groups. Stand groups for the bryoid layer are indicated within the dendrogram; classifications based on other groups are shown at left.

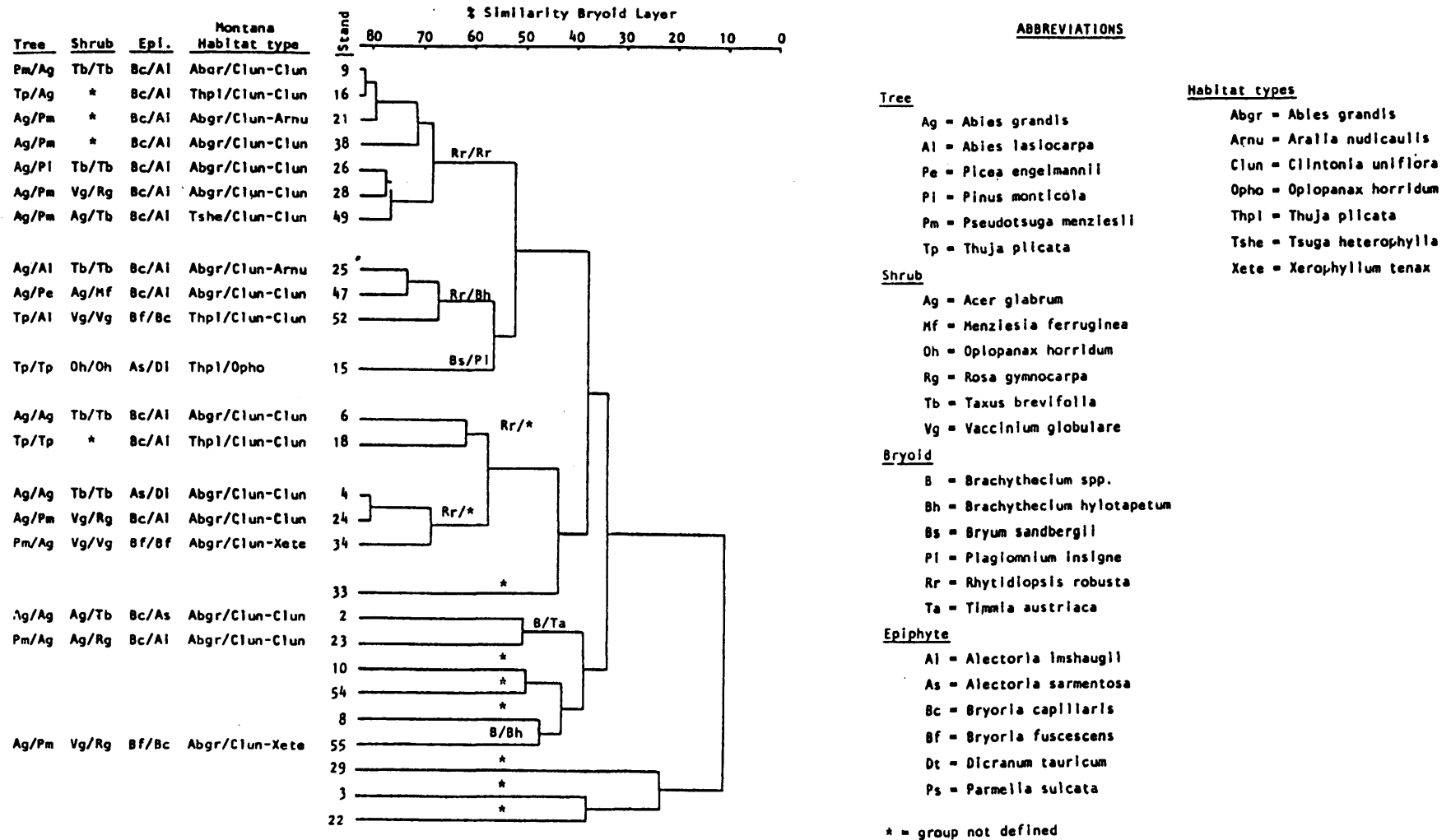
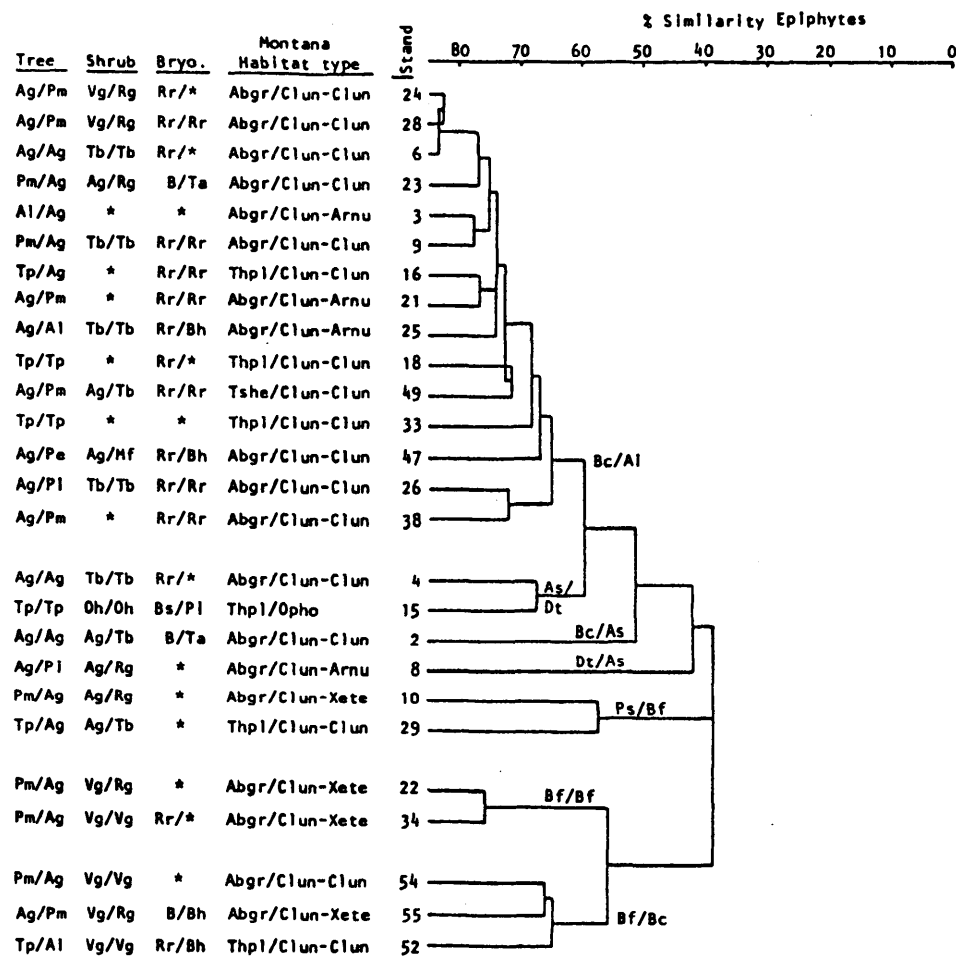


Figure 9. Cluster analysis of the epiphyte groups compared with the Montana Habitat Types (Pfister, et al., 1977) and stand clusters based on other structural groups. Stand groups for the epiphytes are indicated within the dendrogram; classifications based on other groups are shown at left.



ABBREVIATIONS

Tree

- Ag = Abies grandis
- Al = Abies lasiocarpa
- Pe = Picea engelmannii
- Pl = Pinus monticola
- Pm = Pseudotsuga menziesii
- Tp = Thuja plicata

Shrub

- Ag = Acer glabrum
- Mf = Menziesia ferruginea
- Oh = Oplopanax horridum
- Rg = Rosa gymnocarpa
- Tb = Taxus brevifolia
- Vg = Vaccinium globulare

Bryoid

- B = Brachythecium spp.
- Bh = Brachythecium hylotapetum
- Bs = Bryum sandbergii
- Pl = Plagiomnium insigne
- Rr = Rhytidopsis robusta
- Ta = Timmia austriaca

Epiphyte

- Al = Alectoria lmschaugii
- As = Alectoria sarmentosa
- Bc = Bryoria capillaris
- Bf = Bryoria fuscescens
- Dt = Dicranum tauricum
- Ps = Parmella sulcata

* = group not defined

approached directly.

Whittaker (1960) found that "Although percentage similarities for the tree stratum and undergrowth are necessarily correlated, lack of any strict consistency of these is evident in the data." He further stated that "This fact is consistent with what has already been observed on the lack of strong correlation between different strata and community fractions." Daubenmire (1968) strongly stated that "In the northern Rockies, forest overstory and undergrowth occupy the land independently." McIntosh and Hurley (1964) reported that "stands on quite different site types may have similar understory vegetation as measured by the index of similarity." Yet they state that understory and overstory ordinations were significantly correlated at the 1% level, using the Spearman rank correlation coefficient. Only the ten most frequent understory plants were included in their herb layer ordination. Bratton (1975) found that indirect ordinations of understory and overstory vegetation along a moisture axis had similar stand sequences but quite different positions along that axis.

Several other authors have commented briefly on correlations between structural groups. Hoffman and Kazmierski (1969) state that "a close relationship between them [epiphytes and vascular plants] may break down under scrutiny." Yet they allow for the usefulness of herbaceous species indicating conditions favoring certain epiphytic communities. Phillips (1951) noted that "epiphytic

bryophytes are not always correlated with forest tree climaxes." His explanation for this is that tree climaxes are distributed over a wider variety of habitats. Yet he later states that "Many bryophyte communities are much more widely distributed than the tree species upon which they occur..."

Although the independence of forest layers has been observed by ecologists striving to classify vegetation, that awareness has not been satisfactorily incorporated into the methods and philosophy of classification. Recognition of the independence of layers prompted a move towards separate classifications by layers (Gams, 1918; Du Rietz, 1936; Lippmaa, 1935, 1939; Cain, 1936). This approach to classification has largely been abandoned since their time. Some recent efforts towards classification of forest communities have recognized the independence of layers (Daubenmire, 1968; Pfister et al., 1977) but classify the vegetation using combinations of characteristic overstory and understory vegetation. Daubenmire (1968) justifies combining the layers with the reasoning that that method allows the recognition of more ecologically distinct areas than could be recognized on the basis of the understory or overstory alone.

I suspect that the problem of poor correlation between structural groups has been encountered more frequently than is evidenced by the literature. The assumption that structural groups are well correlated is, perhaps, a

comfortable notion that many ecologists have not critically examined in the past. For instance, Lambert and Maycock (1968) state "It is reasonable to assume that species of lichens occurring in the understories of stands of this shifting forest complex [a moisture gradient] might also show patterns similar to the tree species." The view of plant communities as "super-organisms" (in a Clementsian sense) may also have contributed to an unrealistic view of the correlation between structural groups.

Why are structural groups poorly correlated? Three lines of reasoning provide a tentative explanation for the poor correlation between structural groups. The first suggests that the independence of compositional patterns of structural groups are due to differences in the patterns of environmental factors operating at different levels in the forest. The second is based on differences in rates of biotic response during succession. The third invokes a degree of essentially random factors responsible for plant distribution. These three, non-contradictory ideas are explored below.

The environmental factor complex in a given location is expressed differently towards each structural group. Overstory trees experience the gross macroclimate of a site while successively lower layers experience environments increasingly modified by other structural groups. Shrubs and understory trees occupy an aerial space modified by the overstory but might share a similar root zone. Herbs occupy

an aerial environment drastically modified by higher layers, including modifications of light, temperature, moisture, and nutrient regimes. Soil factors are less likely to directly affect the bryoid layer. Epiphytes are strongly dependent on the host, both from the standpoint of immediate substrate differences between host species, and from differences in microclimates induced by the hosts' canopies. Specific details of some of these factor effects are discussed below. The important point is that different structural groups experience radically different factor complexes and I see no reason why the factor complexes should vary in concert. Therefore, it seems reasonable that compositional patterns of structural groups are weakly correlated.

The rate of response by each layer of vegetation to fire differs between structural groups, weakening the compositional correlation between them. For instance, middle aged stands (say 75 to 100 yr) will support a herb flora often quite similar to older stands on similar sites. Yet the shade intolerant pioneer trees still dominate the overstory. Thus, the tree layer of that stand is similar in composition to younger stands, while the herb layer is already more similar to older stands. Achuff and La Roi (1977) state that the faster recovery rate of lower strata is due to their faster rates of maturation and turnover. This is certainly supported by examples such as *Larix occidentalis*, a pioneer species, persisting for hundreds of years into late seral communities. However, the situation

is complicated by several considerations. For instance, dispersal rates may differ greatly between structural groups (can "climax" mosses immigrate as easily as "climax" herbs?). Differences in colonization strategies also complicate considerations of maturation rates and turnover (eg. the tendency for many shrubs to resprout after fire while mosses may be destroyed completely over small areas).

Essentially random distributional accidents may also contribute to the weak correlation between structural groups. Apparently, only a few authors have recognized the influence of historical factors on the composition of relatively stable communities (Palmgren, 1922; Kujala, 1925; Gleason, 1926, 1936; Braun, 1950). I believe, as did Gleason (1926, 1936), that ecologists have been somewhat carried away with deterministic explanations of plant distribution. Gleason (1926) gave due recognition to the importance of essentially random factors in control of vegetation: "...the vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment." Braun (1950) states that, "Climatic control, although determining the relative positions of the several major climaxes, does not in general appear to determine regional boundaries. Instead, most of these appear to be determined largely by historical factors--changing climates and physiography of past ages." No doubt exists as to the validity of many environmental

explanations of plant distribution. However, as the width of the environmental variation being considered decreases, the relative importance of random sources of variation increases. These random sources of variation include dispersal "accidents", variations in disease and fire history, and variation in nearby propagule sources at the critical times of earlier stand initiations. Distributional accidents may be perpetuated to a degree through successive fire cycles in the northern Rockies. The composition of a regenerating stand is often largely dependent upon the composition of the pre-burn stand (Lyon and Stickney, 1976).

The preceding paragraph points to a problem of scale that arises when comparing compositional patterns of structural groups. It seems likely that the correlation between structural groups would increase with broader geographic or environmental scale. That is, as the beta diversity of the sample increased, I would expect the correlation between compositional shifts of structural groups to increase. This would be manifested by increasing correspondence between stand groups as defined by cluster analysis. Probably the most important reason why this might be true is that the proportion of compositional variation due to essentially random historical events would be minimized relative to environmental differences. In the Swan Valley the overall beta diversity was rather low. At that scale of variation in community and environment, uncoupling of compositional patterns of structural groups

was rather pronounced. Essentially random historical events may have contributed significantly to that uncoupling.

I do not mean to imply that community composition is unpredictable. On the contrary, cover of most species was readily predictable from the cover values of species in another structural group. Prediction equations from multiple regression analysis with coefficients of determination near 1.0 were usually possible with ten or fewer species as independent variables. Thus, while compositional patterns may be predictable, structural groups did not shift composition along environmental gradients at the same rate or in the same pattern.

B. Diversity.

The following section explores the differences between structural groups in alpha diversity, beta diversity, and species equitability in the Swan Valley forests. Whittaker (1960) states that "diversity relations to environment are clearly different for different community fractions and groups of organisms." Control of floristic diversity is complex and poorly understood (Whittaker, 1960, 1965, 1972) and has been the subject of much study and speculation. Yet it remains a community parameter of considerable interest to ecologists.

Pronounced differences in alpha and beta diversities were found between the structural groups (Table 4). Differences in species equitability were slight.

Table 4. Species counts, beta diversity, and equitability for each structural group.

	average species count	beta diversity	average equitability
Tree	6.5	2.0	.64
Shrub	8.2	2.9	.60
Herb	20.7	4.3	.71
Bryoid	28.1	5.8	.72
Epiphyte	28.7	3.0	.73

Alpha diversity: Alpha diversity was calculated here as the mean number of species in a given layer for all stands. Differences in sampling methods used for vascular and nonvascular plants complicate the comparison. Within each stand, the area sampled for nonvascular plants was considerably smaller than the area sampled for vascular plants. To adjust for this difference, nonvascular species lists for four stands were used to calculate a correction factor (2.7 for epiphytes and 3.6 for bryoids). These correction factors were multiplied against the richness values based on the smaller samples, thus deriving a comparable estimate of species richness for the two non-vascular groups.

Alpha diversity was greatest in the epiphytes. An interesting trend is apparent: a high species count in the bryoid layer, decreasing through the herb and shrub layers, to the lowest value for trees. Similar results were reported for vascular strata by Whittaker (1960), La Roi (1967), and Zobel *et al.* (1976), although Glenn-Lewin (1975) found the lowest richness in the shrub layer. Achuff and La Roi (1977) reported another instance of the vertical trend in species richness and extended it by including the bryoid layer. A reasonable explanation for this result is that species diversity parallels environmental diversity. This explanation is consistent with del Moral's suggestion (1972) that "hypotheses based on habitat heterogeneity, environmental rigor, and competition may be most relevant to

understanding patterns of diversity within a small region." I feel that the higher habitat heterogeneity of lower forest layers is the result of two primary factors: microclimatic differentiation and substrate diversity. Microclimatic differentiation is greater at lower layers, in part because of the variability induced by the irregularity in cover of higher layers. The wider range of substrate orientation and form also contributes to microclimatic differentiation. Counteracting these effects is the moderating influence of vegetative cover (Geiger, 1950). A wider range of substrates is present in the lower layers particularly the bryoid layer. Most stands had primarily four substrates available to the bryoid layer: litter-covered forest floor, rock, bare soil, and rotting logs. Each substrate type supports a characteristic group of species. Species comprising the lower layers are able to occupy these microhabitats only by virtue of their size. Continued survival and success of the bryoid layer has been guaranteed by adaptation to utilizing resource fragments left in the wake of the competitive trend towards increasing vascularization and size.

Beta diversity: Beta diversity, or the rate of species change across environmental gradients, was lowest in the tree layer and was progressively greater in lower layers. Beta diversity paralleled alpha diversity except that epiphytes had a low beta diversity yet a high alpha diversity. In other words, while many epiphyte species are

present in most stands, the same species are likely to be present in the majority of stands. This differs from the bryoid and herb layers in that a large number of species are present in each stand but compositions of these layers are more variable across the range of stands sampled.

The pattern of increasing beta diversity in lower strata was reported by Whittaker (1956, 1960) and Bratton (1975) for vascular plants. Whittaker also noted that alpha and beta diversities increased and decreased in parallel. My results are in agreement with his and extend the conclusion to the bryoid layer as well. However, epiphytes did not show this parallel between alpha and beta diversity, as discussed below.

It is tempting to invoke differences in tolerance amplitudes as an explanation for the differences in beta diversity. For instance, one could say that mosses are more sensitive to differences in environment than are trees. Such a statement has, in fact, been made repeatedly in the literature, although there has been little evidence to that effect. It seems more likely that the differences in beta diversity between layers may be explained largely on the basis of the range of environmental variation present at the scale of that structural group. In other words, the forest structure creates a wide variety of small-scale differences in habitats. The variety of microhabitats is reflected by the diversity relations of the structural groups. Trees, by virtue of their size, must exist in a narrower range of

habitats than the smaller plants, within the multi-layered forest structure. Therefore, the beta diversity of trees would be expected to be low, reflecting the relatively uniform environment at the scale of trees. Clearly, this line of reasoning cannot be extended to all forests. In the case of tropical forests, the diversity relations are probably under greater control by biotic factors (Ashton, 1969).

Beta diversity of epiphytes does not neatly fit the size-diversity pattern shown by the other structural groups. Based on the hypothesis that uniformity in environment results in less species diversity in my study area, the fact that epiphytes had a high alpha diversity and low beta diversity may be explained as follows. The high alpha diversity is the result of a wide variety of possible microhabitats created by the structure of trees. These microhabitats are readily observable in the field and have been documented in many cases (eg. Barkman, 1958; Pearson and Lawrence, 1965; Hoffman and Kazmierski, 1969; Hale, 1952, 1965). However, the range of microhabitats shifts less for epiphytes than for bryoids or herbs across environmental gradients. This relative insensitivity of epiphytes to the environmental differences expressed by other structural groups, may result from a similarity in the microhabitats present on trees growing in a variety of habitats. Thus the surface of *Abies grandis* in drier stands may have a similar range of microhabitats to the surface of

Abies grandis in wetter stands. For example, in almost any forest in the Swan Valley a microhabitat exists that will support the lichen *Hypogymnia imshaugii*. However, the position of suitable microhabitats varies depending on such factors as the moisture status of the site and available hosts. *H. imshaugii* may be abundant at low levels in open *Pinus contorta* forests but present only on higher exposed branches in wetter forests.

Exceptions to this were observed. For instance, trees bordering streams in narrow gorges or other areas with high humidity often support a distinctive epiphyte flora. *Lobaria pulmonaria*, *Nephroma helveticum*, and *N. resupinatum*, otherwise uncommon in the study area, were locally common in these pockets of high humidity. Furthermore, the success of these species appears to be somewhat dependent upon the canopy openings associated with stream courses. Nevertheless, much of the epiphyte biomass in such locations is composed of relatively rank growth of species common in the drier forests of the Swan Valley (eg. *Platismatia glauca*).

The wide range of epiphytic habitats in a given stand complicates the study of their compositional patterns. In the wettest of the stands, fallen branches may be observed that support an epiphyte flora typical of drier stands in the area (eg. *Letharia vulpina*, *Bryocia abbreviata*, and *Cetraria platyphylla*). Thus, the range of epiphytic microhabitats in a given upland stand may approach the range

of epiphytic microhabitats present in a much broader geographical area.

Equitability: Species equitability, or the evenness with which the total estimated cover is spread among species, was very similar for the herb, bryoid, and epiphyte groups (Table 4). Species cover in the tree and shrub layers was somewhat less equitable than the other structural groups. This possibly bears on the question of competitive relationships within groups as discussed below. However, Whittaker (1965) reported quite variable dominance concentrations (dominance concentration is inversely related to equitability) for vascular strata in a variety of Great Smoky Mountain forests. In addition, no marked correlations were found between dominance concentrations for the three layers.

Dominance-diversity curves are presented for the total Swan Valley sample, as well as for each structural group, in Figures 10 and 11. The curves for the tree, shrub, herb, epiphyte, and the combined groups approach a geometric series. The curve for the bryoid layer differs in that it has a decreased slope at the lower end of the curve. However, I believe that that is an artifact introduced by the sampling method; specifically, the assignment of trace cover values to the numerous species that were infrequently encountered in sampling and had very low cover within quadrats. Similar curves have been found by Whittaker (1965) although he reported sigmoid curves for most

Figure 10. Dominance-diversity curve for the total Swan Valley sample. Species are ranked by percent cover on a logarithmic scale.

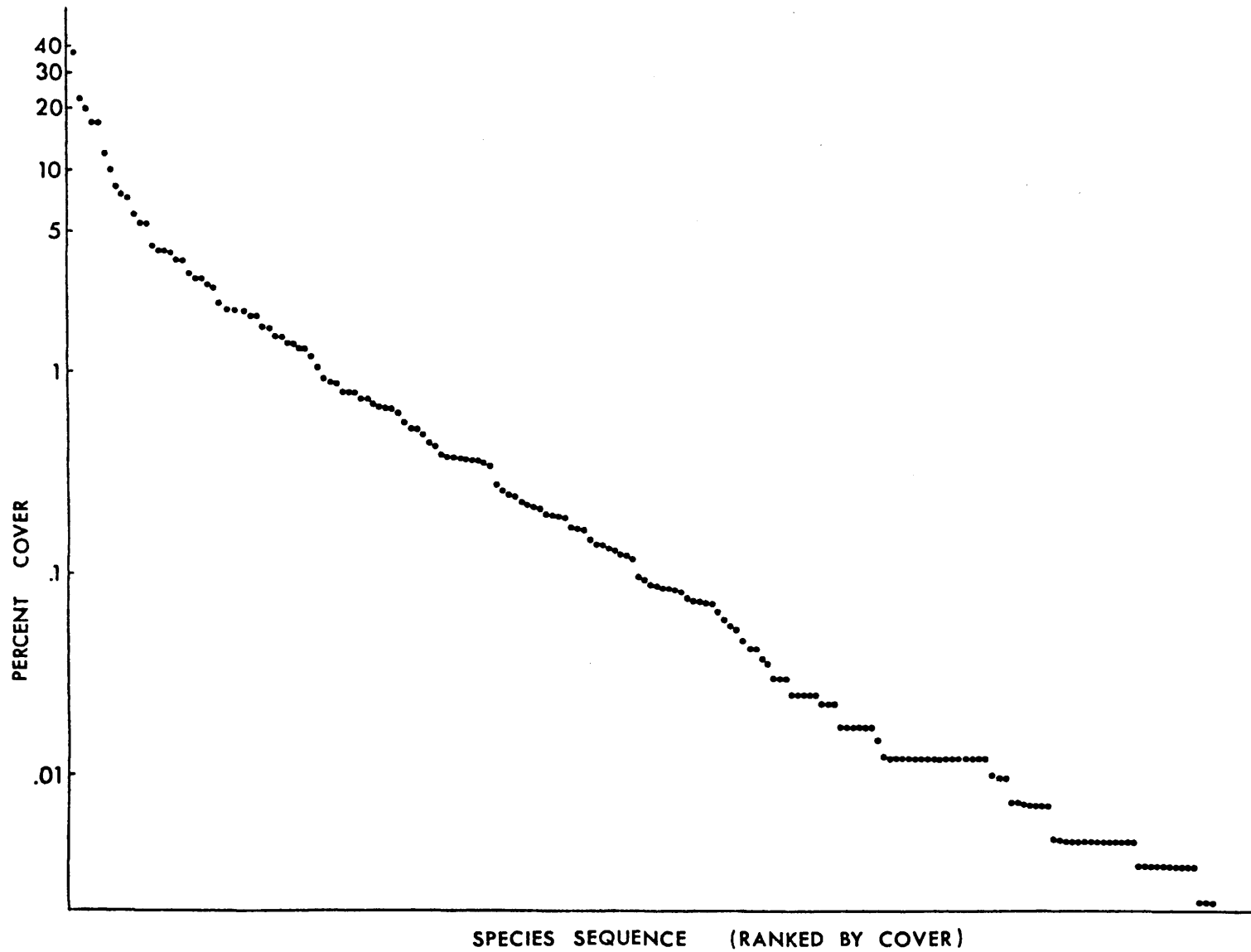
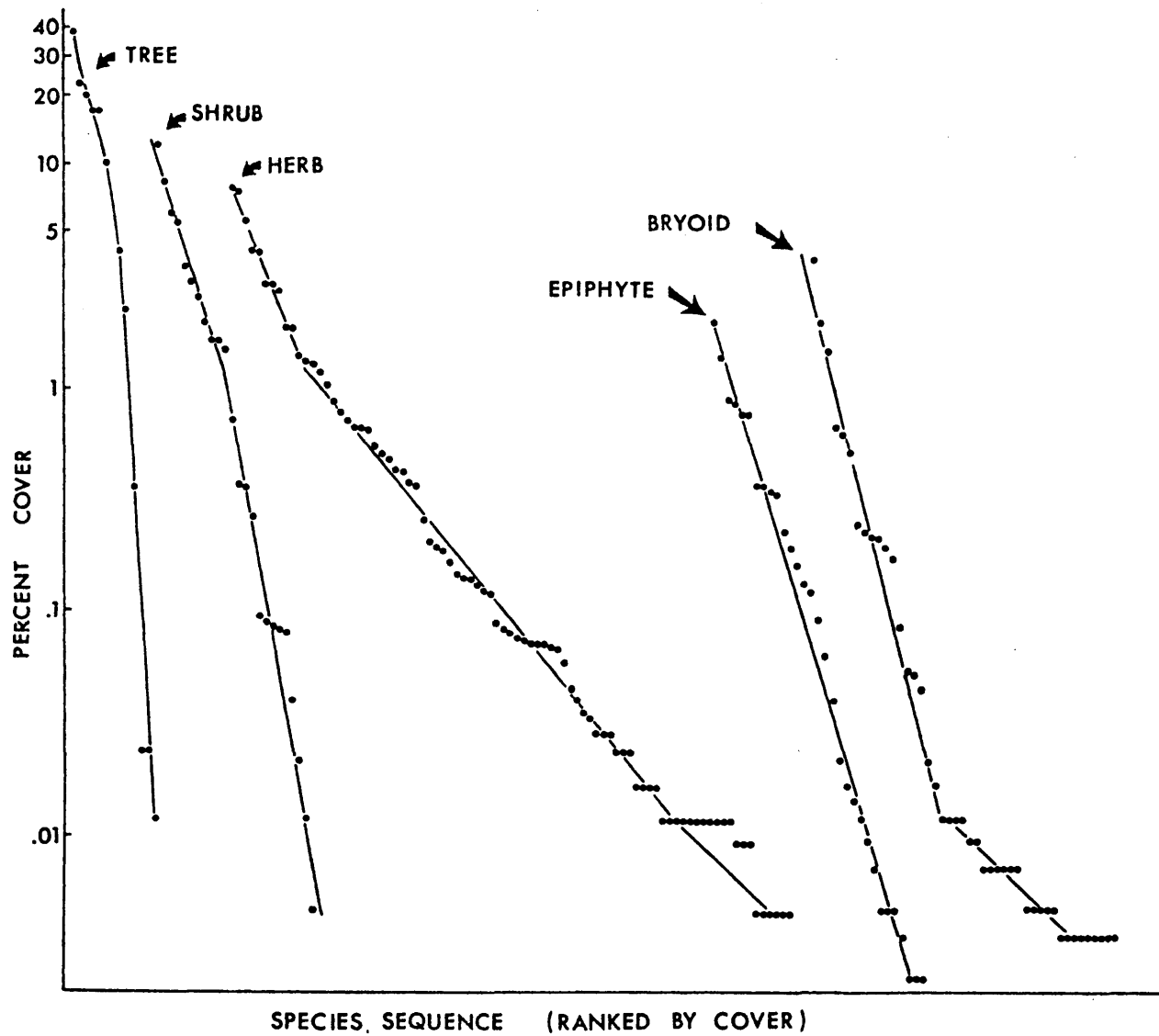


Figure 11. Dominance-diversity curves for each structural group, the species within each group ranked by percent cover on a logarithmic scale. The curves were placed within the same axes for ease of comparison. The horizontal position of the curves is arbitrary.



communities. Whittaker suggests that the geometric series may be a "plausible representation of competitive relations ... in some communities with few species."

The geometric series may be a reasonable, though oversimplified, model for resource utilization and competitive relations of species in the Swan Valley forests. Such a model implies that the most successful species utilizes a fraction of the total environmental resources, the second utilizes the same fraction of the remainder, and so on (Whittaker, 1965). It appears that the model is appropriate in this case for the structural groups considered alone or combined. However, one should be cautious in this interpretation because cover is not an accurate measure of resource utilization when making comparisons between structural groups.

Correlation of species counts between all pairs of structural groups revealed no strong positive or negative correlations (Table 5). This result has also been found for vascular strata by Zobel *et al.* (1976), Whittaker (1956, 1950), and Daubenmire and Daubenmire (1968). A contrary result was reported by Auclair and Goff (1971) from the Great Lakes area where herb and shrub diversities were positively correlated. Whittaker (1965) states that he sees no reason why diversity relations for different strata should parallel one another: different strata are "subject to different environmental factors and modes of population limitation."

Table 5. Coefficients of determination (r^2) for correlations between species richness of structural groups. Significant positive correlations at the .05 level is indicated by (*).

	Epi- phyte	Bryoid	Herb	Shrub
Tree	.03	.00	.00	.00
Shrub	.00	.00	.10*	
Herb	.10*	.02		
Bryoid	.01			

C. Resource Utilization by Structural Groups

Vegetation structure affects the availability of resources to the structural groups. In particular I was concerned with structural effects on the light and moisture factors. It is clear that canopy density affects the success of individuals below the canopy, although the mechanism of control is uncertain. In more general terms, increased cover in higher levels results in decreased cover at lower levels (Reiners, 1967). My results are somewhat equivocal on this point. Total cover of a structural group was negatively correlated with canopy cover in only the herb layer ($r^2=.24$, $p<.001$). Attempts to correlate cover of a given layer with the sum of the higher layers were abandoned. Difficulties were encountered in attempting to sum cover values derived from the different sampling methods used for the various structural groups. Observational evidence, however, supports the hypothesis of high cover in a given layer suppressing cover of lower layers.

Canopy openings support a ground flora differing in composition from areas of canopy closure. Dense canopies may affect lower layers by decreasing light and moisture and increasing litter fall. There is a long history of debate on whether light or moisture or both cause the observed differences in composition (Anderson et al., 1969). Many authors state emphatically that understory growth is controlled by light (eg. Rowe, 1956). However, most quantitative and experimental studies indicate that

variations in throughfall precipitation are of greater importance, although low light also limits understory growth to a degree (Anderson *et al.*, 1969; Touney, 1931; Fricke, 1904; Fabricius, 1927, 1929).

I set up trenched plots in the study area in order to assess the relative importance of light and moisture in understory suppression within the study area. The two stands chosen for study have dense canopies with very sparse understories. It is too early to report the results of this experiment. Nevertheless, qualitative observations allow a preliminary assessment of the problem in the Swan Valley.

It seems likely that moisture is usually an important limiting factor for undergrowth development in dense forests of the Swan Valley, based on the following rationale. Rain showers in the Swan Valley tend to be relatively gentle or brief during the summer season when soil moisture levels become critical. Summer showers are often largely intercepted by the canopy. At the same time, root competition has reduced soil moisture to low levels, and the surface litter and humus are dry. Under such conditions survival of herbaceous species, especially early in their life history, is probably dependent upon addition of moisture to the soil by precipitation. Because canopy cover is so effective in intercepting the normally light and/or brief summer showers, I feel that canopy cover is probably important in determining survival of young or shallow-rooted vascular plants. Interception of snowfall by canopies may

also be important in locally decreasing soil moisture and affecting understory success.

Some canopy openings in the Swan forests are dominated by shrubs, some by herbs, others by bryophytes. The factors controlling which structural group dominates below a canopy opening remain uncertain. The circumstance during stand initiation may affect the contribution of shrubs to the stand and in turn, to canopy openings. In any event, the composition of understory layers under the surrounding canopy may be of primary importance in determining which structural group will dominate under a canopy opening. However, in some cases the mosses tend to dominate because of local thin spots in the soil mantle over bedrock. In those situations thinly buried rock creates and temporarily maintains the opening. Still other sites may have a soil depth adequate for the success of rooted plants, yet support mainly mosses. Light compensation points may be relatively low for mosses. Thus, these sites may allow enough moisture for mosses or herbs but not enough light for significant development of the herb layer. However, limited data indicate that the light compensation points for forest floor bryophytes and shade-grown vascular plants may be similar (Stalfelt, 1960).

The vertical gradient in light intensity in a forest is closely related to a gradient in plant form. Plants successfully growing in lower layers tend to have proportionately greater photosynthetic tissue than plants in

higher layers. Trees and bryophytes are at the two extremes: the former with much respiring but non-photosynthetic support tissues, the latter with virtually all photosynthetic tissue.

Lichens, however, do not fit this pattern, having relatively few photosynthetic cells. Perhaps lichens are plentiful under the canopies of the Swan Valley forests by virtue of a strategy of slow and intermittent growth. Long term resistance to decay and herbivory is probably afforded by high internal concentrations of "lichen substances", predominantly organic acids. This protection plus physiological adaptation for survival at low thallus water contents permits opportunistic photosynthesis--a facility that apparently is required for an epiphytic existence in this study area.

Some hypotheses as to the environmental and competitive relations of structural groups may be drawn by analysis of the species correlation matrix. Table 6 presents the percent of possible within-group and out-of-group correlations for each structural group.

Conditions that favor one tree species are unlikely to favor another. This is suggested by the uniquely low percent of possible within-group positive correlations as well as the uniquely high percent of possible within-group negative correlations. The abundance of negative correlations in the tree layer appears to be due in part to differing environmental requirements and perhaps competitive

Table 6. Percent of possible interspecific correlations, significant at $p < .05$.

structural group	positive correlations		negative correlations	
	within group	out of group	within group	out of group
Tree	4.4	12.2	15.6	3.5
Shrub	19.2	12.6	0.0	2.6
Herb	15.8	11.6	0.3	1.2
Bryoid	17.5	9.2	0.0	0.5
Epiphytes	19.3	11.0	2.9	2.5

effects. For instance, *Picea engelmannii* is negatively correlated with *Pinus contorta*, probably because of differing environmental requirements. Within the stands sampled the former is most common in old ravine stands, the latter occurring in young stands over a wide range of moisture conditions. Competition may also contribute to the negative correlations. For example, both *Abies grandis* and *Pinus contorta* may become established soon after a burn (Antos, 1977). In the early years of succession, *Pinus contorta* is able to outcompete *Abies grandis*. The fir remains as a somewhat suppressed component of the stand until the pine begins to die, usually from bark beetles. *Abies grandis* may then increase and assume dominance.

Shrubs were distributed more cohesively. In other words, conditions favoring one shrub species are likely to favor the other shrub species. Supporting evidence from the species correlation matrix includes an absence of negative within-group correlations and a greater proportion of possible positive within-group correlations than out-of-group positive correlations.

Bryoids, epiphytes, and herbs also tended towards cohesive distributions (listed in order of decreasing group cohesion). These groups show similar patterns in Table 6: the proportion of positive correlations was high within each structural group relative to out-of-group positive correlations. For each of these groups, negative

correlations were rare both within and out of the group.

Thus, with the exception of trees, the general observation was that factors favoring a given species are more likely to favor other species in the same structural group than species of other structural groups.

Overall, noticeably more positive correlations were found than negative correlations. This resulted from the presence of many zero-cover values in the data matrix. Because of this, meaningful comparisons of the number of positive to the number of negative correlations within a group are not possible.

D. Implications Concerning Habitat Typing.

Habitat type systems exist for much of the northern Rocky Mountain forests (Pfister *et al.*, 1977; Daubenmire and Daubenmire, 1968; R. Steele *et al.*, 1976). The basic objective of this approach is to provide a classification and description of late seral to climax vegetation that would allow improved resource management. The general philosophy and methodology of this approach is described by Daubenmire (1966).

Forest habitat types are generally based on both overstory and understory vegetation. This practice was probably initiated by Scandinavian and European workers who found more variation in the understory than in the canopy (Gams, 1918; Du Rietz, 1936; Braun-Blanquet, 1932; Cajander, 1909, 1949; Cajander and Ilvessalo, 1921).

However it has been recognized that associations of undergrowth are not always predictable subgroups of larger types defined by trees (Gams, 1918; Cain, 1936; Gleason 1926, 1936; Lippmaa, 1939; Whittaker, 1960; McIntosh and Hurley, 1964; Daubenmire, 1968; Hoffman and Kazmierski, 1969; La Roi and Stringer, 1976; Pfister *et al.*, 1977; A. Steele, 1978). My data are in agreement with their observations: independently defined types for each structural group are related neither by a simple hierarchy nor a one-to-one correspondence. The relationships between stratal types in the Swan Valley appear to be quite complex (Figures 6 through 9). This lack of correspondence between stratal types is even more disturbing in view of the low correspondence between the Montana habitat type system (Pfister *et al.*, 1977) and the groups produced by cluster analysis of the late seral Swan Valley stands.

I do not mean to belittle the habitat typing efforts. While I have doubts concerning the assumptions that that approach is based on, I recognize the value of a classification scheme for management purposes. However, I do wish to emphasize that my results indicate that the habitat type systems that we have today should be considered to be first approximations. There appears to be a danger of mechanistic reliance on habitat types as management units, a reliance that overlooks the uncertain status of the biological foundation for the types.

Much of the bulk of plant ecological literature is

directed towards pigeonholing vegetation. My results indicate that pigeonholes that work well for one layer are not necessarily good for other layers. This independence of layers has long been recognized by Scandanavian and European workers in their stratal and synusial approaches to vegetation classification (Gams, 1918; Du Rietz, 1936; Lippmaa, 1935, 1939; Cain, 1935). In these approaches, structural groups are classified independently. However, as Krajina (1960) infers, an understanding of ecosystems is not possible by studying structural groups separately. As discussed above, a satisfactory reconciliation between the independence of layers and classification methodology has not been reached.

E. Bryophytes and Lichens as Indicator Species.

It has been written, over and over, that bryophytes and lichens are exceptionally sensitive to their environment. (eg. Lambert and Maycock, 1968; Stringer and Stringer, 1974; Shacklette, 1961; Scott, 1970; Phillips, 1951; Jesberger, 1973; Cantlon, 1953; Culberson, 1955). Furthermore, it has been repeatedly suggested that because of that sensitivity they should be good indicator species. However, cryptogams have been used as indicator species in relatively few studies in North America (Krajina, 1965, 1969; Orloci, 1965; Bell, 1965; Brooke, 1965; Brooke *et al.*, 1969; Achuff and La Roi, 1977) Except for the well documented sensitivity to pollutants, I am not convinced that lichens are more sensitive (i.e. narrower amplitudes

of tolerance) to their environment than other life form groups. The appearance of sensitivity results from frequently high diversity and obvious small-scale distributional patterns. As discussed above, these observations have an alternative explanation: the high diversity of cryptogams results from the complex array of within-stand microhabitats. Obviously, the presence and diversity of microhabitats can only be given visible expression by plants small enough to occupy them. Thus, cryptogams are more likely to indicate microenvironments available primarily to cryptogams than to indicate environments relevant to vascular plants. Perhaps this partially explains the large discrepancy between the many claims of the utility of cryptogams as indicator species and the rarity of their use as such.

Other difficulties impede the adoption of lichens and bryophytes as indicators. In addition to a narrow amplitude of tolerance and constancy within that amplitude, an ideal indicator species should be readily identifiable in the field. Unfortunately, only a few cryptogams in this area are so distinct in appearance that they could be accurately identified by a non-specialist in the field (eg. *Letharia vulpina*, *Lobaria pulmonaria*, *Rhytidiopsis robusta*, and *Hylocomium splendens*). Most species of cryptogams in the northern Rockies have closely related species with significantly different ecological requirements.

F. Species Responses

Antos (1977) discussed in detail the species responses of vascular plants in the Swan Valley. The main focus of this section is on cryptogamic species.

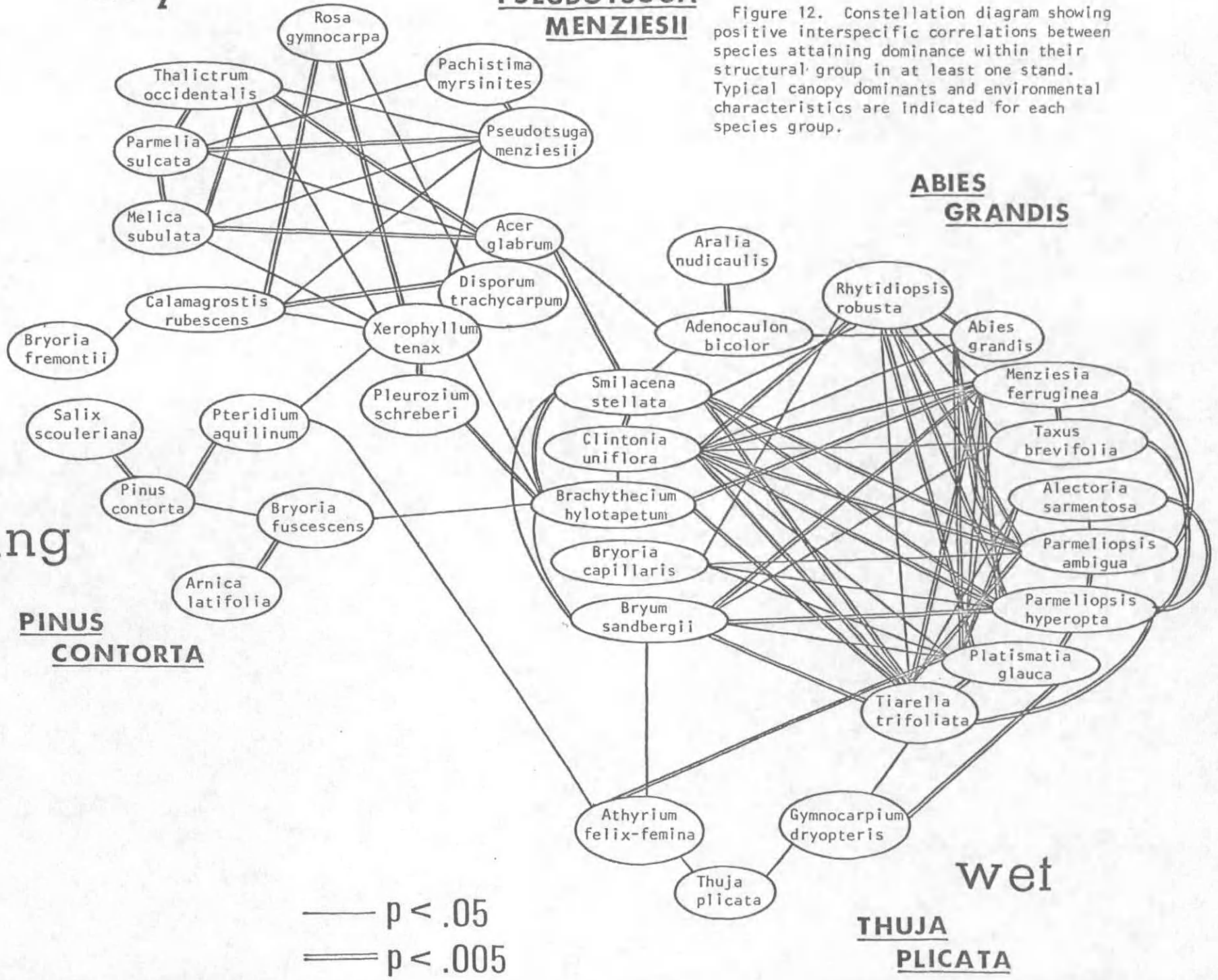
Figure 12 is a constellation diagram for major species from all structural groups. Only those species achieving dominance within a structural group in at least one stand are included. Lines connecting the species represent positive interspecific correlations. Four species groups are suggested by the diagram, each group with a characteristic dominant tree species. *Abies grandis* and its associated species are typical of modal sites in the Swan Valley. Composition on drier sites shifts towards the species grouped with *Pseudotsuga mezziesii*. On wetter sites, especially in stream bottoms, the species grouped with *Thuja plicata* may be dominant. Species associated with *Pinus contorta* may dominate their layer in young stands. The positions of vascular species within this diagram are consistent with other studies in this area (eg. Antos, 1977; Pfister et al., 1977; Habeck, 1967, 1968).

Epiphytes: Positive interspecific correlations between epiphytes are shown in Figure 13. The group of species at the lower left are characteristic of young *Pinus contorta* stands or dry exposed sites. The mosses *Dicranum tauricum* and *Ptilidium pulcherrimum* are well developed as epiphytes only in wetter stands, especially on the bark of leaning, old trees. The remainder of the species shown can be found

dry

PSEUDOTSUGA
MENZIESII

Figure 12. Constellation diagram showing positive interspecific correlations between species attaining dominance within their structural group in at least one stand. Typical canopy dominants and environmental characteristics are indicated for each species group.



ABIES
GRANDIS

PINUS
CONTORTA

THUJA
PLICATA

— $p < .05$
= $p < .005$

young

wet

Figure 13. Constellation diagram showing positive interspecific correlations between epiphytes. General environmental conditions favoring the species groups are indicated.

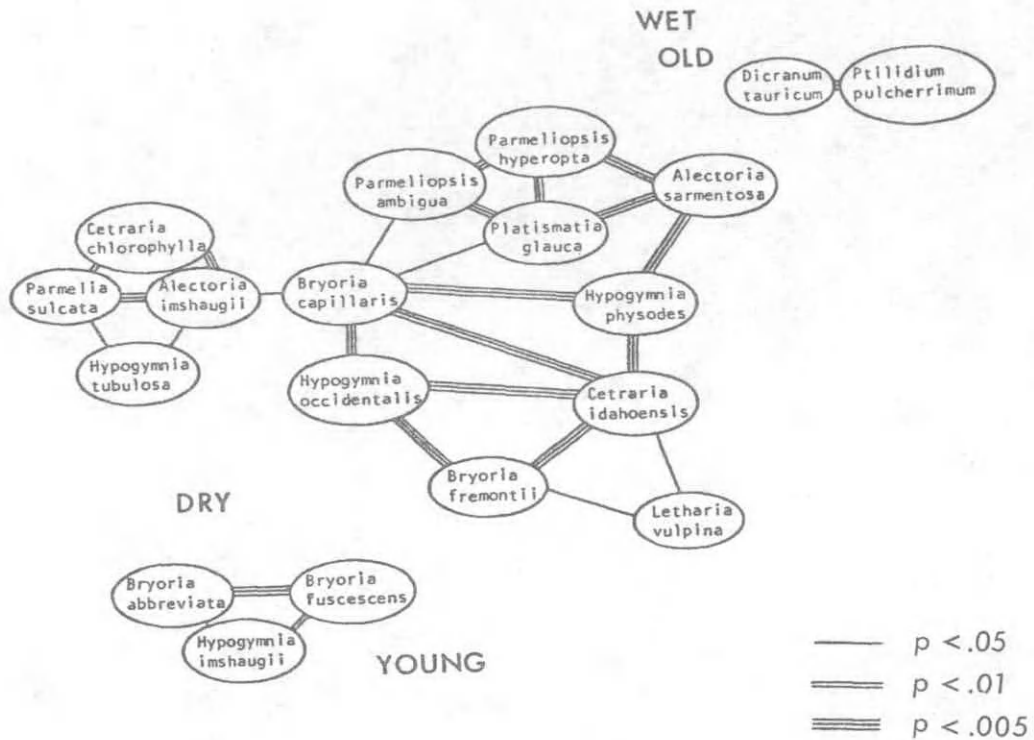
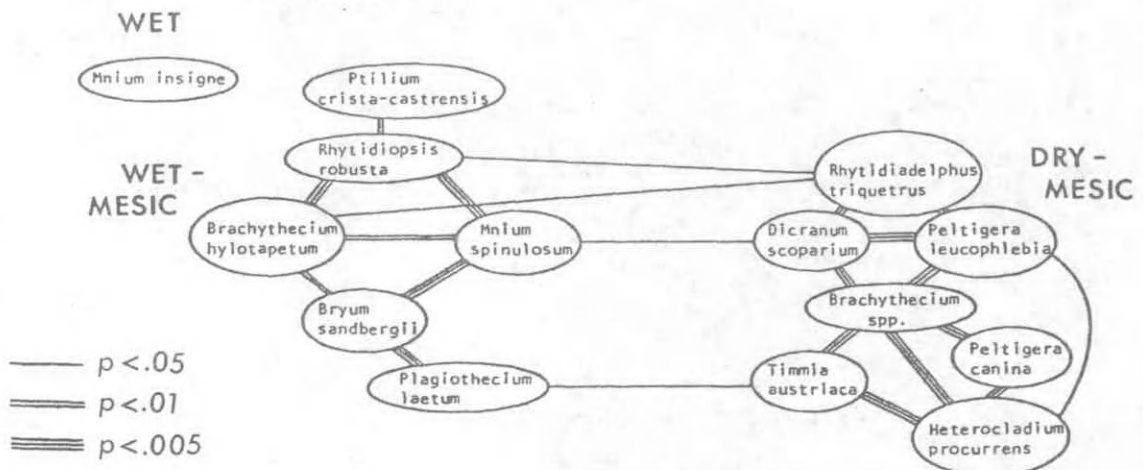


Figure 14. Constellation diagram showing positive interspecific correlations within the bryoid layer. General environmental conditions favoring the species groups are indicated.



in most *Abies grandis* stands in the study area. A list of epiphytic lichens is included in Appendix A.

Bryoid layer: Positive correlations between species in the bryoid layer are shown in Figure 14. The species groups are roughly related to a moisture gradient as indicated in the figure. Some of the more common species found on the forest floor are discussed below. A list of all species known from this layer in the Swan Valley is included in Appendix B.

Rhytidiopsis robusta was the most abundant species in the bryoid layer. Percent cover of *R. robusta* ranged up to about 20% in individual stands and averaged about 4%. In western Montana *R. robusta* is typical of older stands on moist upland sites, and is frequently found in stands dominated by *Abies grandis*, *Thuja plicata*, *Picea engelmannii*, or *Tsuga heterophylla*. This robust moss appears to be a strong competitor in the bryoid layer and is capable of maintaining populations in mature forests. As with most of the mosses growing on the forest floor, the most luxuriant cover occurs in patches associated with openings in the canopy. *Ptilium crista-castrensis* and *Pleurozium schreberi* are also large mosses characteristic of wetter forests in the study area, but these species are generally less abundant than *R. robusta*.

Rhytidiadelphus triquetrus has a habit similar to *R. robusta* but appears to be tolerant of drier sites. Although these two species often grow intermixed, *R. triquetrus* is

commonly found in drier *Pseudotsuga menziesii* stands without *R. rostrata*.

I believe that the four species discussed above are primarily K-selected. They spread mainly by vegetative growth, can easily overgrow smaller mosses, and are typical of mature forests.

Mnium spinulosum was present in most stands but reached maximum cover in the wetter stands. Because this species is relatively small and frequently bears spores, populations of *M. spinulosum* are probably relatively ephemeral and mobile. Furthermore, rather than forming continuous cover, this species frequently occurs as scattered individuals -- a feature probably related to its abundant spore production.

Bryum sandbergii is similar to *Mnium spinulosum* in habit, and frequently grows intermixed with it. I believe that the former differs in being more shade tolerant and more restricted to wetter sites. *B. sandbergii* is one of the few plants that can survive under dense stands of *Taxus brevifolia* or *Menziesia ferruginea*.

Mnium insigne is usually found in moist depressions in stream bottoms and along springs or creeks. Wherever *M. insigne* occurs groundwater is at or close to the surface. This moss and its substrate are generally wet to the touch for most of the year. *M. insigne* occurs in shady wet microsites from the wettest to the driest forests in northwestern Montana.

Brachythecium hylotapezum is nearly ubiquitous on

upland sites in the Swan Valley. It typically is well dispersed throughout a stand, probably because of frequent reproduction by spores and a creeping habit. It is able to occupy a wide range of substrates but rarely forms continuous cover. It was frequently found threaded through masses of living or dead plant material, such as clumps of *Xerophyllum tenax*. *B. hylocomium* appears to have evolved the strategy of continual tip growth into favorable environments while abandoning old shoots to burial by litter. *B. hylocomium* is probably the most successful moss in *Abies grandis* stands having a dense herb layer.

It is unfortunate that several *Brachythecium* species had to be lumped, because those species appear to differ ecologically. *B. leibergii* was apparently more abundant in the wetter stands, while *B. albicans* and *B. collinum* were found in the driest stands. *B. salebrosum* and *B. starckeii* were more restricted to rotten wood, but may also occur on the forest floor in moist stands.

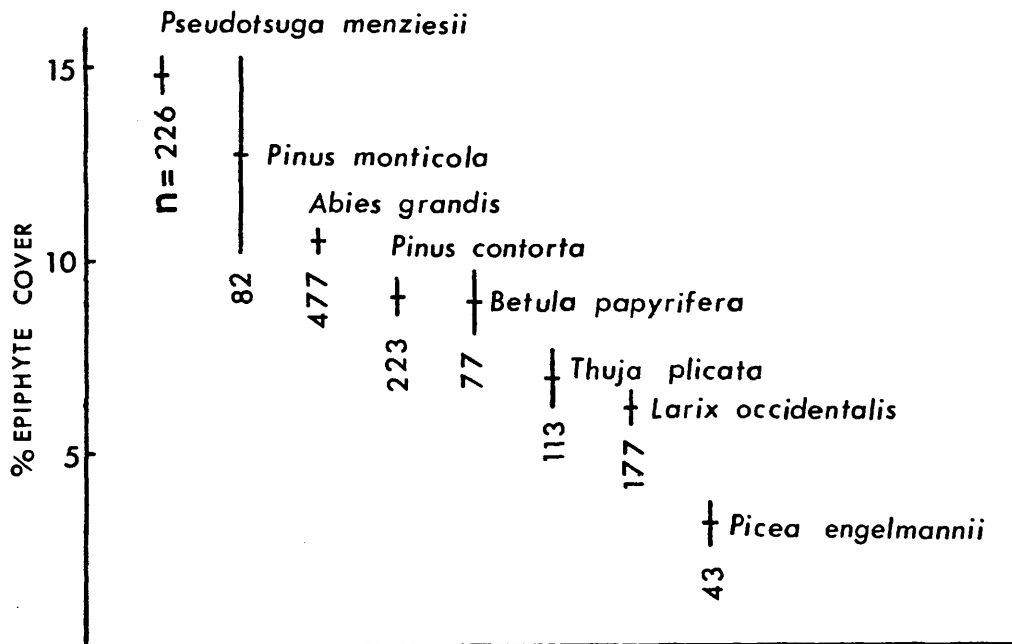
The large foliose lichens *Peltigera leucophlebia* and *P. canina* are common in the Swan Valley in an amazing variety of habitats ranging from exposed soil on clearcuts to rotting logs along streams in *Thuja* forests. Specimens of *P. canina* from exposed sites approach the morphology, and may be, *P. rufescens*. No attempt was made to separate these species during quantitative sampling because of the baffling array of specimens with characteristics of both species.

G. Host-Epiphyte Relations

Lichen cover was found to vary greatly between different host tree species (Figure 15). Similar observations as well as cases of host specificity have been explained on the basis of bark characteristics including roughness, sloughing rates, pH, nutrient status, presence of tannins and resins, and moisture absorbance and retention. Of course, factors other than bark characteristics also influence epiphyte cover on trees, including the light-temperature-moisture factor complex, canopy characteristics, host age, air pollution, and so on. Reviews of factors controlling epiphyte distribution are included in Barkman (1958) and Brodo (1974).

I believe that the differences in total cover of epiphytes on conifers in the Swan Valley (Figure 15) can be adequately explained on the basis of canopy characteristics, bark texture, and bark durability. Differences in bark chemistry may also be important. However, with the exception of *Betula papyrifera*, all the hosts were conifers. Conifers have been shown to have similar bark pH values as compared with deciduous trees (Culberson, 1955; Kalgutkar Bird, 1969; Patterson, 1940; Billings and Drew, 1938). Differences in nutrient status due to stem flow are not important in the Swan Valley because stemflow rarely occurs. Conifer bark as well as *Betula papyrifera* bark are all "oligotrophic" as evidenced by low ash content (Barkman, 1958). However, tannin content of bark appears to differ

Figure 15. Mean percent cover of epiphytes on major tree species. Vertical bars indicate 95% confidence intervals. The number of trees sampled for epiphytes is shown for each tree species.



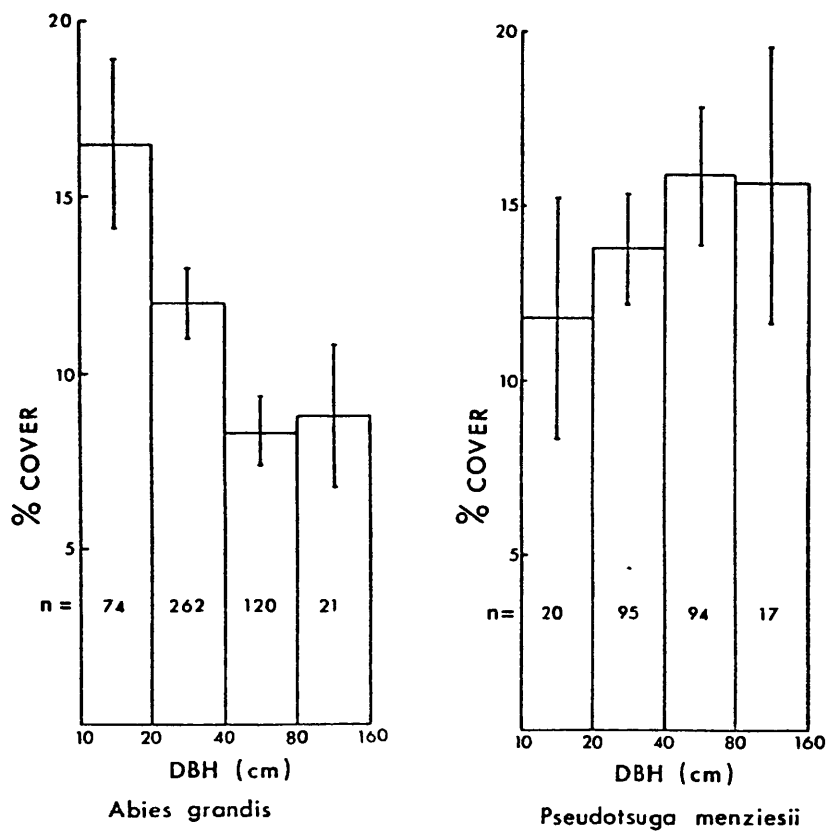
significantly among conifers and differences in resin contents have apparently not been studied (Barkman, 1958).

Pseudotsuga menziesii had the highest epiphyte cover. This species has a durable bark that becomes very rough and absorbent when old, promoting epiphyte development. High epiphyte cover on Pinus monticola probably occurs because of its dense very durable bark and the tendency for this species to have a moderately open crown. Abies grandis has a durable bark becoming quite rough with age, although these epiphyte-promoting characteristics are offset somewhat by its tendency to form dense crowns when in a dominant position in the forest. Abies grandis was commonly present as small old suppressed trees that often supported a dense lichen cover. Pinus contorta forests often have thin canopies which promote epiphyte development. However, Pinus contorta is relatively short-lived and has a moderately flaky bark which tends to reduce the epiphyte cover values. Betula papyrifera has very smooth bark which discourages lichen establishment. However, thalli (especially of Parmelia sulcata) frequently originate on the rough limb scars and rapidly expand over the smooth areas. Lichen cover is further promoted by the generally thin crown of the host during the growing season and the increased light and moisture after leaf fall. Thuja plicata forms dense canopies which tend to retard lichen growth on its trunks. Moisture interception by the canopy may be offset to a degree by the tendency for Thuja plicata to grow in

relatively moist streambottoms. *Larix occidentalis* has very loose scaly bark which strongly reduces lichen cover on its trunk. *Picea engelmannii* had the least epiphyte cover on its trunks. It has a moderately flaky bark, but perhaps more importantly, it often forms dense canopies that result in low trunk illumination and moisture levels.

Epiphyte cover as a function of trunk diameter was examined for the two host species, *Abies grandis* and *Pseudotsuga menziesii*, for which a sample adequate for such an analysis was obtained. Quite different patterns were found for the two species (Figure 15). *Abies grandis* had higher percent cover on smaller trees, the reverse was true of *Pseudotsuga menziesii*. It should be realized that diameter and height are not well correlated with age for *Abies grandis* because this species can survive in deep shade, maintaining a suppressed condition in the stand (Antos, 1977). These small, suppressed grand firs of moderate to old age usually support a dense epiphyte cover. The canopies of the suppressed individuals are generally thin and poorly developed permitting more light and throughfall precipitation to reach its trunk, as compared to adjacent dominant individuals. The slow rate of bark surface expansion resulting from slow growth may also contribute to higher cover on the trunks of suppressed individuals. While the curve of percent cover as a function of DBH for grand fir is controlled by the tendency for the host to exist in a suppressed state, the curve for douglas

Figure 16. Mean percent cover of epiphytes at breast height on trunks of *Pseudotsuga menziesii* and *Abies grandis* as a function of trunk diameter. Vertical lines indicate 95% confidence intervals. Sample sizes are shown within each bar.



fir reflects changes occurring with age. Douglas fir bark becomes very thick, soft, and absorbent with age, yet remains fairly durable. These changes allow a well developed epiphyte flora to expand and persist on older individuals. Thus, for the two tree species studied, percent cover as a function of diameter appears to be dependent not only on changing bark characteristics and surface age, but also on the tendency for the tree to exist in a suppressed condition.

LITERATURE CITED

- Acuff, P. L. and G. H. La Roi. 1977. Picea-Abies forests in the highlands of northern Alberta. *Vegetatio* 33: 127-146.
- Anderson, R. C., O. L. Loucks, and A. M. Swain. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecol.* 50: 255-263.
- Antos, J. A. 1977. Grand fir (*Abies grandis* (Dougl.) Forbes) forests of the Swan Valley, Montana. M.A. Thesis, Univ. of Montana, Missoula. 220 p.
- Ashton, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc. London* 1:155-196.
- Auclair, A. N. and F. G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. *Am. Nat.* 105: 499-528.
- Balogh, J. 1938. Biosozologische Studien über die Spinnenfauna des Sashegy (Adler-Berg) bei Budapest. *Festschr. Strand* 4: 464-499.
- Banberg, S. A. and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecol. Monogr.* 38: 127-167.
- Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum and Co., Ltd., Assen, Neth. 628 p.
- Barkman, J. J. 1973. Synusial approaches to classification. in *Handbook of Vegetation Science Vol. 5, Ordination and classification of communities*. R.H. Whittaker, (ed.) 82. p. 437-482.
- Bell, M. A. M. 1965. The dry subzone of the interior western hemlock zone. *Ecology of Western North America* 1: 42-56.
- Billings, W. D. and W. B. Drew. 1924. Bark factors affecting the distribution of corticolous bryophytic communities. *Am. Midl. Nat.* 20: 302-330.
- Bowler, P. A. and P. W. Rundel. 1977. Synopsis of a new lichen genus, *Eistulariella* Bowler and Rundel (Ramalinaceae). *Mycotaxon* 6: 195-202.
- Bratton, S. P. 1975. A comparison of the beta functions of the overstory and herbaceous understory of a deciduous forest. *Bull. Torr. Bot. Club* 102: 55-50.

- Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia. 596 p.
- Braun-Blanquet, J. 1928. Pflanzensoziologie: Grundzuge der Vegetationskunde. 1st Ed. Springer, Berlin. 330 p.
- Braun-Blanquet, J. 1932. Plant sociology, the study of plant communities. Transl. by G. D. Fuller and H. S. Conard. McGraw-Hill, New York. 439 p.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.
- Brodo, I. M. 1973. Substrate ecology. in V. Ahmadjian and M. E. Hale (eds.), The lichens. p. 401-441. Academic Press, New York.
- Brodo, I. M. and D. L. Hawksworth. 1977. Alectoria and allied genera in North America. Op. Bot. 42: 1-164.
- Brooke, R. C. 1965. The subalpine mountain hemlock zone. Part II. Ecotypes and biogeocoenotic units. Ecol. of West. North Amer. 1: 79-101.
- Brooke, R. C., E. B. Peterson, and V. J. Krajina. 1969. The subalpine mountain hemlock zone. Ecol. of West. North Amer. 2: 147-349.
- Cain, S. A. 1936. Synusia as a basis for plant sociological field work. Amer. Midl. Nat. 17: 665-725.
- Cajander, A. K. 1909. Ueber Waldtypen. Acta For. Fenn. 1: 1-175.
- Cajander, A. K. 1949. Forest types and their significance. Acta. Forest. Fennica 56: 1-71.
- Cajander, A. K. and Y. Ilvessalo. 1921. Uber Waldtypen II. For. Fenn. 20: 1-77.
- Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. Ecol. Monogr. 23: 241-270.
- Clements, F. F. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.
- Cooke, W. B. 1955. Fungi, lichens, and mosses in relation to vascular plant communities in eastern Washington. Ecol. Monogr. 25: 119-180.
- Crum, H. A., W. C. Steere, and L. E. Anderson. 1973. A new list of mosses of North America north of Mexico. Bryol. 76: 85-130.

- Culberson, W. L. 1955. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. *Ecol. Monogr.* 25: 215-231.
- Daubenmire, R. 1966. Vegetation: identification of typical communities. *Science* 151: 291-298.
- Daubenmire, R. and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. Agric. Exp. Sta., Tech. Bull.* 60. 104p.
- Du Rietz, G. F. 1936. Classification and nomenclature of vegetation units 1930-1935. *Svensk. Bot. Tidskr.* 30: 580-589.
- Esslinger, T. L. 1977. A chemosystematic revision of the brown *Parmellia*e. *J. Hatt. Bot. Lab.* 42: 1-211.
- Esslinger, T. L. 1978. Studies in the lichen family *Physciaceae*. II the genus *Phaeophyscia* in North America. *Mycotaxon* 7: 283-320.
- Fabricius, L. 1927. Der einfluss des wurzelwettbewerbs des schirmstandes auf die Entwicklung des Jungwuchses. *Forstwiss. Centralb.* 49:329-345.
- Fabricius, L. 1929. Neue versuche zur Feststellung des Einflusses von Wurzelwettbewerb und lichtentzug des schirmstandes auf den Jungwuchs. *Forstwiss. Centralb.* 51: 477-506.
- Ferry, B. W., M. S. Baddeley, and D. L. Hawksworth (eds.). 1973. Air pollution and lichens. Univ. of Toronto Press, Toronto.
- Flint, H. R. 1932. Some observations on lichens as factors in Northern Rocky Mountain forest succession. *Northwest Science* 6: 14-16.
- Fricke, K. 1904. "Licht und schattenholzarten", ein wissenschaftlich nicht begründetes dogma. *Centralb. f.d.g. Forst.* 30: 315-325.
- Gams, H. 1918. Prinzipienfragen der Vegetationsforschung. *Vierteljahrsschr. d. Naturf. Ges. Zurich* 63: 293-493.
- Gauch, H. G. and R. H. Whittaker. 1972. Comparison of ordination techniques. *Ecol.* 53: 868-875.
- Geiger, R. 1950. The climate near the ground. Harvard Univ. Press, Cambridge. 459 p.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torr. Bot. Club* 53: 7-27.
- Gleason, H. A. 1939. The individualistic concept of the plant

- association. Amer. Midl. Nat. 21: 92-108.
- Glenn-Lewin, D. C. 1975. Plant species diversity in ravines of the southern Finger Lakes region, New York. Can. J. Bot. 53: 1465-1472.
- Habeck, J. R. 1953. Lichen distribution in the Lake Macdonald forest communities in Glacier National Park. Proc. Mont. Acad. Sci. 23: 34-36.
- Habeck, J. R. 1957. The vegetation of Northwestern Montana. A preliminary report. Univ. of Montana, Missoula. 57 p.
- Habeck, J. R. 1958. Forest succession in the Glacier Park cedar-hemlock forest. Ecol. 49: 872-880.
- Hale, M. E., Jr. 1952. Vertical distribution of cryptogams in a virgin forest in Wisconsin. Ecol. 33: 398-406.
- Hale, M. E., Jr. 1965. Vertical distribution of cryptogams in a red maple swamp in Connecticut. Bryologist 68: 193-197.
- Hale, M. E., Jr. 1974. Bulbothrix, Parmelina, Relicina, and Xanthoparmelia, four new genera in the Parmeliaceae (Lichenes). Phytologia 28: 479-490.
- Hale, M. E., Jr. and W. L. Culberson. 1970. A fourth checklist of the lichens of continental United States and Canada. Bryologist 73: 499-543.
- Harris, W. P. and C. W. Harris. 1934. Lichens and mosses of Montana. Univ. of Mont. Bull. No. 19, Biol. Ser. 7: 308-330.
- Hawksworth, D. L. and F. Rose. 1975. Lichens as pollution monitors. Arnold, London.
- Herman, F. J. 1969. Bryophytes of Glacier National Park, Montana. Bryologist 72: 358-376.
- Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Wash. Press, Seattle. 730 p.
- Hoffman, G. R. 1971. An ecological study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. II. Diversity of the vegetation. Bryologist 74: 413-427.
- Hoffman, G. R. and R. G. Kazmierski. 1969. An ecologic study of bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington I. A description of the vegetation. Bryologist 72: 1-19.
- Hong, W. S. 1968. Hepaticae of the Lolo National Forest,

- Montana. Bryologist 71: 362-365.
- Hong, W. S. 1975. Leafy hepaticae of Montana and phyto-geographic relationships to neighboring states and provinces. Bryologist 78: 304-327.
- Hong, W. S. 1977. Thalloid hepaticae of Montana and phyto-geographical relationships to neighboring states and provinces. Bryologist 80: 270-278.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecol. 52: 577-586.
- Imshaug, H. A. 1957. Alpine lichens of western United States and adjacent Canada. I. the macrolichens. Bryologist 60: 177-272.
- Jesberger, J. A. 1973. An ordination of corticolous lichen communities in the Popple River basin of northern Wisconsin. Trans. Wisc. Acad. Sci., Arts, Lett. 61: 267-284.
- Kalgutkar, R. M. and C. D. Bird. 1969. Lichens found on *Larix laricina* and *Pinus albicaulis* in southwestern Alberta, Canada. Can. J. Bot. 47: 627-648.
- Kessell, S. R. and R. H. Whittaker. 1976. Comparisons of three ordination techniques. Vegetatio 32: 21-29.
- Korchagin, A. A. 1964. Synusial structure of forest communities. Proc. X Int. Bot. Congr. Edinburgh 1964, Abstracts. p. 403.
- Kujala, V. 1925. Über die Begrenzung der Siedelungen. Commun. ex Inst. Quaest. Forestal. Finlandiae editae 10.
- Krajina, V. J. 1960. The role of corticolous, lignicolous and epilithic bryophyte and lichen communities in an ecosystem classification of the forest. Sympos. on the Ecol. of Bryophytes and Lichens, A.I.B.S. Annual Mtg., Stillwater, Okla.
- Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecol. of West. North Amer. 1: 1-17.
- Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecol. of West. North Amer. 2: 1-146.
- Lambert, J. D. H. and P. F. Maycock. 1968. The ecology of terricolous lichens of the northern coniferous-hardwood central eastern Canada. Can. J. Bot. 46: 1043-1078.
- Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori Botanical Lab., Nichinan, Miyazaki, Japan. 362 p.
- Leuckert, C., J. Poelt, and G. Hahnel. 1976. Zur chemotaxonomie der Eurasischen arten der flechtengattung

- Rhizoplaca. *Nova Hedwigia* 28: 71-129.
- Lippmaa, T. 1935. La methode des associations unistrates et le systeme ecologique des associations. *Act. Instit. Hort. Bot. Univ. Tart.* 4, 1934: 7 p.
- Lippmaa, T. 1939. The unistratal concept of plant communities (the unions). *Amer. Midl. Nat.* 21: 111-143.
- Lyon, L. J. and P. F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. *Proc. Tall Timbers Fire Ecol. Conf.* 14: 355-375.
- McCune, B. 1977. Vegetation development on a low elevation talus slope in western Montana. *Northwest Sci.* 51: 198-206.
- McIntosh, R. P. and R. T. Hurley. 1964. The spruce-fir forests of the Catskill Mountains. *Ecol.* 45: 314-320.
- Moral, R. del. 1972. Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. *Bull. Torr. Bot. Club* 99: 57-64.
- Moss, E. H. 1953. Forest communities in northwest Alberta. *Can. J. Bot.* 31: 212-252.
- Mueller, Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.. 547 p.
- Orloci, L. 1965. The coastal western hemlock zone on the southwestern British Columbia mainland. *Ecol. of West. North Amer* 1: 18-34.
- Palmgren, A. 1922. Uber Artenzahl und Areal sowie uber die Konstitution der vegetation. *Acta Forest. Fennica* 22.
- Patterson, P. M. 1940. Corticolous bryophyte societies at Mountain Lake, Virginia. *Am. Midl. Nat.* 23: 421-441.
- Pearson, L. C. and D. B. Lawrence. 1965. Lichens as micro-climatic indicators in northwestern Minnesota. *Am. Midl. Nat.* 74: 257-268.
- Pfister, R. D., R. L. Kovalchik, S. F. Arno, and R. C. Presby. 1974. Forest habitat types of Montana. U.S.D.A. Forest Service, Gen. Tech. Rpt. INT-34. 213 p.
- Phillips, E. H. 1951. The associations of bark-inhabiting bryophytes in Michigan. *Ecol. Monogr.* 21: 301-316.
- Pielou, E. C. 1966. Shannon's formula as a measure of species diversity: its use and disuse. *Amer. Nat.* 100: 463-465.

- Reiners, W. A. 1967. Relationships between vegetational strata in the pine barrens of central Long Island. *Bull. Torr. Bot. Club* 94: 87-98.
- Ross, C. P., D. A. Andrews, and I. J. Witkind. 1955. Geologic map of Montana. *Mont. Bur. Mines and Geol.*
- Ross, R. L. and H. E. Hunter. 1976. Climax vegetation of Montana based on soils and climate. U.S.D.A. S.C.S., Bozeman, Montana. 64 p. + maps.
- Robertson, P. A. 1978. Comparisons of techniques for ordinating and classifying old-growth floodplain forests in southern Illinois. *Vegetatio* 37: 43-51.
- Rowe, J. S. 1956. The use of undergrowth plant species in forestry. *Ecol.* 37: 461-473.
- Scott, G. A. M. 1970. Vegetation studies on Secretary Island, Fjordland. Part II: Epiphytic and ground cryptogamic vegetation on the north slopes. *New Zeal. J. Bot.* 8: 30-50.
- Shacklette, H. T. 1965. Bryophytes associated with mineral deposits and solutions in Alaska. *Geol. Surv. Bull.* 1198-C.
- Shannon, C. E. and W. Weaver. 1963. The mathematical theory of communication. Univ. of Illinois Press, Urbana. 117 p.
- Stalfelt, M. G. 1960. Flechten und moose. p. 364-375 in E. Ashby et al., (eds.) *Encyclopedia of Plant Physiology* Vol. V. The assimilation of carbon dioxide, Part 2. Springer-Verlag, Berlin.
- Steele, A. M. 1974. Moss communities of central Idaho forests. M.S. Thesis, Univ. of Idaho, Moscow, Idaho. 52 p.
- Steele, A. 1978. Bryophyte communities of central Idaho forests. *Northwest Sci.* 52: 310-322.
- Steele, R., S. F. Arno, and R. O. Pfister. 1976. Preliminary forest habitat types of the Nezperce National Forest. U.S.D.A. Forest Service Intermtn. For. and Range Exp. Sta. 71 p.
- Stotler, R. and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. *Bryol.* 80: 405-428.
- Stringer, P. W. and N. H. L. Stringer. 1974. Studies on the bryophytes of southern Manitoba. VI. An ecological study of the bryophytes of coniferous forests in Bird's Hill Provincial Park. *Bryologist* 77: 1-16.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts

- and terms. *Ecol.* 16: 284-307.
- Toumey, J. J. 1929. The vegetation of the forest floor; light v. soil moisture. *Int. Congr. Plant Sci. Proc.* 1: 575-590.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 270-338.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-260.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Whittaker, R. H. and H. G. Gauch. 1973. Evaluation of ordination techniques. in R. H. Whittaker (ed.) *Ordination and classification of communities. Handbook of Vegetation Science* 5: 287-321. Junk, The Hague.
- Zobel, D. B., A. McKee, and G. M. Hawk. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecol. Monogr.* 46: 135-156.

APPENDIX A

BRYOPHYTES OF THE SWAN VALLEY

Bryophyte taxa known for the Swan Valley are listed alphabetically in three sections; Musci, Sphagnales, and Hepaticae. The list represents my collections except that the Hepaticae section has been supplemented with published reports by Hong (1975, 1977). Species reported by Hong but not collected by myself are referenced to Hong. A total of 183 taxa are reported here. Species collected only at high elevations (>1800 m) are excluded from the list.

MUSCI

Ablystegium juratzkanum Schimp.

Aphidium mougeotii (B.S.G.) Schimp.

Antitrichia curtispindula (Hedw.) Brid.

Atrichum selwynii Aust.

Aulacomnium androgynum Schwaegr.

Aulacomnium palustre (Web. & Mohr) Schwaegr.

Bartramia pomiformis Hedw.

Brachythecium albicans (Hedw.) Brid.

Brachythecium collinum (C. Mull.) Besch.

Brachythecium frigidum (C. Mull.) Besch.

Brachythecium hylotapetum N. Hig. & B. Hig.

Brachythecium leibergii Grout

Brachythecium rivulare B.S.G.

Brachythecium salebrosum (Web. & Mohr) B.S.G.

Brachythecium starkei (Brid.) B.S.G.

Brachythecium turgidum (C.J.Hartm.) Kindb.

Bryoerythrophyllum recurvirostrum (Hedw.) Chen.

Bryum argenteum Hedw.

Bryum caespiticium Hedw.

Bryum capillare Hedw.
Bryum pallescens Schwaegr.
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Schreb.
Bryum sandbergii Holz.
Bryum turbinatum (Hedw.) Schwaegr.
Bryum weigellii Spreng.

Buxbaumia piperi Best.
Buxbaumia viridis (DC.) Moug. & Nestl.

Calliergon giganteum (Schimp.) Kindb.

Campylium chrysophyllum (Brid.) J. Lange
Campylium stellatum (Hedw.) C. Jens.

Ceratodon purpureus (Hedw.) Brid.

Claopodium bolanderi Best

Climacium dendroides (Hedw.) Web. & Monr.

Cratoneuron falcatum (Brid.) Roth.
Cratoneuron filicinum (Hedw.) Spruce

Desmatodon obtusifolius (Schwaegr.) Schimp.

Dichodontium pellucidum (Hedw.) Schimp.

Dicranella crispa (Hedw.) Schimp.

Dicranoweisia crispula var. *contermina* (Holz.) Grout

Dicranum fuscescens Turn.
Dicranum polysetum (Holz.) Irel.
Dicranum scoparium Hedw.
Dicranum tauricum Sap.

Distichium capillaceum (Hedw.) B.S.G.

Drepanocladus aduncus (Hedw.) Warnst.
Drepanocladus uncinatus (Hedw.) Warnst.
Drepanocladus uncinatus (Hedw.) Warnst var. *symmetricus*
 (Ren. & Card.) Grout

Eurhynchium pulchellum (Hedw.) Jenl.
Eurhynchium stokesii (Turn.) B.S.G.

Fissidens adianthoides Hedw.
Fissidens bryoides Hedw.
Fissidens grandifrons Brid.

Funaria hygrometrica Hedw.

Grimmia agassizii (Sull. & Lesq.) Lesq. & James
Grimmia alpestris (Web. & Mohr) Nees

- Grimmia alpicola* var. *rivularis* (Brid.) Wahl.
Grimmia apocarpa var. *apocarpa* Hedw.
Grimmia apocarpa var. *stricta* (Turn.) Hook. & Tayl.
Grimmia affinis Hoppe & Hornsch. ex Hornsch.
Grimmia calyptrata Hook.
Grimmia montana B.S.G.
- Hedwigia ciliata* Hedw.
- Heterocladium dimorphum* (Brid.) B.S.G.
Heterocladium procurrens (Mitt.) Rau & Herv.
- Homalothecium aeneum* (Mitt.) Lawt.
Homalothecium megaptilum (Sull.) Robins.
Homalothecium nevadense (Lesq.) Rea. & Card.
- Hygroamblystegium noterophilum* (Sull. & Lesq. ex Sull.)
 Warnst.
- Hygrohypnum bestii* (Ren.) Broth.
Hygrohypnum luridum (Hedw.) Jenn.
Hygrohypnum ochraceum (Wils.) Loeske
- Hylocomium splendens* (Hedw.) B.S.G.
- Hypnum circinale* Hook.
Hypnum lindbergii Mitt.
Hypnum pallescens (Hedw.) P. Beauv.
Hypnum pratense Spruce
Hypnum revolutum (Mitt.) Lindb.
Hypnum subimponens Lesq.
- Isopterygium seligeri* (Brid.) Dix.
- Isothecium spiculiferum* (Mitt.) Ren. & Card.
- Leptobryum pyriforme* (Hedw.) Wils.
- Leptodictyum riparium* (Hedw.) Warnst.
- Lescuraea incurvata* (Hedw.) Lawt.
Lescuraea patens (Lindl.) H. Arn. & C. Jens.
Lescuraea radicata var. *radicata* (Mitt.) Moenk.
Lescuraea stenophylla (Roll.) Kindb.
- Mnium dlytii* B.S.G.
Mnium orthorrhynchum Brid.
Mnium spinulosum B.S.G.
- Neckera menziesii* Drumm.
- Oncophorus virens* (Hedw.) Brid.
- Orthotrichum affine* Brid.
Orthotrichum hallii Sull. & Lesq. ex Sull.

Orthotrichum obtusifolium Brid.
Orthotrichum rupestre Schleich. ex Schwaegr.
Orthotrichum speciosum Nees.

Philonotis fontana (Hedw.) Brid.

Plagiomnium ciliare (C. Mull.) Kopon.
Plagiomnium insigne (Mitt.) Kopon.
Plagiomnium rostratum (Schröd.) Kopon.
Plagiomnium rugicum (Laur.) Kopon.
Plagiomnium venustum (Mitt.) Kopon.

Plagiothecium denticulatum (Hedw.) B.S.G.
Plagiothecium laetum B.S.G.
Plagiothecium piliferum (Hartm) B.S.G.

Pleurozium schreberi (Brid.) Mitt.

Pogonatum alpinum var. *alpinum* (Hedw.) Rohl.
Pogonatum urnigerum (Hedw.) Brid.

Pohlia cruda (Hedw.) Lindb.
Pohlia nutans (Hedw.) Lindb.
Pohlia wahlenbergii (Web. & Mohr) Andr.

Polytrichum juniperinum Hedw.
Polytrichum piliferum Hedw.

Pseudoleskeella tectorum (Brid.) Roth.

Pterigynandrum filiforme Hedw.

Ptilium crista-castrensis (Hedw.) De Not.

Rhacomitrium canescens Brid. var. *ericoides* (Hedw.) Hampe
Rhacomitrium heterostichum var. *heterostichum* (Hedw.) Brid.
Rhacomitrium patens (Hedw.) Huben.

Rhizomnium nudum (Williams) Kopon.
Rhizomnium personii Kopon.
Rhizomnium pseudopunctatum (Bruch & Schimp.) Kopon.

Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb.

Rhytidiadelphus loreus (Hedw.) Warnst.
Rhytidiadelphus triquetrus (Hedw.) Warnst.

Rhytidiopsis robusta (Hook.) Benth.

Scleropodium obtusifolium (Drumm.) Mac. & Kindb.

Scouleria aquatica Hook.

Tetraphis pellucida Hedw.

Thuidium recognitum (Hedw.) Lindb.

Timmia austriaca Hedw.

Tortella tortuosa (Hedw.) Limpr.

Tortula mucronifolia Schwaegr.

Tortula princeps De Not.

Tortula ruralis (Hedw.) Gaertn.

Tortula ruraliformis (Besch.) Dix.

Tortula subulata Hedw.

SPHAGNALES

Sphagnum spp.

HEPATICAE

Aneura pinguis (L.) Dum.

Apometzgeria pubescens (Schrank) Kuwah.

Barbilophozia barbata (Schmid. ex Schreb.) Loeske

Barbilophozia hatcheri (Evans) Loeske

Barbilophozia lycopodiodes (Wallr.) Loeske

Blepharostoma trichophyllum (L.) Dum. (Hong, 1975)

Calypogeia muelleriana (Schiffn.) (Mull. (Hong, 1975)

Cephalozia lunulifolia (Dum.) Dum.

Cephalozia pleniceps (Aust.) Lindb. (Hong, 1975)

Chiloscyphus pallescens (Ehrh.) Dum. (Hong, 1975)

Chiloscyphus polyanthus (L.) Corda.

Conocephalum conicum (L.) Lindb.

Jamesoniella autumnalis (DC.) Steph.

Jungermannia atrovirens Dum. [= *J. lanceolata* Schrad.]

Jungermannia cordifolia Hook.

Jungermannia pumila With.

Lepidozia reptans (L.) Dum. (Hong, 1975)

Lophocolea minor Nees (Hong, 1975)

Lophozia ascendens (Warnst.) Schust.

Lophozia collaris (Nees) Dum. [= *L. muelleri* (Nees) Jorg.]

Lophozia gillmanni (Aust.) Schust. (Hong, 1975)

Lophozia guttulata (Lindb. & H. Arnell) Evans [= *L. porphyroleuca*]

Lophozia heterocolpos (Thed.) M. A. Howe (Hong, 1975)
Lophozia incisa (Schrad.) Dum.
Lophozia longidens (Lindb.) Mac.
Lophozia ventricosa (Dicks.) Dum. (Hong, 1975)

Mannia fragrans (Balb.) Frye & Clark

Marchantia polymorpha L.

Metzgeria pubescens [see *Apometzgeria*]

Plagiochila asplenoides (L.) Dum.

Porella cordaeana (Hub.) Moore
Porella platyphylla (L.) Pfeiff.
Porella roellii Steph. (Hong, 1975)

Ptilidium californicum (Aust.) Underw. (Hong, 1975)
Ptilidium pulcherrimum (G. Web.) Hampe

Radula complanata (L.) Dum.

Riccardia multifida (L.) S. Gray (Hong, 1977)

Riccia fluitans L.

Ricciocarpus natans (L.) Corda

Scapania umbrosa (Schrad.) Dum. (Hong, 1975)
Scapania undulata (L.) Dum. (Hong, 1975)

Tritomaria exsecta (Schrad.) Loeske
Tritomaria exsectiformis (Breidl.) Loeske
Tritomaria scitula (Tayl.) Joerg. (Hong, 1975)

APPENDIX B

LICHENS OF THE SWAN VALLEY

A list of the 195 taxa that I collected in the Swan Valley is presented below. Species collected only at high elevations (>1800 m) are excluded from this list. The list is admittedly weak with respect to crustose lichens occurring on rock. Other groups that are probably more diverse than the list would indicate include the brown *Parmeliae* and *Physcia*.

Two of the species listed are particularly interesting finds. *Cladonia pseudomacilentia* has previously been reported from only Japan and Alaska. *Cladonia graciliformis* is new to North America. While *C. pseudomacilentia* appears to be fairly common in the wetter Swan Valley forests, *C. graciliformis* was collected in only one location. Dr. J. W. Thomson has confirmed the identity of specimens of both species.

Acarospora chlorophana (Wahl. ex Ach.) Mass.
Acarospora fuscata (Schrad.) Arn.

Alectoria imshaugii Brodo & D. Hawksw.
Alectoria sarmentosa (Ach.) Ach.

Bacidia obscurata (Somm.) Zahlbr.
Bacidia sabuletorum (Schreb.) Lett.
Bacidia sphaeroides (Dicks.) Zahlbr.

Bryoria abbreviata (Mull. Arg.) Brodo & D. Hawksw.
Bryoria capillaris (Ach.) Brodo & D. Hawksw.
Bryoria fremontii (Tuck.) Brodo & D. Hawksw.
Bryoria friabilis Brodo & D. Hawksw.
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.
Bryoria lanestris (Ach.) Brodo & D. Hawksw.
Bryoria oregana (Tuck.) Brodo & D. Hawksw.

Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.

Buellia papillata (Somm.) Tuck.

Buellia penichra (Tuck.) Hasse

Buellia punctata (Hoffm) Mass.

Buellia retrovertens Tuck.

Calicium viride

Caloplaca spp.

Candelariella vitellina (Ehrh.) Mull. Arg.

Cetraria canadensis (Ras.) Ras.

Cetraria chlorophylla (Willd.) Vain.

Cetraria ericetorum Opiz

Cetraria idahoensis Essl.

Cetraria merrillii Du Rietz

Cetraria orbata (Nyl.) Fink

Cetraria pinastri (Scop.) S. Gray

Cetraria platyphylla Tuck.

Cladina arbuscula (Wallr.) Hale & W.Culb.

Cladina mitis (Sandst.) Hale & W.Culb.

Cladonia bacillaris (Ach.) Nyl.

Cladonia cariosa (Ach.) Spreng.

Cladonia carneola (Fr.) Fr.

Cladonia cenotea (Ach.) Schaer.

Cladonia chlorophaea (Florke ex Somm.) Spreng.

Cladonia coccifera (L.) Willd.

Cladonia coniocraea (Florke) Spreng.

Cladonia cornuta (L.) Hoffm.

Cladonia deformis (L.) Hoffm.

Cladonia ecmocyna (Ach.) Nyl.

Cladonia fimbriata (L.) Fr.

Cladonia furcata (Huds.) Schrad.

Cladonia gonecha (Ach.) Asah.

Cladonia graciliformis Zahlbr.

Cladonia multiformis Merr.

Cladonia norrlinii Vain.

Cladonia phyllophora Hoffm.

Cladonia pleurota (Florke) Schaer.

Cladonia pseudomacilenta Asah.

Cladonia pyxidata (L.) Hoffm.

Cladonia squamosa (Scop.) Hoffm.

Cladonia subulata (L.) Wigg.

Cladonia verticellata (Hoffm.) Schaer.

Collema nigrescens (Huds.) DC.

Collema tenax (Sw.) Ach.

Coniocybe furfuracea (L.) Ach.

Cyphelium inquinans (Sm.) Trev.

- Dermatocarpon mniatum* (L.) Mann.
Dermatocarpon moulinii (Mont.) Zahlbr.
Dermatocarpon reticulatum Magn.
- Dimelaena oreina* (Ach.) Norm.
- Dimerella diluta* (Pers.) Trev.
- Diploschistes scruposus* (Schreb.) Norm.
- Evernia prunastri* (L.) Ach.
- Fistulariella minuscula* (Nyl.) Bowler and Rundel
- Hypogymnia austerodes* (Nyl.) Ras.
Hypogymnia imshaugii Krog
Hypogymnia metaphysodes (Asah.) Rass.
Hypogymnia occidentalis Pike in ed.
Hypogymnia physodes (L.) Nyl.
Hypogymnia rugosa (Merrill) Pike in ed.
Hypogymnia tubulosa (Schaer.) Hav.
- Icmadophila ericetorum* (L.) Zahlbr.
- Lecania syringea* (Ach.) Th. Fr.
- Lecanora cadubriae* (Mass.) Hedl.
Lecanora calcarea (L.) Somm.
Lecanora cinerea (L.) Somm.
Lecanora hageni (Ach.) Ach.
Lecanora muralis (Schreb.) Rabenh.
Lecanora pacifica Tuck.
Lecanora pergibbosa Magn.
Lecanora piniperda Korb.
Lecanora polytropa (Ehrh.) Rabenh.
Lecanora rolleana (Hue) Zahlbr.
Lecanora rupicola (L.) Zahlbr.
Lecanora subfusca sens. lat.
Lecanora varia (Ehrh.) Ach.
Lecanora verrucosa Ach.
- Lecidea atrobrunnea* (Ram.) Schaer.
Lecidea auriculata Th. Fr.
Lecidea berengeriana (Mass.) Nyl.
Lecidea cinnabarina Somm.
Lecidea dolodes Nyl.
Lecidea glomerulosa (DC.) Steud.
Lecidea granulosa (Ehrh.) Ach.
Lecidea hypocrita Massal.
Lecidea insularis Nyl.
Lecidea tessellata (Ach.) Florke
- Lepraria* spp.
- Leptogium lichenoides* (L.) Zahlbr.

- Leptogium saturninum* (Dicks.) Nyl.
Letharia columbiana (Nutt.) Thoms.
Letharia vulpina (L.) Hue

Lobaria hallii (Tuck.) Zahlbr.
Lobaria pulmonaria (L.) Hoffm.

Lopadium pezizoideum (Ach.) Korb.

Massalongia carnosa (Dicks.) Korb.

Microthelia aterrima (Anzi) Zahlbr.

Mycoblastus sanguinarius (L.) Norm.

Mycocalicium sp.

Nephroma bellum (Spreng.) Tuck.
Nephroma helveticum Ach.
Nephroma parile (Ach.) Ach.
Nephroma resupinatum (L.) Ach.

Ochrolechia pallescens (L.) Mass.

Pannaria microphylla (Sw.) Mass.

Parmelia disjuncta Erichs.
Parmelia elegantula (Zahlbr.) Szat.
Parmelia infumata Nyl.
Parmelia multispora Schneid.
Parmelia saxatilis (L.) Ach.
Parmelia solediosa Almb.
Parmelia subaurifera Nyl.
Parmelia subelegantula Essl.
Parmelia subolivacea Nyl.
Parmelia sulcata Tayl.

Parmeliopsis aleurites (Ach.) Nyl.
Parmeliopsis ambigua (Wulf.) Nyl.
Parmeliopsis hyperopta (Ach.) Arn.

Peltigera canina (L.) Willd.
Peltigera collina (Ach.) Ach.
Peltigera elisabethae Gyeln.
Peltigera leucophlebia (Nyl.) Gyeln.
Peltigera malacea (Ach.) Funck
Peltigera polydactyla (Neck.) Hoffm.
Peltigera rufescens (Weis.) Humb.
Peltigera spuria (Ach.) DC.
Peltigera venosa (L.) Baumg.

Pertusaria amara (Ach.) Nyl.
Pertusaria multipuncta (Turn.) Nyl.
Pertusaria trochisea Norm.

Phaeophyscia constipata (Norrl. ex Nyl.) Moberg
 Phaeophyscia decolor (Kashi.) Essl.
 Phaeophyscia imbricata (Vain.) Essl.
 Phaeophyscia sciastra (Ach.) Moberg

Physcia adscendens (Th. Fr.) Oliv.
 Physcia aipolia (Ehrh.) Hampe
 Physcia dubia (Hoffm) Lett.
 Physcia phaea (Tuck.) Thoms.
 Physcia semipinnata (Gmel.) Moberg
 Physcia stellaris (L.) Nyl.

Physconia muscigena (Ach.) Poelt
 Physconia perisidiosa (Erichs.) Moberg

Platismatia glauca (L.) W.Culb. & C.Culb.

Polychidium muscicola (Sw.) S.Gray

Psora novomexicana B. de Lesd.
 Psora rubiformis (Wahl.) Hook.
 Psora scalaris (Ach.) Hook.

Psoroma hypnorum (Vahl) S.Gray

Ramalina farinacea (L.) Ach.
 Ramalina pollinaria (Westr.) Ach.
 Ramalina thrausta (Ach.) Nyl.

Rhizocarpon badioatrum (Florke ex Spreng.) Th.Fr.
 Rhizocarpon disporum (Naeg. ex Hepp) Mull. Arg.
 Rhizocarpon geographicum (L.) DC.
 Rhizocarpon grande (Florke ex Flot.) Arn.
 Rhizocarpon riparium Ras.

Rhizoplaca chrysoleuca
 Rhizoplaca melanophthalma

Rinodina exigua (Ach.) S. Gray
 Rinodina pyrina (Ach.) Arn.
 Rinodina turfacea (Wahl.) ex Ach.

Stereocaulon albicans Th.Fr.
 Stereocaulon sp.

Thrombium epigaeum (Pers.) Wallr.

Toninia aromatica (Turn.) Mass.
 Toninia caeruleonigricans (Lightf.) Th. Fr.
 Toninia candida (Web.) Th. Fr.

Umbilicaria deusta (L.) Baumg.
 Umbilicaria hyperborea (Ach.) Ach.
 Umbilicaria phaea Tuck.
 Umbilicaria polyphylla (L.) Baumg.

Umbilicaria torrefacta (Lightf.) Schrad.
Umbilicaria vellea (L.) Ach.

Usnea spp.

Verrucaria spp.

Xanthoparmelia cumberlandia (Gyeln.) Hale
Xanthoparmelia plittii (Gyeln.) Hale
Xanthoparmelia sphaerosporella (Mull.Arg.) Hale

Xanthoria candelaria (L.) Th.Fr.
Xanthoria elegans (Link) Th.Fr.
Xanthoria polycarpa (Ehrh.) Oliv.
Xanthoria sorediata (Vain.) Poelt