

Ordination of epiphytic bryophyte communities in a wet-temperate coniferous forest, South-Coastal British Columbia*

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Abstract

Three coniferous tree species (*Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*) at Capilano Canyon, British Columbia, were studied for their epiphytic communities. Quantitative data were obtained for fourteen bryophyte species by sampling at heights of 0.5 m, 1 m and 2 m above ground level. *Scapania bolanderi* is an abundant and widely distributed species; *Dicranum fuscescens*, *Bazzania denudata*, *Lepidozia reptans* and *Hypnum circinale* are also common. An environmentally uniform study area was chosen to minimize the effects of factors other than bark and elevation on the distribution of epiphytes. In general, tree species are similar in terms of their epiphytic assemblages, but ordination methods using quantitative data exposed compositional variation that may be explained by differences in microclimate and bark-type. In this respect, the results point the way to further studies to examine epiphyte associations in closer detail, and to relate these associations to specific factors in the microenvironment.

Introduction

Ecologists have long recognized that bryophytes and lichens are sensitive indicators of small-scale environmental variation, and thus may assist in the delineation of vegetational units to a degree not possible with vascular plants (Barkman, 1958, 1973; Sjögren, 1961; Westhoff & van der Maarel, 1973). Studies have shown that nonvascular cryptogams are useful indicators of site conditions (Hoffman & Kazmierski, 1969; Szczawinski, 1953; Jonescu, 1970), and may play an important role in the cycling of nutrients through certain ecosystems (Pike, 1971; Pike *et al.*, 1977; Forman, 1975). In

some areas, epiphytic bryophytes are a significant component of a site's vegetation (Iwatsuki, 1960; Scott, 1970, 1971; Pike *et al.*, 1975).

A tree presents a variety of microhabitats that are open to colonization by corticolous species (Barkman, 1958). Environmental gradients relating to changing height, aspect and inclination can be recognized. Compositional changes in epiphytic communities with elevation along the tree bole have been reported for lichens (Hale, 1952; Kershaw, 1964; Harris, 1971; Yarranton, 1972), and for bryophytes (Slack, 1976; Rasmussen, 1975; Rasmussen & Hertig, 1977; Stringer & Stringer, 1974; Iwatsuki, 1960). Hosokawa & Odani (1957) and Hosokawa *et al.* (1964) reported that light intensity increases and relative humidity decreases with increasing elevation, noting that epiphytes adapted to more xeric conditions occur at higher levels. It has been suggested that the bole may be divided into height zones representing unique combinations of habitat factors and associated vegetational

* Nomenclature for vascular plants follows Hitchcock & Cronquist (1973); bryophyte nomenclature follows Schofield (1976) for mosses and Stotler & Crandall-Stotler (1977) for hepatics.

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components (Barkman, 1958; Iwatsuki, 1960); however, the delineation of such zones may be somewhat arbitrary (Pike *et al.*, 1975).

Epiphytic communities also vary circumferentially at a constant level on the bole. This variation is usually correlated with aspect and inclination. The effect of aspect tends to be greater in open stands where differential exposure to wind and light is more pronounced (Barkman, 1958); Yarranton (1972) and Gough (1975) reported compositional changes with aspect for epiphytic lichens. In closed forests, inclination may be more important. An upward facing bark surface will receive more moisture through precipitation and stemflow than the underside which may remain dry even after a rainstorm (Sjögren, 1961; Pike *et al.*, 1975). Rasmussen (1975) found differences in epiphyte species composition and diversity to be correlated with inclination.

Relationships between substrate (bark) and epiphytes have also been examined. Barkman (1958) lists relief, hardness, scaling, water-holding capacity, nutrient availability, acidity, and chemistry as factors of potential influence. Stringer & Stringer (1974) concluded that bark texture was important for lichen establishment, but that microclimate was more important for bryophytes. Jesberger & Sheard (1973) identified substrate, water availability, and stand age as important factors.

Ordination methods have been used to examine structure in epiphytic vegetation. Beals (1965), using polar ordination, determined that substrate represents a mainly continuous environmental variable. Jesberger & Sheard (1973) reached a similar conclusion in a study of eight tree species using principal components analysis. In another study, results from principal components analysis suggested that site factors including moisture stress, nutrient status, and light regime were more important than aspect in determining the performance of epiphytes (Sheard & Jonsescu, 1974).

In the present study, ordination methods were used to answer specific questions pertaining to the structure of the epiphytic vegetation of a wet-temperate coniferous forest in south-coastal British Columbia. The distinguishability of three tree species with respect to their epiphytic communities, and compositional changes with height above ground, were examined with principal components analysis and canonical variates analysis. The extent to which patterns of association among epiphytes

are similar on different tree species was examined with principal coordinates analysis.

Study area

The study area is located adjacent to the Capilano River gorge in North Vancouver at an elevation of about 150 m above sea level. Geologically, the area is characterised by alluvial deposits laid down during the last glaciation over a complex of plutonic and metamorphic rock (Armstrong, 1968). Meteorological data for Cloverly (ca. 2 km from the study area), suggest an average annual precipitation of about 2000 mm, most of which is rain, and an average annual temperature of 9.8 °C. The microclimate of the forest understorey is characterised by consistently high humidity maintained partly by the closed forest structure, and partly by the canyon topography. The area lies within Krajina's (1959) Coastal Western Hemlock biogeoclimatic zone, and the vegetation is similar to that of nearby Lynn Canyon, described by Krause & Schofield (1977). The dominant trees are *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*, *Thuja plicata* Donn., and *Tsuga heterophylla* (Raf.) Sarg., which form a relatively closed canopy extending from about 20 m (where branching begins) to about 50 m. Scattered understorey trees include *Taxus brevifolia* Nutt. and *Acer circinatum* Pursh. A discontinuous low shrub layer contains *Gaultheria shallon* Pursh, *Rubus spectabilis* Pursh, *Vaccinium parvifolium* Smith, as well as depauperate saplings of *Tsuga heterophylla*. The ferns, *Polystichum munitum* (Kaulf.) Presl, *Blechnum spicant* (L.) Roth, and *Athyrium filix-femina* (L.) Roth, are conspicuous. Dominant forest-floor bryophytes include *Rhytidiadelphus loreus* (Hedw.) Warnst., *Plagiothecium undulatum* (Hedw.) B.S.G., *Hylocomium splendens* (Hedw.) B.S.G., and a number of *Mniaceae*.

There is evidence of logging at higher elevations in the canyon, although the study area apparently was not extensively logged and for many years has been a park.

Methods

A preliminary survey of the epiphytic vegetation indicated that inclination of the tree bole from the

vertical is important in determining where epiphytes grow. Trees rarely grow exactly vertically and bryophytes are normally confined to the upper (wetter) side of the trunk. Lichens (mostly indeterminable species of *Cladonia*) are often present on the lower side. To minimize the effect of inclination, sampling was confined to the upper side of trees where bryophytes are most abundant.

A total of 72 trees comprising 25 each of *Thuja plicata* and *Pseudotsuga menziesii*, and 22 *Tsuga heterophylla* were selected for the study in a pseudorandom fashion, excluding trees devoid of bryophytes and those showing signs of disturbance near trails. Trees were sampled at three height levels (0.5 m, 1.0 m, and 2.0 m from the base) using a 15 cm × 15 cm quadrat to obtain percentage cover estimates for fourteen bryophyte species in 216 quadrats.

Three ordination methods including principal components analysis (PCA), principal coordinates (axes) analysis (P-Co-A, Gower, 1966; Orłóci, 1978) and canonical variates analysis (CVA, Seal, 1964) were used to analyse the data. As eigenvector techniques, these methods assume linear relationships between variables and ordination axes. This assumption may sometimes be ecologically unrealistic thereby limiting the successful exposure of vegetation gradients that are linked to underlying environmental gradients; however, for summarizing information and displaying overall relationships in a set of data, the methods are appropriate (Nichols, 1977).

Four PCA's were run, one on the data from each of the three sampling heights, and one on the combined data for trees formed by averaging species coverage values across three quadrats. This approach made possible the inspection of patterns of variation within and between tree species at separate and combined levels. Each analysis was based on an unstandardized covariance matrix for 14 species.

CVA was run after the data were arranged into groups composed of quadrats from similar heights on each tree species. Nine quadrat-groups were formed, corresponding to the nine height-species combinations. The ordination axes calculated by CVA coincide with the lines of 'best' linear discrimination among the quadrat-group centroids; thus, the results display an optimum configuration of the data from which various aspects of group interrelationships can be inferred.

The similarity relations among bryophyte species on separate tree species were examined with P-Co-A. Before the analyses were run, bryophytes occurring in less than five quadrats on any tree species were removed from the data. Similarities between bryophytes were defined by the cos theta (angular separation) function expressed as:

$$\text{COS}(\theta_{i,h}) = \frac{\sum_j X_{ij}X_{hj}}{(\sum_j X_{ij}^2 \sum_j X_{hj}^2)^{1/2}} \quad j = 1, \dots, n$$

where X_{ij} and X_{hj} denote the cover recorded for species i and h in quadrat j , and n is the total number of quadrats. Geometrically, the expression relates to the angle subtending species positional vectors in n -dimensional (quadrat) space; thus, the lengths of the vectors, which are determined by the abundances of species, do not influence the similarity measure.

Computer programs for PCA and P-Co-A were developed by one of us (Bradfield); CVA was run using a program from the MIDAS statistical package (Fox & Guire, 1976). All analyses were performed on an AMDAHL 470 V/6-II computer at the University of British Columbia Computing Centre.

Results

The mean percent cover data for the fourteen epiphytic bryophytes observed during sampling are given in Table 1. Of the five most common species, *Scapania bolanderi* is clearly the leading dominant at all heights examined. *Bazzania denudata*, *Scapania bolanderi*, and *Lepidozia reptans* show a tendency to decline in cover with increasing height; *Hypnum circinale* shows the opposite trend. The cover of *Dicranum fuscescens* is highest on *Tsuga heterophylla* and lowest on *Thuja plicata*.

The remaining nine species occur with generally low frequency and cover making interpretation of their distributional patterns more difficult. Species such as *Rhizomnium glabrescens*, *Plagiothecium undulatum*, *Hylocomium splendens*, and *Rhytidadelphus loreus* are fairly common on the forest floor, but occasionally grow epiphytically on tree bases; *Isothecium stoloniferum* is a more common epiphyte at higher levels.

Table 1. Mean percent cover data for epiphytic bryophytes at 0.5 m, 1 m and 2 m on *Thuja plicata*, *Pseudotsuga menziesii* and *Tsuga heterophylla*.

	<i>Thuja plicata</i> (n = 25)			<i>Pseudotsuga menziesii</i> (n = 25)			<i>Tsuga heterophylla</i> (n = 22)		
	.5 m	1 m	2 m	.5 m	1 m	2 m	.5 m	1 m	2 m
<i>Scapania bolanderi</i> Aust.	44.2	28.2	15.6	40.8	33.4	21.2	40.2	40.0	32.7
<i>Dicranum fuscescens</i> Turn.	0.6	0.8	0.2	4.8	11.8	7.0	21.4	28.2	25.0
<i>Bazzania denudata</i> (Torrey ex Gott. et al.) Trev.	7.4	3.0	2.0	6.8	1.6	3.2	19.1	5.7	3.2
<i>Lepidozia reptans</i> (L.) Dum.	5.0	3.6	0.6	12.6	4.0	3.4	3.6	2.3	0.7
<i>Hypnum circinale</i> Hook.	6.4	8.2	11.4	3.2	7.6	13.0	1.4	6.1	13.6
<i>Plagiochila porelloides</i> (Torrey ex Nees) Linderb.	-	0.2	-	2.2	0.2	-	2.3	0.5	-
<i>Ptilidium californicum</i> (Aust.) Underw.	0.4	-	0.4	-	2.4	0.4	0.5	0.5	0.7
<i>Rhizomnium glabrescens</i> (Kindb.) Kop.	1.2	-	-	1.4	-	-	1.4	-	-
<i>Plagiothecium undulatum</i> (Hedw.) B.S.G.	1.6	-	-	5.6	-	-	4.1	-	-
<i>Isothecium stoloniferum</i> Brid.	-	-	-	-	0.4	1.4	-	0.2	1.3
<i>Hylocomium splendens</i> (Hedw.) B.S.G.	-	-	-	0.8	-	-	-	-	-
<i>Cephalozia lunulifolia</i> (Dum.) Dum.	-	-	-	0.6	0.4	0.2	-	-	-
<i>Lophocolea heterophylla</i> (Schrad.) Dumort	-	-	-	0.4	1.6	0.4	-	-	-
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.	-	-	-	-	-	-	0.9	0.5	-

Table 2. Eigenvectors from principal components analysis of the separate and combined levels data. Dashes indicate species absence.

	.5 m		1 m		2 m		Combined	
	I	II	I	II	I	II	I	II
	54.7% ¹	15.7%	40.6%	33.6%	47.6%	25.3%	46.5%	27.0%
SCA BOL ²	.957	.090	.780	.624	.902	-.388	.934	-.258
DIC FUS	-.056	.802	-.618	.773	.235	.802	.264	.955
BAZ DEN	-.259	.340	.035	.006	.042	.021	.104	.007
LEP REP	-.099	-.474	.056	-.078	.009	.025	.050	-.138
HYP CIR	-.029	-.075	.064	-.071	-.359	-.446	-.211	.025
PLA POR	-.016	.038	.001	.001	-	-	.019	.006
PTI CAL	.000	.002	.040	-.017	.006	-.012	-.008	-.005
RHI GLA	-.030	.014	-.003	-.007	-	-	.011	-.007
PLA UND	-.041	.013	-	-	-	-	.013	.002
ISO STO	-	-	-.009	.007	.009	.082	-.004	.050
HYL SPL	-.006	.009	-	-	-	-	-.004	-.000
CEP LUN	-.008	-.007	-.004	-.002	-.002	.005	-.002	-.004
LOP HET	.003	.002	-.015	-.141	-.005	.003	-.006	-.006
RHY LOR	-.011	.025	-.016	.009	-	-	.004	.012

¹ percent variation explained

² abbreviated epiphyte species name

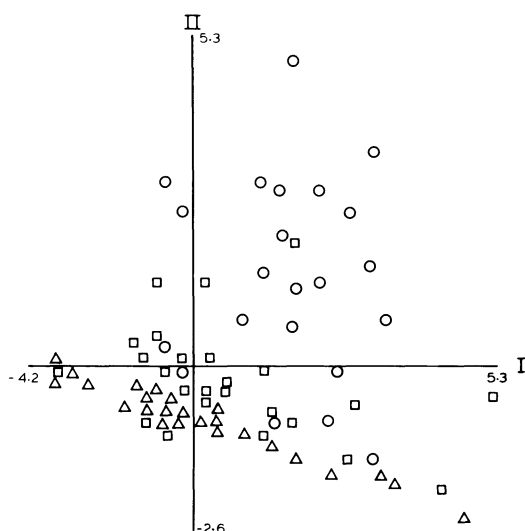


Fig. 1. Ordination of trees on the first two axes derived by principal components analysis of the combined levels data. Symbols code: Δ (*Thuja plicata*), \square (*Pseudotsuga menziesii*), \circ (*Tsuga heterophylla*).

Principal components analysis

Table 2 contains the eigenvectors pertaining to the first two axes for each PCA performed. Since the results from separate analyses were considered to be reasonably similar, only those from the PCA using averaged data are discussed. In fact, this ordination seemed to clarify trends noted when the sampling heights were analysed separately. The scatter diagram for this analysis is shown in Figure 1.

The first axis explains about 47% of the variance and is strongly influenced by the degree of *Scapania bolanderi* cover (increasing from left to right). Considerable overlap among tree species is evident.

The second axis explains an additional 27% of the variance and primarily displays a cover gradient of *Dicranum fuscescens* (increasing from bottom to top). Tree species tend to be positioned along the gradient in the order, *Thuja plicata* – *Pseudotsuga menziesii* – *Tsuga heterophylla*. A group of *Tsuga heterophylla* trees growing along the ravine edge which are exposed to increased light levels and river spray are positioned toward the top of the second axis.

In general, the PCA results demonstrate that variation in the epiphytic vegetation is continuous and mainly related to cover changes in *Scapania*

bolanderi and *Dicranum fuscescens*. The results suggest that microclimate exerts a stronger influence than bark-type in controlling the distribution of epiphytes.

Canonical variates analysis

CVA gave results that were, in general, consistent with those of PCA; however, grouping the data into height-species categories proved to be instructive. The ordination of quadrat group-centroids on the first two canonical axes is shown in Figure 2. Four aspects of the results are noteworthy. First, the axes account for 79% of the variation among group means, and thus may be considered successful in summarizing major relationships in the data. Second, the distinctiveness of *Tsuga heterophylla* is somewhat over-emphasized since the means are being influenced by a few trees growing along the ravine edge where the microenvironment is different. Third, the lowest level sample of *Pseudotsuga menziesii* appears distinctive because of the combined influence of a few rare (primarily forest floor) species in this group (Table 1). Fourth, this ordination, more so than the PCA's, demonstrates variation related to changing height and substrate conditions.

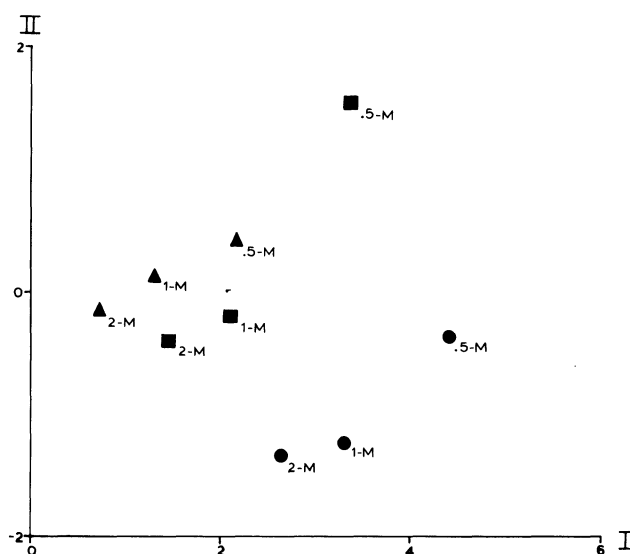


Fig. 2. Ordination of quadrat group centroids on the first two axes derived by canonical variates analysis. Symbols code: \blacktriangle (*Thuja plicata*), \blacksquare (*Pseudotsuga menziesii*), \bullet (*Tsuga heterophylla*).

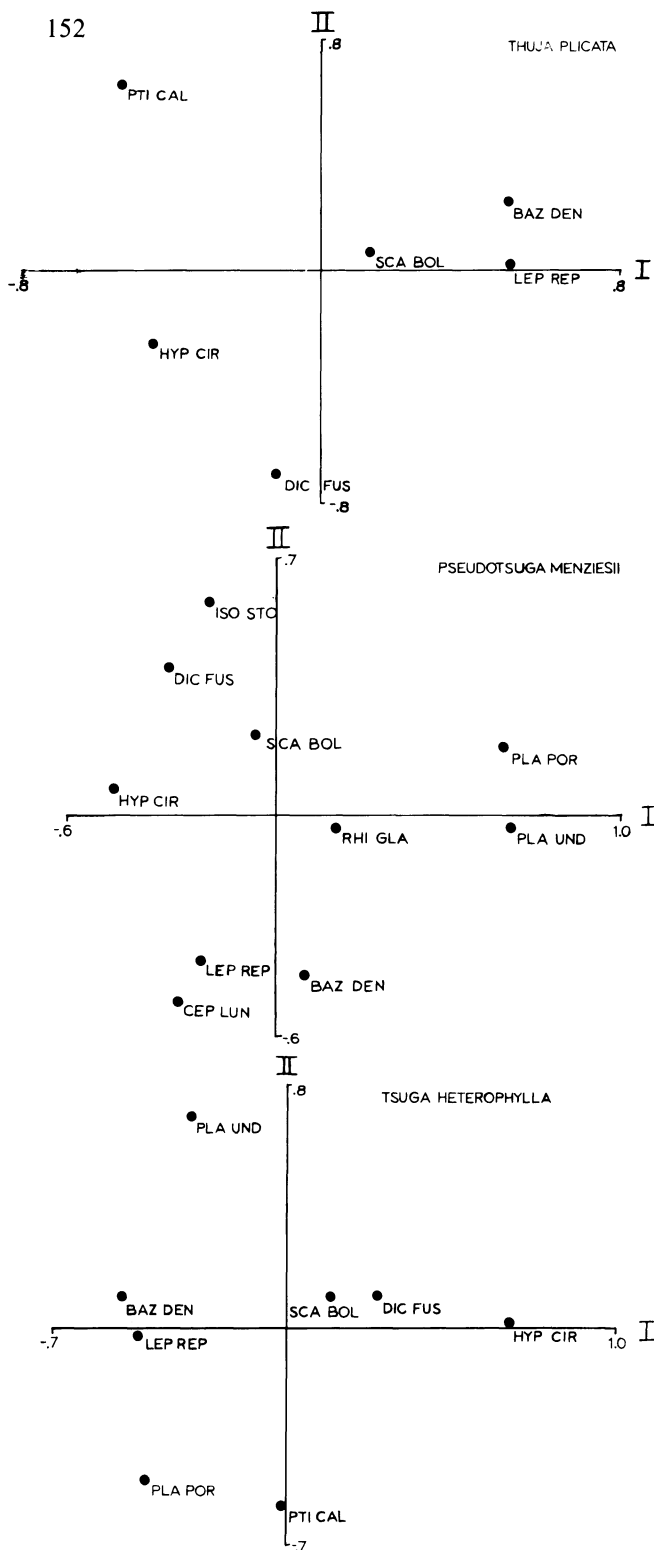


Fig. 3. Ordinations of epiphyte species on the first two axes derived by principal coordinates analysis. Variance explained by axes: *Thuja plicata*, axis I, 26.6%, axis II, 24.7%; *Pseudotsuga menziesii*, axis I, 17.9%, axis II, 16.8%; *Tsuga heterophylla*, axis I, 21.3%, axis II, 19.2%.

Principal coordinates analysis

Scatter diagrams of epiphytes obtained by analysing the data from each tree species separately with P-Co-A are presented in Figure 3. Measures of ordination efficiency, expressed as the proportion of variance explained by the first two axes, range from 37% with *Pseudotsuga menziesii* to 51% with *Thuja plicata*. In comparison with the quadrat ordinations obtained with PCA and CVA, the P-Co-A results display associations among epiphytes based on their distributional patterns; thus, the closeness of species in the ordinations reflects the degree to which they were recorded growing together in quadrats. Further insight into the strengths of the associations may be gained by comparing the three sets of results giving particular attention to the five most common bryophyte species. *Scapania bolanderi*, the leading community dominant, occurs near the center of each ordination; other species are arranged peripherally in accord with their associations with *S. bolanderi* and with each other. *Bazzania denudata* and *Lepidozia reptans* both decline in cover with increasing height, exhibiting a relatively strong association on all tree species; *Hypnum circinale* shows the opposite trend, increasing its cover at higher levels, and is thus well separated from the preceding group. *Dicranum fuscescens* varies positionally in the ordinations, and no distinct height preferences are indicated in the data (Table 1). It occurs commonly on both *Pseudotsuga menziesii* and *Tsuga heterophylla*, where it tends to be associated with the higher levels group of species; on *Thuja plicata*, it is markedly separated from *Ptilidium californicum* (both relatively rare species) owing to their mutual exclusiveness in quadrats.

In general, the species ordinations suggest that patterns of association among epiphytes are similar on different tree species. Microclimatic variation seems to be the overriding influence in determining where epiphytes grow.

Discussion

Variation in microclimate and bark characteristics results in continuous compositional changes in the epiphytic communities of *Thuja plicata*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* at Capilano Canyon. These findings are in general agreement with those of comparable studies of epiphytes done elsewhere (Beals, 1965; Jesberger & Sheard, 1973; Szczawinsky, 1953). Concerning

bark factors, the physical nature of the substrate appears to exert a stronger influence on epiphytes than does its chemistry (average bark pH's of 4.4, 4.2 and 4.4 were determined for ten trees each of *T. plicata*, *P. menziesii*, and *T. heterophylla*); however, bark chemistry probably accounts for the more marked differences observed between the three conifers of this study and other tree species in the area such as *Taxus brevifolia* and *Acer macrophyllum*. The bark of *Pseudotsuga menziesii* is up to 30 cm thick on mature trees, is deeply fissured and exfoliates in plates when kept wet. The accumulation of decomposing organic matter in fissures near the tree base favours establishment by bryophytes, especially species such as *Rhizomnium glabrescens*, *Plagiothecium undulatum*, *Hylocomium splendens*, and *Rhytidiadelphus loreus* which commonly occur on fallen logs. In this respect, the tree base represents an extension of the forest floor environment. *Tsuga heterophylla* bark is deeply furrowed with flat, scaly ridges; exfoliation appears to occur only on trees exposed to continuous river spray. The bark of *Thuja plicata* is thin and fibrous, and may be peeled off in long, vertical strips; the bark surface is relatively smooth, with little fissuring. Observations suggest that the bark of all three species remains moist for considerable periods after wetting.

The sensitivity of epiphytes to variation in physical factors of the bark appears to be mainly growth form dependent. *Dicranum fuscescens*, an erect, tuft-forming acrocarpous moss, may have difficulty establishing on the relatively smooth bark of *Thuja plicata*. A similar explanation may account for the decline in cover of the sub-erect, tuft-forming hepatic, *Scapania bolanderi*, at heights above 1 m on *Thuja plicata*. Also, forest floor species which often colonize the bases of *Pseudotsuga menziesii* and *Tsuga heterophylla*, rarely occur on *Thuja plicata*. In contrast, the mat forming hepatics, *Bazzania denudata* and *Lepidozia reptans*, and the appressed, pleurocarpous moss, *Hypnum circinale*, seem to be less sensitive to differences in bark-type.

It seems likely that epiphytes are also responding to a light-moisture complex gradient operating along the bole. Microclimate may change significantly over a vertical distance of a few meters. Consistently high humidity near the ground, maintained partly by the shelter afforded by neighbouring understorey plants, creates a suitable

microenvironment for the growth of many bryophytes. Also, the splayed tree base receives a greater proportion of the total precipitation than higher parts of the bole which undoubtedly experience wider ranges in light and moisture conditions. Of the 14 epiphyte species recorded, the majority show a decline in cover with increasing height; however, *Hypnum circinale* and *Isothecium stoloniferum* show the opposite trend well beyond the upper limit of sampling at 2 m. Both of these species grow closely appressed to the bark surface. Presumably, this growth form is an adaptation to the more xeric conditions and nearly vertical bark surface at higher levels. Species which grow in loose-erect to sub-erect tufts, including *Scapania bolanderi*, *Dicranum fuscescens*, and *Rhizomnium glabrescens*, are more abundant near the base of the tree, as are the prostrate, mat-forming hepatics, *Lepidozia reptans*, *Bazzania denudata*, and *Ptilidium californicum*.

The results also show variation related to microclimatic changes on a larger scale within the study area. A group of *Tsuga heterophylla* trees growing along the ravine edge above the river have been identified as supporting a distinctive epiphytic assemblage. This appears to be caused by a different set of microenvironmental conditions (river spray, increased light) which, in particular, favours the growth of species such as *Dicranum fuscescens* and *Scapania bolanderi*.

The ordination methods used have provided an efficient summarization of a complex body of data with minimal information loss. Major properties of the structure and inherent variability of the epiphytic vegetation have been exposed. Several directions for more detailed study of the relationships between epiphytes, epiphytic communities, and microenvironmental factors are indicated.

References

- Armstrong, J. E., 1968. In: W. H. Mathews (ed.) Guidebook for geological field trips in southwestern British Columbia. Dept. of Geology, U. B. C., Report No. 6.
- Barkman, J. J., 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum, Assen, Netherlands.
- Barkman, J. J., 1973. Synusial approaches to classification, In: R. H. Whittaker (ed.) Handbook of Vegetation Science. Vol. 5. Dr. W. Junk, The Hague, p. 435-491.

- Beals, E. W., 1965. Ordination of some corticolous cryptogamic communities in south-central Wisconsin. *Oikos* 16: 1-8.
- Forman, R. T. T., 1975. Canopy lichens with blue-green algae: a nitrogen source in a Columbian rain forest. *Ecology* 56: 1176-1184.
- Fox, D. J. & Guire, K. E., 1976. Documentation for MIDAS. 3rd edition. Statistical Research Laboratory, Univ. of Michigan.
- Gough, L. P., 1975. Cryptogam distributions on *Pseudotsuga menziesii* and *Abies lasiocarpa* in the Front Range, Boulder County, Colorado. *Bryologist* 78: 124-145.
- Gower, J. C., 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325-338.
- Hale, M. E., 1952. Vertical distribution of cryptogams in a virgin forest of Wisconsin. *Ecology* 33: 398-406.
- Harris, G. P., 1971. The ecology of corticolous lichens. I. The zonation on oak and birch in South Devon. *J. Ecol.* 59: 431-439.
- Hitchcock, C. L. & Cronquist, A., 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle.
- Hoffman, G. R. & Kazmierski, R. G., 1969. An ecological study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. I. A description of the vegetation. *Bryologist* 72: 1-19.
- Hosokawa, T. & Odani, N., 1957. The daily compensation period and vertical ranges of epiphytes in a beech forest. *J. Ecol.* 45: 901-915.
- Hosokawa, T., Odani, N. & Tagawa, H., 1964. Causality of the distribution of corticolous species in forests with special reference to the physioecological approach. *Bryologist* 67: 396-411.
- Iwatsuki, Z., 1960. The epiphytic bryophyte communities in Japan. *J. Hattori Bot. Lab.* 22: 159-352.
- Jesberger, J. A. & Sheard, J. W., 1973. A quantitative study and multivariate analysis of corticolous lichen communities in the southern boreal forest of Saskatchewan. *Can. J. Bot.* 51: 185-201.
- Jonescu, M. E., 1970. Lichens on *Populus tremuloides* in west-central Canada. *Bryologist* 73: 557-578.
- Kershaw, K. A., 1964. Preliminary observations on the distribution and ecology of epiphytic lichens in Wales. *Lichenologist* 2: 263-276.
- Krajina, V. J., 1959. Bioclimatic zones in British Columbia. U.B.C., Botanical series 1: 1-47.
- Krause, G. & Schofield, W. B., 1977. The moss flora of Lynn Canyon Park, North Vancouver, British Columbia. *Syesis* 10: 97-110.
- Nichols, S., 1977. On the interpretation of principal components analysis in ecological contexts. *Vegetatio* 34: 191-197.
- Orlóci, L., 1978. *Multivariate analysis in vegetation research*. 2nd ed. Dr. W. Junk, The Hague.
- Pike, L. H., 1971. The role of epiphytic lichens and mosses in production and nutrient cycling in an oak forest. Ph.D. thesis, Dept. of Biology, Univ. of Oregon.
- Pike, L. H., Denison, W. C., Tracy, D. M., Sherwood, M. A. & Rhoades, F. M., 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *Bryologist* 78: 391-404.
- Pike, L. H., Rydell, R. A. & Denison, W. C., 1977. A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions. *Can. J. For. Res.* 7: 680-699.
- Rasmussen, L., 1975. The bryophytic epiphyte vegetation in the forest Slotved Skov, Northern Jutland. *Lindbergia* 3: 15-38.
- Rasmussen, L. & Hertig, J., 1977. Statistical investigation of interspecific phytosociological relations in epiphytic bryophyte communities. *Rev. Bryol. Lichenol.* 43: 207-217.
- Schofield, W. B., 1976. *Bryophytes of British Columbia. III. Habitat and distributional information for selected mosses*. *Syesis* 9: 317-354.
- Scott, G. A. M., 1970. Vegetation studies on Secretary Island, Fiordland. Part II. Epiphytic and ground cryptogamic vegetation on the northern slopes. *New Zealand J. Bot.* 8: 30-50.
- Scott, G. A. M., 1971. Some problems in the quantitative ecology of bryophytes. *New Zealand J. Bot.* 9: 744-749.
- Seal, H. L., 1964. *Multivariate statistical analysis for biologists*. Methuen, London.
- Sheard, J. W. & Jonescu, M. E., 1974. A multivariate analysis of the distribution of lichens on *Populus tremuloides* in west-central Canada. *Bryologist* 77: 514-550.
- Sjögren, E., 1961. Epiphytische Moosvegetation in Laubwäldern der Insel Öland. *Acta Phytogeographica Suecica* 44 (english summary).
- Slack, N. G., 1976. Host specificity of bryophytic epiphytes in eastern North America. *J. Hattori Bot. Lab.* 41: 107-132.
- Stotler, R. & Crandall-Stotler, B., 1977. A checklist of the liverworts and hornworts of North America. *Bryologist* 80: 405-428.
- Stringer, P. W. & Stringer, M. H. L., 1974. A quantitative study of corticolous bryophytes in the vicinity of Winnipeg, Manitoba. *Bryologist* 77: 551-560.
- Szczawinski, A., 1953. Corticolous and lignicolous plant communities in the forest associations of the Douglas-fir forest on Vancouver Island. Ph.D. thesis, Department of Botany and Biology, U.B.C.
- Westhoff, V. & van der Maarel, E., 1973. The Braun-Blanquet approach. In R. H. Whittaker (ed.), *Handbook of Vegetation Science*. Vol. 5. Dr. W. Junk, The Hague, p. 617-726.
- Yarranton, G. A., 1972. Distribution and succession of epiphytic lichens on black spruce near Cochrane, Ontario. *Bryologist* 75: 462-480.