Notes on the Assessment of Lichen Diversity in Old-growth Engelmann Spruce – Subalpine Fir Forests

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ABSTRACT

Qualitative and quantitative methods are used to determine an optimal sampling strategy for assessing and monitoring lichen abundance and distribution in different silvicultural treatments in high-elevation Engelmann spruce – subalpine fir forests near Sicamous, British Columbia. The resulting sampling methods are described in detail, and a list of 99 species reliably identifiable in the field is provided. Based on principal components and cluster analysis, we propose that lichen diversity in the study area may adequately be monitored on the basis of nine substrate units.

INTRODUCTION

Central to the maintenance of lichen diversity in British Columbia is the question whether lichens occur randomly in forests of different ages, or whether some species depend on old-growth forests (Goward 1996). Old-growth dependency among lichens is already well documented in western Europe (Rose 1976; Esseen et al. 1981; Tibell 1991) and eastern North America (Maass 1980; Selva 1994). Indeed, lichens have long been used as indicators of environmental continuity within forest ecosystems. There is now growing evidence that they may serve a similar function in western North America (e.g., Neitlich 1993; Goward 1993, 1994).

Forest ecosystems of the Engelmann Spruce – Subalpine Fir (ESSF) zone of British Columbia have received little attention from lichenologists. Some information is contained incidentally in the floristic studies of McCune (1982), Goward and Ahti (1992), and Debolt and McCune (1993). However, no comprehensive floristic studies have yet been undertaken on the lichens of the ESSF zone, nor is much information available regarding the ecological behaviour of even the more common species within this zone.

Most existing data on the lichens of the ESSF zone has derived from the work of wildlife biologists (e.g., Edwards and Ritcey 1960; Edwards et al. 1960; Stevenson 1979; Palmer 1982; Antifeau 1987; Rominger et al. 1994) studying various epiphytic "forage lichens" (in the genera *Alectoria* and *Bryoria*) that are a primary winter food of the mountain caribou. These and other authors consistently stress the existence of a strong positive correlation between forage lichen biomass and forest age. Field observations suggest a similar correlation may exist between forest age and species diversity, but no published data are available on this subject.

In August 1993, the senior author initiated a detailed study on the lichens of the ESSF zone at Sicamous Creek. This study is intended to reveal the extent to which lichens depend on old-growth ecosystems. It consists of three phases. Phase 1 was initiated during the 1993 and 1994 field seasons. The primary objectives were:

- to document all non-saxicolous woodland lichen species present in the study area; and
- to summarize the local status and distributional ecology of these species.

This work continued through 1995, with the further phase 2 objective of describing lichen floristics and abundance in plots laid out to reflect different silvicultural practices. Phase 3 will begin in 1997 or 1998. Its objective is to monitor the plots at intervals for evidence of disturbance-related changes in lichen floristics and community structure. Simultaneously, other studies will specifically examine substrates strongly associated with old-growth ecosystems, especially large snags, tip-up mounds, and large logs. Over the duration of this project, comprehensive identification keys and detailed species accounts will be prepared; these, together with findings not included in the present paper, will be published at a later date.

The objectives of this paper are primarily methodological:

1. to give a brief account of sampling methods used for phases 2 and 3 of this study;
2. to identify the largest possible subset of the lichen flora that can be reliably sampled in the field; and
3. to determine the minimum number of substrates required for a comprehensive sampling of the lichen flora (i.e., without loss of ecologically significant information).

These points should be of interest to others who wish to investigate lichen floristics and ecology in high-elevation conifer forests.

Study Area

This study is part of the Sicamous Creek Silvicultural Systems Project and is located in the Sicamous Creek research area, approximately 12 km southeast of Sicamous (50°49'N 118°50'W) at an elevation of between 1450 and 1770 m. The forests here belong to the Wet Cold subzone of the Engelmann Spruce –Subalpine Fir zone (ESSFwc2) (Meidinger and Pojar 1991), and are dominated by *Abies lasiocarpa* and *Picea engelmannii* in the overstorey. (See Lloyd and Inselberg [this proceedings, page 79] for a more complete description of the study area.)

METHODS

Sampling

Owing to problems of scheduling, we were unable to sample the study area prior to silvicultural treatment. Though initially this was of concern to us, we now believe our post-logging assessments have provided an appropriate starting point from which to monitor future changes in lichen community structure: plots sampled prior to logging would have been subject to varied and unpredictable disturbance as a result of cutting, depending on harvesting methods, ground saturation, snow depth, etc.

Sampling was thus initiated four to five months after logging had terminated. During this interval, a few foliose and fruticose lichens had apparently died as a result of disturbance, whereas others were showing signs (e.g., discoloration) of physiological stress. We found no evidence, however, that any species had yet decayed beyond recognition, making it possible to perform a fairly complete inventory of lichen community structure as it would have existed at the time of logging.

Our sampling plots measured 20 × 20 m and were clustered in four silvicultural treatments:

- partial cuts (12 plots);
- 0.1-ha cuts (13 plots);
- 1-ha cuts (15 plots); and
- 10-ha cuts (13 plots).

A similar number of plots will be established in control stands in 1996. In total, 53 plots were assessed between July 14–25 and August 14–27, 1995. Field work was performed by Trevor Goward, with the assistance of David Miège.

Numerous sampling methods have been developed for the quantification of lichen abundance. Recently, McCune and Lesica (1992) evaluated three of these methods: the whole-plot ocular method, the belt transect method, and the micro-plot method. Each method was found to represent a trade-off between species capture and quantitative accuracy. The whole-plot method, for example, yields the most accurate estimate of species richness, but also provides the least accurate estimate of species cover. Notwithstanding this, McCune and Lesica (1992) judged this method to be adequate for detection of at least the most important changes in community structure over time, and recommended its use in studies such as the present one, in which emphasis is given to rare or infrequent species. A coarse sampling approach would seem appropriate given the potential disturbance to which many plots in the Sicamous Creek research area are subject (e.g., by repeated sampling by various researchers), with resulting impacts on some substrates.

Our use of the whole-plot method was intended to allow maximum species capture with a minimum of sampling effort; for most substrates, this method is considerably more efficient than other available methods (McCune and Lesica 1992). In performing the whole-plot ocular method, a thorough reconnaissance is made of a plot of fixed size. Each lichen species within the plot is assigned an abundance class estimate for each substrate on which it occurs. As required, the estimates are gradually revised to reflect improving knowledge of the plot.

In their study, McCune and Lesica (1992) assessed lichen abundance through use of percent cover classes. It may be argued, however, that percent cover per se may not always provide a sensitive measure of ecological adaptedness. In the first place, different lichen species differ in size by at least two orders of magnitude, depending on growth form. It follows from this that percent covers assigned to species having large thalli (e.g., some foliose and fruticose lichens) will far exceed those accorded to species with minute thalli (e.g., some crust lichens), even when these occur in equal abundance. A similar observation can also be made for large fruticose lichens (e.g., *Alectoria sarmentosa)* attached to their substrate at a single point.

And in the second place, many lichen species routinely occur in low abundance, and thus tend to occupy only a minute percentage of any given substrate. As McCune and Lesica (1992) themselves point out, low abundance values are especially difficult to reliably quantify using percent cover, and are generally greatly overestimated. More problematic still is the assessment of percent cover for arboreal habitats, in which the species occupy three-dimensional space (McCune 1990; Stevenson and Enns 1993).

For all these reasons, we prefer in the following frequency and abundance scale to reserve percent cover classes for the assessment of species having moderate to high abundance; species present in low abundance are assigned by us to frequency classes based on actual numbers of thalli present. Embedded in this approach is the assumption that those species present in low abundance in a given site are more likely than other species to experience substantial shifts in abundance as a result of environmental disturbance; their baseline frequency status therefore warrants careful assessment. A similar argument might be made for species having very high abundance. Hence our decision, in the following scale, to reserve four of five frequency units (i.e., units 1, 2, 4, and 5) for species present in notably low or notably high abundance; by far the majority of lichen species would thus generally be accorded a rating of 3.

Frequency unit	Description
1	2 or fewer colonies per trunk (and associated branches) for epiphytic species, or per $16m^2$ for terricolous species
2	3–5 colonies per tree or per 16 m^2
3	6 colonies as above, or up to 20% cover (under optimum conditions)
4	from 21 to 50% cover (under optimum conditions)
5	51% cover or greater (under optimum conditions)

In interpreting our use of the above scale, four points must be borne in mind:

1. For epiphytic species, ratings are intended to reflect abundance within 2.5 m of the ground; lichens of the middle and upper canopies were not assessed.
2. Our scale is intended to represent lichen occurrence within an area approximately 4 × 4 m, which in our experience is the largest area reliably assessable at mesoscale. Our procedure has thus involved mentally subdividing our 20 × 20-m plots into subplots of appropriate size—a procedure recommended by McCune and Lesica (1992).
3. Ratings were assigned based on lichen performance in those portions of the plot to which a given species appeared to be ecologically most suited. The ratings are thus intended to reflect optimum growing conditions experienced by each species within each plot, as opposed to merely the "average" of the entire plot.
4. Abundance levels for a given substrate in one 4 × 4 m portion of a plot were occasionally found to be more than one suitability unit higher than that expressed elsewhere in the same plot. In such cases, we assigned a whole-plot suitability rating one unit lower than the optimum.

All species of unknown identity were assigned a field name and collected. The specimens were later sorted, curated, and examined in the laboratory using dissecting and compound microscopes, as well as chemical tests. Several crustose specimens were forwarded to various specialists for verification. Voucher specimens will be deposited in the herbaria of the Kamloops Forest Region and the University of British Columbia Department of Botany upon completion of the project.

Definition of Substrates

Lichens are capable of colonizing a wide variety of substrates. To reflect this, our original substrate classification was designed to capture as much ecological information as possible, without, however, overwhelming our sampling methodology. In total, we recognized 21 substrate units (Table 1), each of which was routinely evaluated for lichen abundance. Rock surfaces were excluded from consideration, in order to standardize our assessments for substrates present in all plots.

A snag is defined as a dead standing tree more than 1 m tall. During the summer of 1995, most of the snags present in our plots were felled according to British Columbia Workers' Compensation Board guidelines. A few snags did, however, escape cutting and were assessed as "Bl dead."

A stump, as defined here is a dead standing tree less than 1 m tall, which had died prior to logging. By contrast, the term "cut live" is used for the basal remnant of a live tree felled during logging.

Only a few shrub species were encountered in the study area. The most common was *Rhododendron albiflorum*. Because *Menziesia ferruginea* was rare at Sicamous Creek (it was encountered in only one plot), this species was included with *Rhododendron albiflorum* as "Rhododendron." Likewise, *Vaccinium membranaceum* and *V. ovalifolium* were grouped as "Vaccinium." *Ribes lacustre* and *Lonicera utahensis*—both poor substrates for epiphytes—were excluded from consideration.

TABLE 1 *Definition of 21 substrate units recognized in the Sicamous Creek research area*

Code	Definition
Bl branch	*Abies lasiocarpa* branch
Bl trunk	*Abies* trunk
Bl cut live	*Abies* stump cut as a live tree
Bl dead	*Abies* snag, standing
Bl cut dead	*Abies* stump cut as a snag
Se branch	*Picea engelmannii* branch
Se trunk	*Picea* trunk
Se cut live	*Picea* stump cut as a live tree
Se dead	*Picea* snag, standing
Se cut dead	*Picea* stump cut as a snag
Snag	Dead conifer of uncertain identity
Vacc	*Vaccinium* spp.
Rhodo	*Rhododendron albiflorum* (and *Menziesia ferruginea*)
M logs	Mossy logs present before logging
Logs	Logs present before logging
Up root	Upturned roots, creating tip-up mound
Dec stump	Decayed stump lacking more than half its bark
Moss	Moss on ground
M rock	Mossy rock
Duff	Organic matter on forest floor
Soil	Mineral soil

Our assessments were often complicated by woody debris introduced into the plots as a result of logging. Some plots were further disrupted by the placement of skid roads, as well as by the felling of snags. To maintain sampling consistency among the plots, we assessed only those substrates that would have been present prior to a disturbance. We also excluded all lichen species introduced from the middle and upper canopies by logging activities; such species are unlikely to persist in their new habitats.

Finally, we examined only those trees and shrubs that were actually rooted within the plot perimeter. Portions of trees and shrubs that extended outside the plot boundaries were not considered.

Analysis of Lichen-Substrate Relationships

Lichen community structure and its relationship to substrate was described using ordination methods. Our analysis was restricted to the partial-cut treatments because these supported a more complete assemblage of substrate units than did the clearcut treatments. Principal Components Analysis (PCA) was used on an unstandardized co-variance matrix that contained the abundance and frequency indices for 64 species in 178 plot-substrates. We arrived at the latter figure by combining the total number of substrates in all 12 plots examined. Three of the substrate units, however, lacked an appreciable lichen cover: soil, duff, and dead

Engelmann spruce stumps. The first two PCA axes were used to display variation in species composition and to elucidate relationships with substrate units. In addition, the plot-substrate units were classified numerically using the Ward minimum variance algorithm. This procedure allowed us to determine degrees of similarity between the lichen floras of different substrates.

RESULTS AND DISCUSSION

Species Inclusion

One hundred and seventy-six lichens were recorded at the Sicamous Creek research area during this study (Goward et al., in prep.). This flora encompasses 20 species not previously reported from British Columbia, including eight species new to North America, and at least two species new to science.

Not all of these species were found to be reliably identifiable in the field. Most troublesome are certain crustose lichens, especially species in the Caliciales, as well as *Lecanora*, *Lecidea* s. lat., and *Micarea*. Based on comparisons of consistencies and inconsistencies in our use of field names, only 99 species are judged by us to be sufficiently large or otherwise distinctive to permit reliable recognition under a wide range of field lighting conditions. These species are listed in Table 2, which is drawn from as wide an assortment of substrate types as possible. Only species denoted by an asterisk, however, were actually recorded in the plots under discussion; the remaining species are included primarily on the basis of field work conducted in 1993 and 1994.

For routine field assessments of a few taxonomically or morphologically difficult species, we have found it advisable to broaden our concepts to include closely related species having similar ecologies. Thus we list *Bryoria fuscescens* s. lat. (= *B. fuscescens*, *B. glabra*, and *B. lanestris*), *Cladonia ochrochlora* s. lat. (= *C. norvegica* and *C. ochrochlora*), *Cladonia sulphurina* s. lat. (= *C. pleurota* and *C. sulphurina*), *Cladonia symphycarpia* s. lat. (= *C. cariosa* and *C. symphycarpia*), *Mycoblastus sanguinarius* s. lat. (= *M. affinis* and *M. sanguinarius*), *Ochrolechia oregonensis* s. lat. (= *O. oregonensis* and *O. szatalensis*), and *Pertusaria ophthalmiza* s. lat.(= *P.* cf. *multipuncta* and *P. ophthalmiza*). Some sterile specimens recorded as "*Pyrrhospora cinnabarina*" doubtless include the morphologically very similar *Ochrolechia gowardii*.

Lichen Community Structure

The ordination of 178 plot-substrate units is shown in Figure 1. The first PCA axis explained 35% of the total variation and clearly separated two distinct lichen communities. The group of substrates located on the right side of the ordination corresponds to standing live and recently dead trees and includes branches and trunks of live *Picea engelmannii* and *Abies lasiocarpa*, as well as snags of *Abies lasiocarpa*. This group is associated with many species that occur primarily over the bark of trees (epiphytes), including species in the genera *Bryoria* and *Hypogymnia*. The left portion of the ordination contains the remaining 14 substrate types, and is dominated by lichens that grow on the forest floor, including species of *Cladonia* and *Peltigera*. Although divisions between lichen associations are

TABLE 2 *List of lichen species reliably identified at the Sicamous Creek research area (asterisks denote species which were found in the 53 vegetation monitoring plots)*

* *Agyrium rufum* (Pers.) Fr.
* *Ahtiana pallidula* (Tuck. ex Riddle) Goward & Thell
* *Alectoria sarmentosa* (Ach.) Ach.
Arthrorhaphis citrinella (Ach.) Poelt
* *Baeomyces rufus* (Hudson) Rebent
Biatora flavopunctata (Tønsberg) Hinteregger & Printzen
* *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw.
* *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw. s. lat.
* *Bryoria pseudofuscescens* (Gyelnik) Brodo & D. Hawksw.
* *Calicium glaucellum* Ach.
* *Cetraria chlorophylla* (Willd. *in* Humb.) Vainio
Cetraria ericetorum Opiz subsp. *reticulata* (Räsänen) Kärnefelt
* *Cetraria orbata* (Nyl.) Fink
Cetraria platyphylla Tuck.
* *Cetraria subalpina* Imsh.
* *Chaenotheca furfuracea* (L.) Tibell
* *Chrysothrix candelaris* (L.) J.R. Laundon
* *Cladonia bellidiflora* (Ach.) Schaerer
Cladonia botrytes (K. Hagen) Willd.
* *Cladonia carneola* (Fr.) Fr.
* *Cladonia cenotea* (Ach.) Schaerer
* *Cladonia chlorophaea* (Flörke *ex* Sommerf.) Sprengel
Cladonia cornuta (L.) Hoffm. ssp. *cornuta*
Cladonia crispata (Ach.) Flotow var. *crispata*
* *Cladonia ecmocyna* Leighton ssp. *intermedia* (Robbins) Ahti
* *Cladonia fimbriata* (L.) Fr.
* *Cladonia gracilis* (L.) Willd. ssp. *turbinata* (Ach.) Ahti
* *Cladonia macilenta* Hoffm.
Cladonia macrophyllodes Nyl.
* *Cladonia merochlorophaea* Asah.
Cladonia multiformis G. Merr.
* *Cladonia ochrochlora* Flörke s. lat.
Cladonia pyxidata (L.) Hoffm.
* *Cladonia sulphurina* (Michaux) Fr. s. lat.
Cladonia symphycarpia (Flörke) Fr. s. lat.
* *Cliostomum* sp. nov.
Esslingeriana idahoensis (Essl.) Hale & M.J. Lai
Fuscopannaria mediterranea (Tav.) P.M. Jørg.
* *Hypogymnia austerodes* (Nyl.) Räsänen
* *Hypogymnia imshaugii* Krog
* *Hypogymnia metaphysodes* (Asah.) Rass.
* *Hypogymnia occidentalis* L. Pike
* *Hypogymnia physodes* (L.) Nyl.
* *Hypogymnia rugosa* (G. Merr.) L. Pike
* *Hypogymnia tubulosa* (Schaerer) Hav.
* *Icmadophila ericetorum* (L.) Zahlbr.
Kaernefeltia merrillii (Du Rietz) Thell & Goward
* *Lecanora circumborealis* Brodo & Vitik.
Lepraria cacuminum (Massal.) Lothander
* *Lepraria jackii* Tønsberg
* *Letharia vulpina* (L.) Hue
Lopadium disciforme (Flotow) Kullhem
Massalongia carnosa (Dickson) Körber
* *Melanelia exasperatula* (Nyl.) Essl.
Melanelia subelegantula (Essl.) Essl.
* *Mycoblastus sanguinarius* (L.) Norman s. lat.
* *Nephroma arcticum* (L.) Ach.
* *Nephroma bellum* (Sprengel) Tuck.
Nephroma parile (Ach.) Ach.
Nephroma resupinatum (L.) Ach.
Nodobryoria abbreviata (Müll. Arg.) Common & Brodo
Nodobryoria oregana (Tuck.) Common & Brodo
* *Ochrolechia oregonensis* H. Magn. s. lat.
* *Pannaria pezizoides* (G.H. Weber) Trevisan
* *Parmelia hygrophila* Goward & Ahti
* *Parmelia sulcata* Taylor
* *Parmeliopsis ambigua* (Wulfen *in* Jacq.) Nyl.
* *Parmeliopsis hyperopta* (Ach.) Arnold
* *Peltigera aphthosa* (L.) Willd.
Peltigera britannica (Gyelnik) Holt.-Hartw. & Tønsberg
Peltigera canina (L.) Willd.
* *Peltigera chionophila* Goward, ined.
Peltigera cinnamomea Goward
Peltigera degenii Gyelnik
Peltigera didactyla (With.) J.R. Laundon
Peltigera kristinssonii Vitik.
Peltigera leucophlebia (Nyl.) Gyelnik
Peltigera malacea (Ach.) Funck
* *Peltigera membranacea* (Ach.) Nyl.
* *Peltigera neopolydactyla* (Gyelnik) Gyelnik
Peltigera occidentalis (E. Dahl) Kristinsson
* *Peltigera polydactylon* (Necker) Hoffm.
Peltigera ponojensis Gyelnik
Peltigera praetextata (Flörke *ex* Sommerf.) Zopf
* *Peltigera scabrosa* Th. Fr.
Peltigera venosa (L.) Hoffm.
* *Pertusaria ophthalmiza* (Nyl.) Nyl. s. lat.
* *Platismatia glauca* (L.) Culb. & C. Culb.
* *Psoroma hypnorum* (Vahl) S. Gray
* *Pyrrhospora cinnabarina* (Sommerf.) Choisy
* *Solorina crocea* (L.) Ach.
* *Stereocaulon alpinum* Laurer *ex* Funck
Stereocaulon tomentosum Fr.
Thrombium epigaeum (Pers.) Wallr.
Trapeliopsis granulosa (Hoffm.) Lumbsch
* *Varicellaria rhodocarpa* (Körber) Th. Fr.
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai
* *Xylographa vitiligo* (Ach.) J.R. Laundon

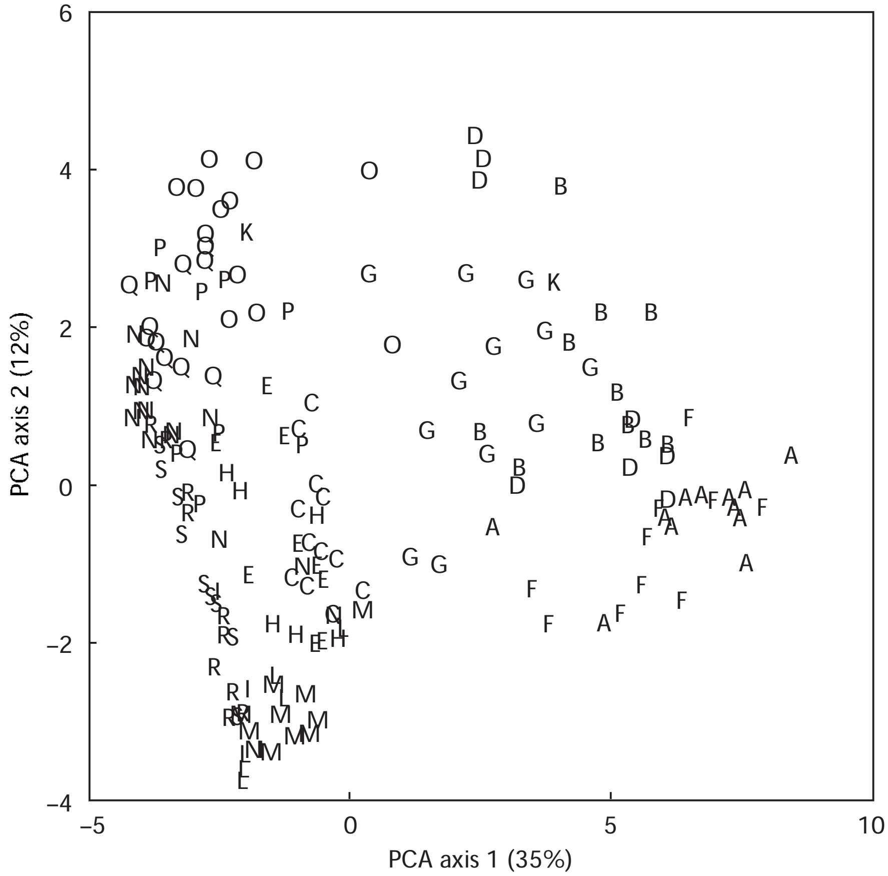

FIGURE 1 *Principal components analysis ordination of 178 plot-substrate units. Substrates are denoted by letter according to the following: A = Bl branch, B = Bl trunk, C = Bl cut live, D = Bl snag, E = Bl cut dead, F = Se branch, G = se trunk, H = Se cut live, I = Se snag, J = Se cut dead, K = Snag, L = Vacc, M = Rhodo, N = M logs, O = Logs, P = Up root, Q = Dec stump, R = Moss, S = M rock.*

not as clear along the second PCA axis, several main groups emerge. Similar assemblages of lichens are found on live *Picea* and *Abies* as shown by the overlap of substrate units associated with these two tree species. However branch and trunk substrates occupy distinct positions along the second axis and represent different lichen communities. Species on subalpine fir snags spread across both groups, apparently because they included samples both on trunks and on branches. It is also possible to divide the main group on the left side into five species subgroups along the second axis which includes:

1. species growing on logs,
2. species growing on decaying stumps,
3. species growing on mossy substrate,
4. species growing on freshly cut stumps, and
5. epiphytes growing on shrubs.

The classification of plot-substrate units accords well with the ordination, and suggests that several substrates may be combined without losing important ecological information (Table 3). Ninety percent of *Picea engelmannii* and *Abies lasiocarpa* branches, for example, were classified as belonging in the same group. The trunks of these two species were also largely classified into one group. Similarly, *Vaccinium* and *Rhododendron* may be combined as a shrub substrate, while mossy logs, mossy rocks, and decaying stumps may likewise be merged. Finally lichen communities occurring on stumps that arise from freshly cut live or dead trees are sufficiently similar to justify their placement in a single substrate unit. The remaining substrates do not classify well and should therefore be sampled separately. This scheme allows the original 21 substrates to be reduced to nine: conifer branch, conifer trunk, snag, hard stump, hard log, tip-up mounds, elevated mossy substrates, soil, and duff. Given that each plot sampled in 1995 required between 2.5 and 4 hours of field time, such a reduction in substrate units, and therefore in sampling effort, seems desirable. This revised methodology will be adopted for the 1996 field season.

TABLE 3 *Relationship between groups classified using Ward minimum variance cluster algorithm and substrate types. Percentages of plot-substrate types classified in the ten clusters are shown.*

	Cluster no.										
Substrates	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	***N*[a]**
Bl branch	92.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	12.0
Se branch	90.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0
Bl trunk	0.0	92.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	12.0
Se trunk	0.0	42.0	16.5	0.0	0.0	0.0	0.0	0.0	16.5	25.0	12.0
Rhodo	0.0	0.0	17.0	67.0	0.0	0.0	8.0	8.0	0.0	0.0	12.0
Vacc	0.0	0.0	9.0	73.0	0.0	0.0	9.0	9.0	0.0	0.0	11.0
Bl cut live	0.0	0.0	67.0	0.0	0.0	0.0	8.0	0.0	25.0	0.0	12.0
Se cut live	0.0	0.0	33.0	0.0	0.0	0.0	67.0	0.0	0.0	0.0	6.0
Bl cut dead	0.0	0.0	67.0	0.0	0.0	0.0	22.0	0.0	11.0	0.0	9.0
Bl snag	13.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.0	8.0
Se snag	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	2.0
Snag	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	2.0
Dec stump	0.0	0.0	0.0	0.0	58.3	33.3	8.3	0.0	0.0	0.0	12.0
Logs	0.0	0.0	0.0	0.0	0.0	75.0	0.0	0.0	25.0	0.0	12.0
Up root	0.0	0.0	0.0	0.0	22.0	33.0	11.0	0.0	33.0	0.0	9.0
M log	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	12.0
M rock	0.0	0.0	0.0	0.0	67.0	0.0	0.0	33.0	0.0	0.0	9.0
Moss	0.0	0.0	0.0	0.0	27.0	0.0	0.0	73.0	0.0	0.0	11.0

[a] *N* is the number of plot-substrate units associated with each substrate.

ACKNOWLEDGEMENTS

The senior author wishes to thank the following people for assistance with this project: Lynn Konowalyk and Walt Klenner for accommodation during field work; Trevor Blenner-Hassett, Todd Manning, Diana O'Brien, and Karen Yearsley for orientation in the field; Dan Burgess, Rick Pelletier, and especially David Miège for field assistance; and Dennis Lloyd and Alan Vyse for funding, helpful discussion, loan of equipment, and moral support. Gary E. Bradfield and Ken Kranrod are also thanked for their reviews of the manuscript.

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