

## Epiphytic vegetation on *Acer macrophyllum*: a multivariate study of species-habitat relationships\*

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**Keywords:** *Acer macrophyllum*; Bark chemistry; Bryophyte; Canonical analysis; Epiphyte; Gradient; Height; Inclination; Lichen; Microenvironment; Procrustes analysis.

### Abstract

Multivariate methods were used to examine epiphytic species composition on the lower trunk of *Acer macrophyllum* at five sites in south-coastal British Columbia, Canada. Differences in species composition and abundance between sites were attributed mainly to variation in relative humidity and light conditions. Bark chemistry differences accounted for only a small portion of the observed variation in epiphytic composition between sites. Within sites, compositional variation was examined over 0.5–5 m from ground level on the upper, vertical, and lower trunk surfaces of leaning trees. Compositional variation of the epiphytic vegetation with height and inclination tended to be more strongly developed at drier sites. Furthermore, at all sites compositional variation tended to be greater on upper (wetter) than on lower (drier) surfaces. Particular epiphytic species tended to occur in similar locations on the trunk surface at different sites, suggesting that some microhabitat specialization has occurred. Observed distributional shifts of epiphytic species appeared to be greatest among sites differing widely in prevailing microenvironmental conditions.

### Introduction

Epiphytes are an important component of many forest ecosystems, particularly those of high rainfall tropical (Pócs, 1983) and temperate (Iwatsuki, 1960; Nadkarni, 1984) regions. They are thought to play an important role in nutrient cycling (Pike, 1978; Nadkarni, 1984), and are often regarded as useful indicators of microenvironmental conditions (Hoffman & Kazmierski, 1969; Jonescu, 1970).

\* Nomenclature follows Hitchcock & Cronquist (1973) Flora of the Pacific Northwest for vascular plants, Schofield (1976) Bryophytes of British Columbia for mosses, Stotler & Crandall-Stotler (1977) A checklist of the liverworts and hornworts of North America for hepatics, and Hale & Culberson (1970) A fourth Checklist of the lichens of the continental United States and Canada for lichens.

\*\* Support from the Natural Sciences and Engineering Research Council, through an operating grant to G.E.B. and a scholarship to N.C.K., is gratefully acknowledged. We thank Dr. H. Kimmins for providing facilities and technical expertise for the analysis of bark nutrients.

The trunk of a tree represents a complex of continuously grading microhabitats which influence the pattern of colonization by epiphytic species. The microenvironmental gradients involved are complex, reflecting simultaneous variation in moisture status, light intensity, and nature of the organic substratum (degree of bark decomposition, substratum nutrient status, pH, etc.). Changes in epiphytic composition with height along a tree trunk have been documented for both lichens (Harris, 1971; Yarranton, 1972) and bryophytes (Rasmussen, 1975; Kenkel & Bradfield, 1981). In open forests circumferential variation at a given height tends to be correlated with aspect (Yarranton, 1972; Gough, 1975). However, in closed forests the angle of inclination of the trunk surface appears to exert a stronger influence than aspect (Sjögren, 1961; Rasmussen, 1975).

Different host species (phorophytes) often support different epiphytic assemblages. Studies have shown that while there may be distinctive differ-

ences among phorophytes in such factors as bark texture, pH, and nutrient status, corresponding variation in epiphytic composition is largely continuous (Rasmussen, 1975; Bates & Brown, 1981; Kenkel & Bradfield, 1981). For a given phorophyte species, variation in epiphytic composition related to environmental differences between sites might be expected. However, other than the pioneering work of Barkman (1958) and Hoffman & Kazmierski (1969), there have been few detailed studies of epiphytic species – site relationships.

This study investigates the compositional variation of epiphytic vegetation on the lower trunk of *Acer macrophyllum* Pursh. (bigleaf maple) at five sites in south-coastal British Columbia. This phorophyte is distinguished by the presence of an extensive epiphytic cover dominated by thick bryophyte mats (Nadkarni, 1984). It is endemic to the west coast of North America, occurring from California to British Columbia. In the northern portion of its distribution it grows on alluvial deposits and river terraces west of the Coast Mountains below an elevation of 1000 m.

The principal objectives of this study are: (1) to determine the extent of variation in epiphytic composition on the lower trunk of *Acer macrophyllum*, (2) to relate between-site variation in epiphytic composition to differences in microenvironment and substratum nutrient status, and (3) to examine intrasite variation of the epiphytic vegetation in relation to height and inclination gradients.

### Study area

The south coast of British Columbia is characterized by a mild maritime climate, with mean daily temperatures in January (the coldest month) remaining above freezing and in July (the warmest month) not exceeding 19°C. The Coast Mountains create an area of relatively high rainfall (averaging over 2000 mm/yr) along the coast, though total precipitation shows considerable local variation as reflected by the proximity of high mountains. Almost all the precipitation at lower elevations occurs as rain, approximately three-quarters of which falls between October and March (Environment Canada, 1970).

Site selection was based on a number of criteria, the foremost being to represent a broad range of

natural habitats of *Acer macrophyllum* in south-coastal British Columbia. Open, recently disturbed forests and solitary trees were avoided, and stands of approximately the same age were selected to minimize differences in epiphytic vegetation attributable to temporal influences. Stand age was estimated using tree DBH since the heartwood of *Acer macrophyllum* rots, making it impossible to age using standard techniques. A description of the five study sites selected is given in Table 1.

### Methods

#### *Field sampling*

Fifteen *Acer macrophyllum* trees (each > 40 cm DBH) within each of the five sites were selected at random, although excessively leaning trees and those with large lower branches were avoided in order to minimize variation in trunkflow patterns. A systematic sampling design was used to enumerate the epiphytic vegetation on the lower trunk of each tree. The sampling unit was a 10 × 20 cm quadrat gridded into fifty 2 × 2 cm squares, which yielded local frequencies (Greig-Smith, 1982) of species at given locations on the trunk. Twenty-four quadrats were placed on each tree, four at each of six heights above ground level (0.5, 1, 2, 3, 4, and 5 m). At each height, quadrats were placed at 90° intervals around the trunk, starting from the most upward facing surface (Fig. 1). Also recorded at each quadrat were the angle of inclination of the trunk surface (measured with a clinometer), the thickness of the bryophyte and organic layers, and a qualitative estimate of the degree of bark decomposition.

#### *Bark chemistry*

A bark sample for chemical analysis was obtained at a height of 1.5 m on the upper trunk surface of each study tree. Bark pH was measured using a 'Radiometer' pH meter after soaking crushed bark in distilled water for 24 hours. Total nitrogen and phosphorus were determined by the semi-micro Kjeldahl method using a 'Technicon' industrial analyzer. Calcium, magnesium, and potassium were measured using a 'Varion-Tectron' atomic absorption spectrophotometer. All nutrient values were expressed as a percent of total oven-dry weight.

### Data handling and analysis

To examine inter-site differences in epiphytic composition, mean local frequencies were calculated for the ten most abundant epiphyte species on each of the 75 study trees. The trees were then discriminated by site using canonical variates analysis (CVA; Gittins, 1985). Among-site variation in bark chemistry was examined using the multivariate version of a Model I analysis of variance (MANOVA; Morrison, 1976). Finally, canonical correlation analysis (Gittins, 1985) was performed between the scores of the 75 trees on the first two CVA axes and the five nutrients plus pH, to determine the extent to which bark chemistry could account for intersite variation in epiphytic composition.

Changing patterns of epiphytic composition and abundance on the lower trunk were examined separately at each site. For this purpose 18 height/inclination categories (three inclinations – upper, middle, and lower – at each of the six heights) were defined and subsequently discriminated using CVA. Note that the upper and lower height combinations contained 15 quadrats each (one from each tree), while the middle height combinations each contained 30 quadrats; see Fig. 1.

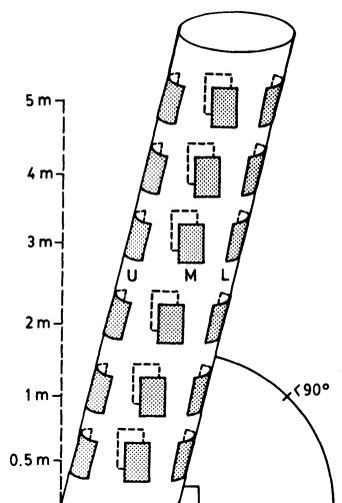


Fig. 1. Diagrammatic representation of the sampling design used in collecting epiphytic vegetation data from the lower bole of *Acer macrophyllum*. At each of six heights above ground level (0.5, 1, 2, 3, 4 and 5 m), quadrats were placed on the 'upper' (U) and 'lower' (L) surfaces of the bole, as well as mid-way (M) between U and L. Inclination angles of upper surfaces exceed 90°, while those of the lower surface are less than 90°.

The two-dimensional ordination configurations (representing the 18 group means) were used to suggest the nature of the response of epiphytic vegetation to environmental gradients operating vertically and circumferentially along the trunk. In an idealized situation, with species responding linearly to independent gradients, the point configuration would approximate a  $3 \times 6$  rectangular grid. Deviation of the observed point configuration from this idealized grid may be attributable to two factors: first, epiphytes may not respond linearly to changes in gradient levels; second, they may be interaction (non-independence) between the two gradients. Interaction could occur, for example, if inclination differences varied with height along the trunk. Deviation between observed and idealized point configurations was determined using Procrustes analysis (Schönemann & Carroll, 1970, with point scores first standardized to unit variance along each discriminant axis to render the five site configurations comparable).

It was also of interest to examine the spatial distribution of individual epiphytic species for evidence of microhabitat specificity. For this purpose three-dimensional response surfaces were produced by plotting mean local frequencies within sites against height and inclination gradients.

## Results

### Site characterization

The physiognomic-environmental characterization of the five study sites (Table 1) is used to subjectively rank them in terms of overall moisture and light availability. The UEL site appears driest, as reflected by the low total precipitation, absence of nearby mountains, and location along the Point Grey cliffs. The BRI site is judged to be wettest owing to high tree density, topographic position, and the continuous mist from a nearby waterfall (see also Vitt *et al.*, 1973). Despite the relative openness of the stand, SQU is also relatively wet because of the surrounding mountains and its foodplain location. The other two sites are intermediate, with FUR wetter than PIT because of greater stand density and the presence of conifers in the canopy. Thus the following ranking of sites in terms of overall relative humidity is inferred:

Table 1. Physiognomic-environmental description of the five study sites. The three-letter abbreviations following site names are used in the text. Climate data are yearly means, 1941–1970 (Environment Canada 1970), except for BRI (from Vitt *et al.*, 1973).<sup>1</sup>

	Squamish River (SQU)	Furry Creek (FUR)	University Endowment Lands (UEL)	Pitt River (PIT)	Bridal Veil Falls (BRI)
Location	49°50'N, 123°13'W	49°35'N, 123°13'W	49°14'N, 123°14'W	49°20'N, 122°39'W	49°11'N, 121°45'W
Elevation (m)	34	5	30	30	76
Site Description	Floodplain of Squamish River; annually flooded. Deep valley surrounded by steep mountains.	Small coastal alluvial fan. Coastal marine (Squamish Inlet). Steep mountains to the east.	Point Grey escarpment. Coastal marine (Georgia Strait), above shoreline cliffs. No mountains nearby.	Gentle slope adjacent to extensive marsh. Sloping to mountains in west.	Base of steep north-facing slope. Enclosed by mountains; high cloud cover. Waterfall nearby creates misty conditions.
Climate					
Precipitation (annual, mm)	2061	2063	1230	2261	2790
Measurable Precip. (days)	167	173	168	163	180
Soil	Recently deposited alluvium. Loamy sand with clay bands.	Recently deposited alluvial sand/wash. Gravelly sand/silt.	Sandy, gravelly gleysol. Well drained (near cliff edge).	Very gravelly, rocky sand/silt.	Gravelly loamy sand.
Physiognomy	Open stands dominated by bigleaf maple. Dense shrub cover (2.5–3 m high); <i>Rubus spectabilis</i> , <i>R. parviflorus</i> , <i>Acer cineratum</i> .	Dense canopy dominated by bigleaf maple and some large conifers. Understory dominated by western hemlock saplings 5–6 m; <i>Rubus spectabilis</i> .	Relatively open, mixed deciduous/coniferous. Occasional conifer saplings. Generally a sparse understorey. <i>Symphoricarpos albus</i> , <i>Rubus spectabilis</i> , <i>R. parviflorus</i> .	Relatively open canopy dominated by bigleaf maple. Dense understorey. 2.5–3 m; <i>Rubus spectabilis</i> , <i>Sambucus racemosa</i> , conifer saplings.	Dense canopy, mixed deciduous/coniferous. Conifer saplings, to 5 m, common; <i>Oplopanax horridus</i> . Understorey sparse.
Tree Dominance (m <sup>2</sup> /ha)					
<i>Acer macrophyllum</i>	30.4	46.5	44.5	37.6	42.8
<i>Alnus rubra</i>	6.8	6.2	–	6.4	1.9
<i>Tsuga heterophylla</i>	1.5	15.7	3.7	1.0	15.7
<i>Thuja plicata</i>	–	26.2	14.6	5.8	26.8
<i>Pseudotsuga menziesii</i>	–	–	9.6	–	5.6
Total	38.7	94.6	72.3	50.8	92.8

<sup>1</sup> Stations: SQU – Squamish, 14.5 km south; FUR – Britannia Beach, 4.8 km south; UEL – Vancouver UBC, 2.4 km north-west; PIT – Pitt Polder, 4.0 km south-east; BRI – Mount Baker, 40 km south.

UEL < PIT < FUR < SQU < BRI. The degree of shading (canopy closure) can also be expected to influence epiphytic vegetation. Good indicators of light availability include tree density and the proportion of conifers in the canopy. Tree dominance values (Table 1) suggest the following ranking of sites in terms of overall light availability: BRI < FUR < UEL < PIT < SQU.

### Site differentiation

Epiphytic species occurring on at least three trees, and their mean local frequencies at each of the five sites, are presented in Table 2. Note that many of the dominant species (e.g. *Metaneckera menziesii*, *Homalothecium fulgescens*, *Neckera douglasii*, and *Claopodium crispifolium*) occur at all sites, though with differing abundance. Other species are more site-specific. For example, *Dendroalsia abietina* was recorded only at FUR and BRI, while *Antitrichia californica* was encountered only at SQU and BRI. *Homalia trichomanoides*, which often grows on tree bases subject to periodic inundation (Barkman, 1958), occurs only at SQU. The only vascular plant species found growing on the trees, the fern *Polypodium glycyrrhiza*, has low cover since sampling was undertaken during the summer when most of the fronds die back.

Table 3 summarizes bark chemistry data for the five sites. In general, the bark of *Acer macrophyllum* is slightly acidic to neutral, with high amounts of calcium. A test of site differences in bark nutrient status using MANOVA indicated rejection of the overall equality of mean vectors (Roy's largest root  $\theta = 0.571$ ,  $p < 0.01$ ;  $s = 4$ ,  $m = 0.5$ ,  $n = 31.5$ ). Nonetheless, pairwise comparisons across all variables (see Morrison, 1976) revealed only a few significant differences. Specifically, the bark at UEL showed significantly lower concentrations of magnesium than at SQU and FUR, and significantly lower pH than at SQU and BRI.

An initial canonical variates analysis of the sites (utilizing the ten most common species) resulted in the strong differentiation of SQU, but relationships among the remaining sites were obscured. This was attributable to the high loading of *Homalia trichomanoides* on the first CVA axis. Since this species is a facultative epiphyte which is here favoured by periodic inundation, it was removed and the analysis performed again. The results are

Table 2. Mean local frequency (maximum = 50) of epiphytic species over the 15 trees sampled at each of the five study sites.

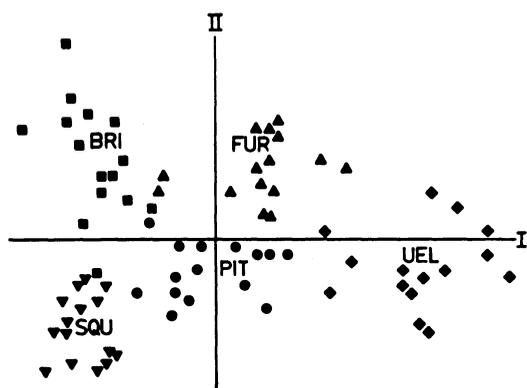
	Site					
	SQU	FUR	UEL	PIT	BRI	
<b>Mosses</b>						
<i>Metaneckera menziesii</i>	9.80	12.96	4.19	15.95	25.43	De <sup>1</sup>
<i>Homalothecium fulgescens</i>	8.69	4.26	5.13	6.93	3.78	De
<i>Neckera douglasii</i>	12.06	6.88	1.96	8.20	3.71	De
<i>Claopodium crispifolium</i>	0.54	11.62	12.41	9.52	4.16	Sp
<i>Isothecium stoloniferum</i>	0.10	7.34	13.05	1.60	-	Dc
<i>Homalothecium nuttallii</i>	1.03	1.20	4.44	3.29	1.17	Sp
<i>Dendroalsia abietina</i>	-	3.78	-	-	7.45	De
<i>Zygodon viridissimus</i>	0.18	2.21	2.03	1.51	0.17	t
<i>Plagiomnium venustum</i>	2.58	0.07	0.99	0.93	0.36	T
<i>Antitrichia californica</i>	2.95	-	-	-	2.12	De
<i>Homalia trichomanoides</i>	6.62	-	-	-	-	Dc
<i>Leucolepis menziesii</i>	0.02	0.10	1.39	1.21	0.16	T
<i>Hypnum subimponens</i>	0.83	0.08	0.13	0.83	0.14	Sp
<i>Stokesiella praelonga</i>						
var. <i>stokesii</i>	0.29	0.14	0.28	0.03	0.05	Dc
<i>Neckera pennata</i>	-	-	-	-	0.61	De
<i>Antitrichia curtispindula</i>	0.39	0.05	-	-	-	De
<i>Orthotrichum lyellii</i>	0.07	0.04	0.02	0.01	0.04	cu
<i>Rhytidiadelphus triquetrus</i>	0.24	-	-	0.27	0.10	De
<i>Rhizomnium glabrescens</i>	-	-	0.27	0.06	0.04	T
<i>Dicranum fluscescens</i>	-	-	0.36	0.01	-	T
<b>Hepatics</b>						
<i>Porella cordeana</i>	2.76	5.98	2.80	1.90	1.42	Sp
<i>Porella navicularis</i>	0.14	2.22	0.09	1.97	0.50	Sp
<i>Frullania tamarisci</i>						
ssp. <i>nisquallensis</i>	-	0.91	2.28	0.26	0.07	Dc
<i>Apometzgeria pubescens</i>	0.15	0.38	-	1.96	1.02	Th
<i>Lophocolea cuspidata</i>	-	0.07	0.54	-	0.02	tr
<i>Metzgeria conjugata</i>	-	-	0.32	-	-	Th
<b>Lichens</b>						
<i>Lepraria membranacea</i>	6.80	7.51	23.71	10.11	4.34	Lp
<i>Graphis scripta</i>	0.09	-	-	0.50	2.91	Cr
<i>Cladonia subsquamosa</i>	-	-	1.44	0.03	-	Sq
<i>Contocybe furfuracea</i>	-	-	1.82	-	0.06	Cr
<i>Parmelia sulcata</i>	-	-	0.08	-	-	Pa
<b>Vascular Plants</b>						
<i>Polypodium glycyrrhiza</i>	0.42	1.42	2.01	0.54	0.04	

<sup>1</sup> Growth forms are modified from Gimingham & Robertson (1950) and Barkman (1958). De = erect dendroid moss; Dc = creeping dendroid; t = short tuft; T = tall tuft; cu = small cushion; Th = thalloid mat; tr = thread-like forms; Sp = spreading-branch wefts; Lp = leprose lichen; Cr = crustose lichen; Sq = squamose lichen; Pa = foliose lichen.

plotted on the first two CVA axes (Fig. 2), with corresponding statistics presented in Table 4a. The results indicate site differentiation along axes corresponding to environmental gradients in moisture

**Table 3.** Mean concentrations of nutrients and mean pH values measured on *Acer macrophyllum* bark samples at each of the five study sites. Nutrient values are expressed as a percentage of sample oven-dry weight. Standard deviations are in parentheses.

	N	P	Ca	Mg	K	pH
SQU	0.78 (0.225)	0.08 (0.016)	5.07 (1.623)	0.32 (0.078)	0.34 (0.159)	7.1 (0.170)
FUR	0.75 (0.182)	0.08 (0.019)	4.69 (1.007)	0.33 (0.070)	0.23 (0.105)	6.7 (0.221)
UEL	0.96 (0.112)	0.10 (0.019)	4.90 (1.906)	0.20 (0.050)	0.14 (0.058)	6.4 (0.302)
PIT	0.77 (0.116)	0.09 (0.016)	5.84 (2.068)	0.29 (0.058)	0.20 (0.070)	6.7 (0.248)
BRI	0.73 (0.732)	0.10 (0.019)	6.50 (1.704)	0.31 (0.085)	0.26 (0.194)	6.9 (0.442)



**Fig. 2.** Axes I and II of the canonical variates analysis of the five sites, based on mean local frequency data for nine epiphytic species. Points represent individual trees whose site affinity is indicated.

availability, increasing from right to left along axis I, and light availability, which increases from top to bottom along axis II. The discriminant weights for species (Table 4b) offer further evidence for these trends. Mosses with high positive weights on the first discriminant axis (*Claopodium crispifolium* and *Isothecium stoloniferum*) have appressed, creeping growth forms which indicate adaptation to conditions of lower relative humidity, while those with high negative weights (*Metaneckera menziesii*, *Neckera douglasii*, and *Dendroalsia abietina*) are erect, dendroid forms indicative of higher relative humidity (Gimingham & Birse, 1957; Rasmussen, 1975).

**Table 4.** Canonical variates analysis of the five sites. (a) Squared canonical correlations ( $R^2$ ), significance tests (Bartlett, 1947, \* = significant at  $\alpha = 0.01$ ), and percent accounted ( $\%A_i$  = percent of total between-sites variance relative to the within sites variance accounted for by a given axis i), (b) Discriminant weights for the nine species on the first two axes.

	Axis			
	1	2	3	4
$R^2$	0.899	0.750	0.411	0.347
$\chi^2$	310.5*	156.9*	64.0*	28.5*
d.f.	36	24	14	6
$\%A_i$	67.81	22.83	5.32	4.03

(b)

Species	Axis	
	I	II
<i>Metaneckera menziesii</i>	-0.512	0.520
<i>Lepraria membranacea</i>	0.765	-0.285
<i>Homalothecium fulgescens</i>	-0.160	-0.520
<i>Neckera douglasii</i>	-0.386	-0.384
<i>Claopodium crispifolium</i>	0.727	0.272
<i>Porella cordeana</i>	0.191	0.176
<i>Isothecium stoloniferum</i>	0.796	0.054
<i>Homalothecium nuttallii</i>	0.441	-0.190
<i>Dendroalsia abietina</i>	-0.299	0.751

$$\%A_i = 100 \left[ \frac{R_i^2/(1-R_i^2)}{\sum R_j^2/(1-R_j^2)} \right] ; i = 1, \dots, 4.$$

The canonical correlation analysis results (Table 5a, b) indicate a significant, though weak, relationship between the first two CVA axes and the six bark chemistry variables. This relationship is attributable primarily to correlations between the first axis and pH, Mg, K and N values. The relationship between bark chemistry and the second CVA axis is not significant. Though the first canonical variate is significant, the redundancy value (Gittins, 1985) measuring the proportion of the variance on the two CVA axes explained by the bark chemistry data is small. It is therefore suggested that while bark chemistry may play a role in determining epiphytic composition on *Acer macrophyllum*, prevailing microclimatic conditions appear to be of greater importance.

**Table 5.** Canonical correlation between discriminant axes I and II (Fig. 2) and the six bark chemistry variables. (a) Redundancies (proportion of variation of discriminant axes I and II accounted for by bark chemistry variables), canonical correlations, and significance tests (Bartlett, 1947, \* = significant at  $\alpha = 0.01$ ). (b) Structure correlations of discriminant axes and bark chemistry variables on the two canonical axes.

	Axis	
	1	2
R <sup>2</sup>	0.508	0.131
$\chi^2$	59.047*	9.735
d.f.	12	5
Redundancy	0.147	0.015

	Axis	
	1	2
I	0.963	0.270
II	0.270	-0.963
N	-0.579	0.070
P	-0.044	-0.511
Ca	0.224	-0.266
Mg	0.582	0.085
K	0.503	0.565
pH	0.868	0.163

### Response to height and inclination gradients

Canonical variates analysis results of the 18 height/inclination habitat categories for each of the five sites are presented in Table 6. Since only the first two discriminant axes were significant in each case, two-dimensional scattergrams were examined to interpret major trends in the data (Fig. 3). At all sites, the first axis reflects changing height, while the second corresponds to inclination differences. However, the pattern of response to these gradients differs considerably across sites. Procrustes error sum of squares values (Table 7) indicate that deviations from an idealized grid are greatest in the wetter sites, particularly SQU and BRI.

The distinction of the basal flora (0.5 m) is a feature common to all sites, particularly the wetter ones (SQU and BRI). At these sites, variation above 0.5 m appears compressed, suggesting that high relative humidity may permit the establishment of a similar epiphytic flora over a wider

**Table 6.** Canonical variate analyses (one for each of the five sites) of the 18 height/inclination categories. Squared canonical correlations (R<sup>2</sup>), significance tests (Bartlett, 1947, \* = significant at  $\alpha = 0.01$ ), and percent accounted (see Table 4) for each of the first three discriminant axes are given.

Axis	R <sup>2</sup>	$\chi^2$	d.f.	%A <sub>i</sub>
<b>Squamish River (SQU)</b>				
1	0.679	761.05*	153	62.34
2	0.409	368.81*	128	20.42
3	0.148	127.12	105	8.15
<b>Furry Creek (FUR)</b>				
1	0.633	558.53*	170	72.15
2	0.227	212.62*	144	12.27
3	0.111	123.88	120	5.21
<b>University Endowment Lands (UEL)</b>				
1	0.533	548.16*	170	54.38
2	0.355	285.41*	144	26.19
3	0.143	134.26	120	7.95
<b>Pitt River (PIT)</b>				
1	0.556	516.59*	170	62.81
2	0.217	236.43*	144	13.94
3	0.151	141.84	120	8.94
<b>Bridal Veil Falls (BRI)</b>				
1	0.599	638.43*	170	65.18
2	0.424	304.21*	144	17.68
3	0.120	128.32	120	7.08

height range. Conversely, at UEL, PIT, and FUR the elevational response is more continuous; the separate heights are more evenly spaced. This appears to indicate a greater sensitivity to microenvironmental variation with height at the drier sites. The scattergrams also indicate that trunk inclination is an important determinant of epiphytic composition, and that changes with height are greater on upper than lower trunk surfaces. An interaction between height and inclination gradients is also apparent, particularly at the drier sites (UEL, PIT, and FUR) where inclination differences are accentuated at higher levels.

### Species-microhabitat relationships

Response surfaces summarizing the distributions of selected species along height and inclination gradients at the five sites are shown in Fig. 4. *Claopodium crispifolium* is the dominant species at 0.5 m at all sites except SQU, where it is largely replaced by *Homalia trichomānoides*. The powdery, leprose lichen *Lepraria membranacea* occurs on the lower (hence, drier) trunk surfaces at all sites, but also occurs on the upper trunk surface at UEL, the driest

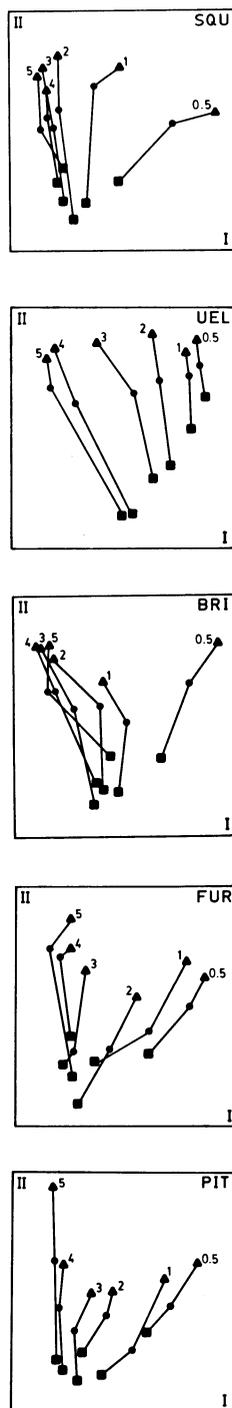


Fig. 3. Canonical variate analyses of the 18 height/inclination combinations for each site. Means of the 18 groups are plotted. Numbers are heights in meters above the tree base. Symbols code for inclination: triangle - 'upper'; circle - 'middle'; square - 'lower' bole surface. See also Table 6.

Table 7. Procrustes analysis results from fitting scattergram configurations (Fig. 3) to an 'ideal gridded response' (see text). Error sums of squares indicate the 'goodness of fit' at each site (the smaller the value, the better the fit), and permit relative comparisons among the five sites.

Site	Error sum of squares
SQU	0.250
FUR	0.219
UEL	0.126
PIT	0.174
BRI	0.249

site. Some species are clearly more prominent at higher levels (>2 m) on upward facing surfaces; these include *Antitrichia californica* (SQU, BRI), *Dendroalsia abietina* (FUR, BRI), and *Neckera douglasii* (all sites). Other species such as *Homalothecium fulgescens* tend to occur over all elevations on upper surfaces. *Isothecium stoloniferum* has a varying distribution across sites. It is uncommon at SQU, PIT, and BRI, but is prevalent at FUR (mainly <2 m) and at UEL (mainly >2 m). *Metaneckera menziesii* is the overall predominant species, tending to occur at all heights and inclinations at the wetter sites. Curiously, in the drier sites (PIT and UEL) it is more common on the drier, lower surfaces, mainly <2 m.

## Discussion

The results suggest that the availability of water (relative humidity) is an important determinant of species composition and abundance relationships of epiphytic communities on *Acer macrophyllum*. Given that epiphytic bryophytes are almost exclusively ectohydric, and that their transpiration rate is directly proportional to the vapour pressure gradient between plant and atmosphere (Hoffman & Gates, 1870; Proctor, 1983), such a result might be expected (Hoffman & Kazmierski, 1969). It is also suggested that light level, as manifested by stand density and the proportion of coniferous species in the canopy, may be an important determinant of epiphytic composition. Previous studies implicating light as an influential factor (e.g. Barkman, 1958; Hosokawa & Odani, 1957) have indicated that temperature, relative humidity and epiphytic

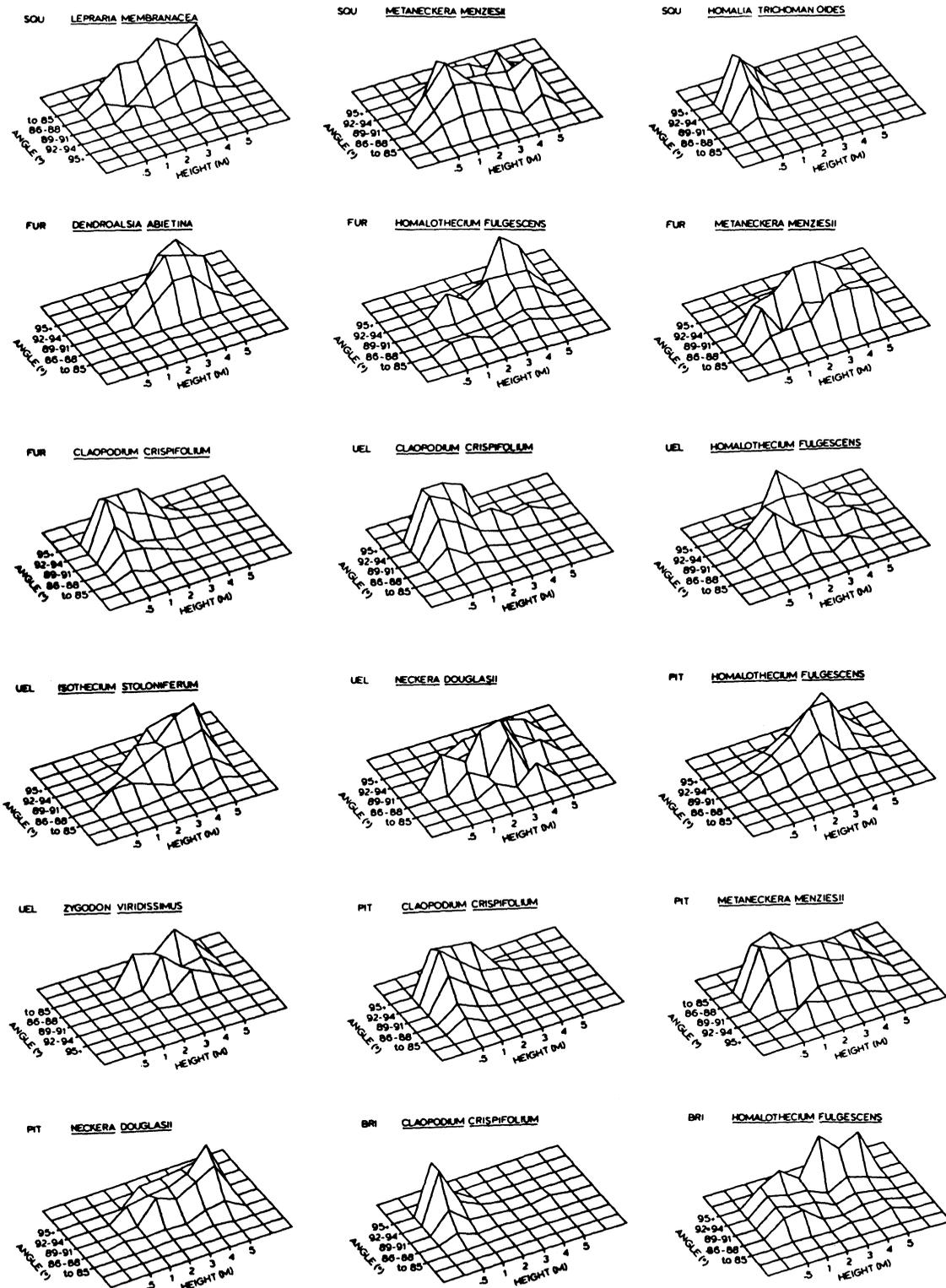


Fig. 4. Response surfaces denoting variation in mean local frequency of epiphyte species (vertical axis) in relation to height and inclination angle on the bole of *Acer macrophyllum* at the five study sites. Note that the order along the 'angle' axis is reversed in some cases to achieve a more effective display of the response surface.

photosynthetic rate may all be influenced by the quantity and quality of light filtering through the canopy. Finally, substrate nutrient status cannot be discounted as a factor influencing intersite differences in epiphytic composition on *Acer macrophyllum*, though it appears to play a limited role. However, it should be noted that the rich epiphytic flora supported by this phorophyte species in comparison with coniferous species occurring in the same sites is very likely attributable to differences in bark chemistry.

Substantial differences in the thickness of the epiphytic mat between sites are also apparent. At the wetter sites (BRI and SQU), the mat is typically 5–12 cm thick on the upper side of the trunk, while in drier sites (particularly UEL) closely appressed epiphytic species, forming mats 1–2 cm thick, are much more common. Proportions of the total mean frequency consisting of dendroid mat-forming species (see Table 2) at each site are: BRI = 0.722; SQU = 0.602; PIT = 0.463; FUR = 0.402; UEL = 0.137, indicating that this growth form is much more prevalent in wetter sites. In such sites transpirational loss can be expected to be lower, permitting the establishment of dendroid forms which have a greater surface area exposed to the atmosphere than do more closely appressed forms (Gimingham & Birse, 1957; Rasmussen, 1975). Accumulation of organic material beneath the epiphytic mat was also observed to be greater at the wetter sites. This may be an important source of water for epiphytes during the drier summer months (see also Nadkarni, 1984).

The degree of variation in epiphytic vegetation with height is site-dependent, though the distinction of the 0.5 m level flora is characteristic of all sites. This suggests that the tree base is a microenvironmentally unique habitat, differing from higher levels in such factors as relative humidity, light, and accumulation of decomposed organic material (Barkman, 1958). Changes in epiphytic composition with height are more pronounced in drier sites, indicating a greater sensitivity to changes in microenvironmental conditions with height at these locations. Light intensity, wind-speed, and saturation deficit have been shown to increase, and relative humidity to decrease, with height along the trunk (Omura *et al.*, 1955; Hosokawa & Odani, 1957).

At all sites trunk inclination appears to be an im-

portant determinant of epiphytic composition, which concurs with a study by Rasmussen (1975) in northern Jutland. Differential growth of epiphytic mats on the upper side of the trunk may further accentuate inclination differences by acting as a 'wick', effectively preventing stemflow from reaching the lower side of the trunk (Barkman, 1958; Pitkin, 1975). Greater change in species composition with height on the upper side of the trunk relative to the lower side is also apparent at all sites. This likely reflects the greatly reduced water availability on the lower side, where only species which are able to tolerate very dry conditions (e.g. *Lepraria membranacea*) are able to survive.

Although this study has suggested the importance of abiotic factors in dictating epiphytic composition, the role of biotic interactions cannot be discounted. Following initial establishment, competition may be important in dictating species composition on a given trunk. At SQU and BRI, dendroid species (particularly *Metaneckera menziesii*) were observed overgrowing closely appressed forms. Only *Apometzgeria pubescens*, *Metzgeria pubescens*, *Porella cordeana*, and *Porellanavicularis*, which are able to grow amongst and over dendroid mats, are able to persist under these conditions. In sites harbouring mat-forming dendroid species, the persistence of more closely appressed growth forms may result from a cyclical pattern of denudation followed by recolonization which occurs when large dendroid mats becoming dislodged from the trunk. Whereas *Dendroalsia abietina* forms an extensive rhizome-like branching system which proliferates among the bark fissures and anchors the mat, *Metaneckera menziesii*, *Neckera douglasii*, and *Homalothecium fulgescens* are less well anchored and may become dislodged as the substrate decomposes. At SQU, BRI, and to a lesser extent FUR and PIT, epiphytic mats (together with adhering organic material and well decomposed bark) were occasionally found around tree bases. Recolonization of bare patches may result from remnants of the dislodged mat, growth of surrounding epiphytic vegetation, or diaspore establishment. The sequence is similar to the cyclical successional processes described by Watt (1947), and may be a mechanism by which higher species diversity of the epiphytic vegetation is maintained (cf. Grubb, 1977).

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Accepted 2.7.1986