DISPERSAL AND COLONIZATION OF ARBOREAL FORAGE LICHENS IN YOUNG FORESTS

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

A cooperative project between the Ministry of Environment and the Ministry of Forests
DISPERSEL AND COLONIZATION OF ARBOREAL FORAGE LICHENS

IN YOUNG FORESTS

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ABSTRACT

Dispersal and colonization of fragments of arboreal lichens (Alectoria spp., Bryoria spp., and Usnea spp.) in selected second-growth stands on Vancouver Island, British Columbia, were studied. Numbers of lichens on twigs in plots adjacent to mature timber with high lichen abundance declined from high values at 100-150 m from the stand edge and levelled off at 300-400 m. Plots adjacent to mature timber with medium or low lichen levels were low in numbers of lichen fragments, regardless of distance to the mature timber. Of the genera studied, Bryoria appeared to be the most effective disperser. Usnea was rare in second growth, and can be discounted in planning for forage production.
ACKNOWLEDGEMENTS

This project was funded by the Integrated Wildlife - Intensive Forestry Research program of the B.C. Ministries of Environment and Parks and Forests and Lands, with direction from D. Eastman, R. Ellis, and B. Nyberg. The fieldwork was conducted by K. Palmer, with the assistance of B. Enns, L. Scheiber, and E. Dobyns. I am grateful to K. Palmer for her insightful field observations and other valuable ideas, including the methodology for estimating lichen abundance on trees in mature forests. I thank the many individuals with Canadian Forest Products Ltd., Crown Forest Industries Ltd., and MacMillan Bloedel Ltd., listed in Appendix 5, who helped us plan and carry out the fieldwork. W. Bergerud, V. Fletcher, R. Page, and L. Stordeur of the Ministry of Forests and Lands gave statistical advice and analyzed the data. D. Stevenson assisted with manuscript preparation.
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1 INTRODUCTION

As old-growth forests on Vancouver Island are increasingly replaced by second growth, resource managers seek means for meeting the habitat needs of wildlife species in young stands. Arboreal lichens, which become available as litterfall, are an important winter forage item for black-tailed deer (*Odocoileus hemionus columbianus*) (Stevenson and Rochelle 1984). The lichens grow abundantly in some old-growth forests, but are typically sparse in second growth. The need for developing means of enhancing the abundance of forage lichens in second growth was recognized by McNay and Davies (1985) in their problem analysis on black-tailed deer and intensive forest management.

Stevenson (1985) discussed the factors that potentially limit the abundance of lichens of the genera *Alectoria*, *Bryoria*, and *Usnea* in young stands. Dispersal ability was identified as one possible limit on lichen abundance in stands distant from mature timber. The dominant means of local dispersal of those lichens appears to be the liberation and transport of thallus fragments through wind action. The effective distance of wind dispersal, and the roles of other propagules in the dispersal of those species, are unknown. Stevenson (1985) speculated that background levels of dispersal adequate to propagate lichens at their present levels may not be maintained, as old-growth forests become habitat islands in a matrix of young stands. She recommended comparative studies of dispersal in areas having different ratios of old-growth to young-growth forests.

The present study, which developed from that recommendation, was expanded to include consideration of several other factors expected to affect the abundance of lichens on twigs in second growth. The number of lichen propagules arriving at a given site during a given time period is hypothesized to depend on:
1. the area of lichen-bearing timber within dispersal range of the site;
2. distance to the lichen-bearing timber;
3. biomass and vertical distribution of lichen in the timber;
4. topographic relationships between lichen sources and the site;
5. lichen species composition in the timber;
6. species-specific dispersal rates (depending on the production and liberation rates of each type of propagule, and the size and shape of propagules);
7. weather conditions during the dispersal period (such as direction and speed of wind, and precipitation).

The number of lichen propagules establishing themselves at the site also depends on: the surface area and distribution of suitable substrate; species-specific characteristics affecting colonization ability; and a variety of microclimatic variables and weather conditions affecting the probability that the propagules will land on the substrate, become entangled with it, form hapters, or germinate.

The study focussed primarily on relationships between the colonization of second growth by lichens and variables 1-3 listed above. Because those relationships could be confounded if residual mature trees in the second growth acted as a source of propagules, veterans and snags in the immediate area of the plots were also considered.

Secondarily, genus-specific differences in rates of dispersal and colonization were examined. Differences were treated at the genus level rather than the species level because identification of thallus fragments at the species level is impracticable, and because apparent differences in colonization at the genus level had been observed. In two local studies,
Brvoria thalli were found to be several times more abundant than Alectoria thalli on 2-year-old twigs in second growth, even though Alectoria was the more abundant genus in adjacent stands of old growth (Stevenson 1985, 1986). It is unknown whether those patterns occur because of genus-specific differences in dispersal ability or in colonization ability.

Finally, the role in dispersal of propagules other than thallus fragments was examined.

The objectives of the study were:

1. To determine the quantitative relationships between number of lichen fragments (Alectoria, Brvoria, and Usnea spp.) occurring on twigs in young second growth, and
   i. distance to nearest mature timber;
   ii. area of mature timber within each of several radii of the plot centres (500 m, 1000 m, 1500 m, etc.);
   iii. abundance of lichens in nearest mature timber.

2. To test the hypothesis that the proportion of Brvoria to Alectoria propagules occurring on twigs in second growth is greater than the proportion of Brvoria to Alectoria dispersed by air, and to explore reasons for the results.

3. To test the hypothesis that the dominant mode of colonization of lichens in second growth is by thallus fragments, rather than by spores or soredia.

4. To describe the management implications of the results.

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The rationales for the objectives and methods are discussed more fully in the working plan (Stevenson 1986\textsuperscript{2}).

\textsuperscript{2} Stevenson, 1986.
2 STUDY AREAS

Sampling was located in two study areas on the east side of Vancouver Island, one in the north and one in the south (Fig. 1). The study areas were selected from the portion of Vancouver Island that has been identified as high in capability for both forestry and deer production (Nyberg 1985). Within that area of conflicting resource values, study areas were chosen on the basis of practical considerations, such as travel distances and availability of sites meeting the criteria for plot selection.

Study Area 1, on northern Vancouver Island, was located in Tree Farm Licenses (TFL’s) 7 and 39 of MacMillan Bloedel Ltd. (Kelsey Bay Division), and included the watersheds of the White and Adam rivers. Plots were located in the Windward Submontane Maritime Variant of the Wetter Coastal Western Hemlock Zone (CWHb1), as mapped by Nuszdorfer et al. (1985). The area is on the windward side of the main Vancouver Island ranges, and therefore has a wetter climate than Study Area 2.

Study Area 2 included portions of the Nanaimo, Chemainus, Cowichan, and Koksilah River watersheds. The northernmost part of the study area, in the Nanaimo Lakes area, was located in TFL 47 of Crown Forest Industries Ltd.; the remainder is administered by MacMillan Bloedel Ltd. through their Cowichan Division. The southern study area was geographically and climatically more diverse than the northern study area. Plots were located in each of the following biogeoclimatic subzones or variants (Nuszdorfer et al. 1985): the Wetter Coastal Douglas Fir Subzone (CDFb), the Vancouver Island Variant of the Drier Maritime Coastal Western Hemlock Subzone (CWHa1), and the Leeward Submontane Maritime and Leeward Montane Maritime Variants of the Wetter Coastal Western Hemlock Subzone (CWHb3 and CWHb4, respectively).
FIGURE 1. The study areas.
3 METHODS

3.1 Colonization of Young Stands by Lichens

This section pertains to procedures for sampling lichen fragments occurring on young twigs, for measuring the independent variables, and for relating the two. Sampling of lichen fragments on twigs was necessary to attain all four study objectives, and measuring the independent variables was necessary to meet Objective 1.

3.1.1 Plot selection

In each study area, 25-30 plots were selected according to the following criteria:

**Stand age.** Stands had to be old enough that most trees were 3 m or more in height. Stands had to be young enough that canopy closure had not yet occurred. Typically, stands aged 10-15 years had those characteristics.

**Tree species.** Douglas-fir (*Pseudotsuga menziesii*) had to be an important component of the study stands, as sampling was limited to that species.

**Aspect and topography.** Stands had to be located on southerly (ESE to WSW) aspects with convex topography, and on middle to upper slope positions with slope $\geq 35\%$. They had to have a soil moisture regime (hygrotrope) of 0-3 (very dry to slightly dry) and a soil nutrient regime (tropho trope) of A-C (very poor to medium) (Green *et al.* 1984). Those criteria were chosen to limit sampling to sites of
the sort that Stevenson (1978) had identified as most suitable for lichen production.

**History of neighbouring stands.** Plots were eliminated if logging of areas larger than 10 ha had occurred within 1.5 km in 1983, 1984, or 1985. That criterion was established to minimize the possible effects of nearby felling of mature trees on the number of lichen fragments in the air.

**Accessibility.** Plots that were distant from passable roads were eliminated.

Potential study sites were selected from forest cover maps or air photographs, and their suitability confirmed with on-site inspections.

### 3.1.2 Field procedures

The location of each plot was recorded on a forest cover map. The circled items on page 1 of the Site Description Form used by government agencies (Walmsley et al. 1980) were completed (Appendix 1).

Each plot was composed of two 120-m transects, 20 m apart and parallel to the contours of the slope (Fig. 2). Occasionally, plot layout had to be modified slightly to conform to the topographic constraints given in Section 3.1.1. Sample points were located at 5-m intervals along the transect lines, including the endpoints. The two living Douglas-fir trees, 3-10 m in height, closest to each sample point were the sample trees. The three branches nearest chest height and closest to the sample point were the sample branches. The central 2-year-old
twig on each sample branch was the sample twig (Fig. 3). Thus, at each plot, 300 twigs were sampled.

The investigator measured the length of each sample twig to the nearest centimetre and inspected it for lichens, using a handlens if necessary. The number of thallus fragments of each lichen genus (Alectoria, Bryoria, and Usnea) were recorded. The sample twig was collected if any of the lichens on it appeared to have originated from a spore or soredium.

The number of veterans or snags within 20 m of the transects was also recorded.

The abundance of arboreal lichens was estimated in the mature timber nearest to each plot. Where two or more plots were closely grouped, estimates were carried out in only one mature timber stand. Typically, the starting point for the mature timber survey was the first visible tree directly upslope from the end of the upper transect. The layout of a typical mature timber survey is shown in Figure 4. If the nearest mature forest was not directly upslope or could not be seen from the plot, it was located on a forest cover map, then surveyed along the edge closest to the plot. The investigator approached to about 60 m from the edge of the mature timber, and used binoculars to conduct the survey.

Proceeding from the starting point, the investigator estimated lichen abundance in the first 20 fully visible trees in the main canopy (the A2 layer, as defined by Walmsley et al. (1980)). Adapting the method of Stevenson (1979), the investigator used a clump of lichen approximately 6 x 10 cm for reference, and counted the number of similar clumps within a horizontal band approximately 2 m wide at the broadest part of the upper crown of each tree. Only lichens that were clearly
FIGURE 3. A sample twig.
FIGURE 4. Layout of a typical mature forest lichen survey.
visible were counted. Lichen clumps were tallied as either *Alectoria* or *Bryoria*. *Usnea* spp., if present, could not be distinguished under those conditions and were grouped with *Alectoria*.

3.1.3 Office procedures

The sample twigs that were collected in the field were examined under a dissecting microscope. Thalli that appeared to have a point source were judged to have originated from a soredium or spore if they met the following criteria:

- the thallus was attached to the substrate at only one location;
- the diameter of the thallus just above the point of attachment was not exceeded elsewhere;
- only one main branch came directly from the point of attachment; and
- the main branch was more or less perpendicular to the substrate.

Stands of mature timber (aged 100 years or more) within 1.5 km of each plot centre were outlined on 1:20 000 forest cover maps. Horizontal distance from the plot centre to the nearest mature timber was measured. The amount of mature timber, in hectares, within a 500-, 1000-, and 1500-m (horizontal distance) radius of each plot centre was measured with a dot grid.

3.1.4 Data analysis

The computer programs DISCRETE (R. Page and F. Hovey, B.C. Ministry of Forests and Lands, Research Branch, Victoria, B.C.) and NEGBIN (White and Eberhardt
1980) were used to analyze the frequency distributions of the data. The Statistical Analysis System (SAS Institute Inc. 1985) was used for the remainder of the data analysis. A variety of procedures, including correlation, multiple regression, and logistic regression, were used, but only those results that contributed substantially to an understanding of the data are presented here.

The independent variables which were considered in analysis are listed and defined in Table 1. The first six variables were expected to be related to the dependent variable SUMLICH, total number of lichen fragments per plot. The last six variables were included for descriptive purposes and because of the possibility that variations in topographic characteristics of plots might affect results.

3.2 Genus Composition of Lichens in Young Stands

This section pertains to procedures for sampling airborne lichen fragments as they arrived in young stands, and for comparing their genus composition to that of lichen fragments occurring on twigs. Sampling of airborne lichen fragments was necessary to attain Objective 2.

3.2.1 Plot selection

Airborne lichen fragments settling to the ground were measured in a subset of the plots in which lichen fragments on twigs were measured. In each study area, the potential plots for sampling lichens on twigs ("twig plots") were stratified into two groups: more than 400 m from mature timber, and less than 400 m from mature timber. From each group, three plots were randomly
<table>
<thead>
<tr>
<th>Variable name</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>DISTMT</td>
<td>Distance to nearest mature timber (m)</td>
</tr>
<tr>
<td>HA500</td>
<td>Area of mature timber within 500 m of plot centre (ha)</td>
</tr>
<tr>
<td>HA1000</td>
<td>Area of mature timber within 1000 m of plot centre (ha)</td>
</tr>
<tr>
<td>HA1500</td>
<td>Area of mature timber within 1500 m of plot centre (ha)</td>
</tr>
<tr>
<td>VETS</td>
<td>Number of veterans or snags within 20 m of transects</td>
</tr>
<tr>
<td>MLICH</td>
<td>Mean number of standardized clumps of lichen on trees surveyed in nearest mature timber</td>
</tr>
<tr>
<td>ASPECT</td>
<td>Aspect of plot (degrees)</td>
</tr>
<tr>
<td>DEGS</td>
<td>Departure of aspect from due south (degrees)</td>
</tr>
<tr>
<td>SLOPE</td>
<td>Slope of plot (%)</td>
</tr>
<tr>
<td>ELEV</td>
<td>Elevation of plot (m)</td>
</tr>
<tr>
<td>SITEPOS</td>
<td>Site position of plot (1=crest; 2=upper slope; 3=middle slope; 4=lower slope; 5=toe; 6=depression; 7=level)</td>
</tr>
<tr>
<td>HYGRO</td>
<td>Ecological moisture regime (1=very xeric; 2=xeric; 3=subxeric; 4=submesic; 5=mesic; 6=subhygric; 7=hygric; 8=subhydric; 9=hydric)</td>
</tr>
</tbody>
</table>
selected for studying lichen dispersal ("trap plots"), making a total of six in each study area.

3.2.2 Field procedures

Lichen fragments were trapped in 4-L plastic buckets (diameter at top, 22.3 cm) filled with approximately 500 ml of water. At each plot, 30 buckets were laid out at 4-m intervals along a transect located halfway between the two transects used for sampling twigs (Fig. 2). Each bucket was placed as close as possible to the 4-m point, at a location where there was no overhanging tree canopy. Understory vegetation overhanging the buckets was clipped.

The buckets were collected after approximately 4 days. The contents of each bucket were filtered through a No. 6 coffee filter. The bucket was rinsed with clean water to remove any fragments clinging to the sides, and the clean water was run through the same filter. The filter was placed flat in a Zip-Lock plastic bag. The sealed bags were packaged together, labelled with the plot number, and frozen for storage as soon as possible.

In hot weather, some buckets were found dry when collected. Subsequently, the amount of water in the buckets was increased and the buckets were collected sooner, usually after 3 days.

3.2.3 Office procedures

In the laboratory, the filters were examined under a dissecting microscope. For each filter, the following information was recorded:

- number of fragments of each genus (Alectoria, Bryoria, Usnea);
length of each fragment, measured along the longest dimension.

Fragments less than 0.5 mm in length were excluded because of the likelihood that they would be missed or misidentified.

3.2.4 Data analysis

Two-by-two contingency tables using chi-square as a non-parametric statistic were used to test the two-tailed hypothesis that for each plot the proportion Bryoria:Alectoria on twigs differed from the proportion Bryoria:Alectoria in traps.
4 RESULTS

4.1 Colonization of Young Stands by Lichens

4.1.1 Characteristics of the data

The frequency distributions of the lichen fragment data at the twig level were strongly skewed right, and characterized by a large number of zero values. In the northern study area, for example, Alectoria and Bryoria were absent from 95.5 and 94%, respectively, of all twigs sampled. Goodness of fit tests on a sample of plots showed that in most cases the data fitted the negative binomial distribution, the logarithmic distribution, or both. Clumping of the data occurred commonly; that is, the observation of one lichen fragment on a twig increased the probability that others were observed.

Analysis of preliminary data sets had suggested that the most efficient sampling units were the trees, and population means for lichen fragments were to be calculated for clustered samples. Because the number of zero values was proportionately greater in the data from the main study than in the preliminary data sets that plan was abandoned, and the data were treated at the plot level instead. This way, there were few zero values, the data were more strongly clumped, and they fitted the negative binomial distribution better than the logarithmic distribution.

The statistical analyses were carried out on untransformed data for two reasons. First, neither the inverse hyperbolic sin transformation nor the logarithmic transformation satisfactorily normalized the data. Second, large sample sizes (300 twigs per plot) had been

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3 Stevenson, 1986.
deliberately chosen in anticipation of that problem. According to the Central Limit Theorem, the distribution of means approaches normality as sample size increases; when sample sizes are large, normality can be assumed for the purposes of calculating and comparing means (V. Fletcher, pers. comm., April 1985, B.C. Ministry of Forests). Because of the variation in the number of zeroes in the samples, the data may not meet the assumption of homogeneity of variance common to most statistical procedures. The statistical analyses are nevertheless useful for informal data interpretation (W. Bergerud, pers. comm., April 1986, B.C. Ministry of Forests). Data interpretations were based primarily on graphic presentations; statistical analyses were used to identify the variables that merited attention.

The lichen fragment data were originally to be expressed as lichens per unit length of twig, on the assumption that longer twigs had a greater chance of supporting lichens than shorter twigs. However, the field investigators had the impression that lichens were less common on long twigs than on twigs of average length. Because tests showed that twig length and the number of lichen fragments on twigs were uncorrelated (r ranged from -0.029 to 0.009), lichen numbers were expressed per twig rather than per unit length of twig. To eliminate the possibility of any spurious confounding with independent variables, the relationship between mean twig length and distance from mature timber was tested, and no correlation was found.

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4 Stevenson, 1986.
4.1.2 Lichen colonization and independent variables

The values of the 1 dependent variable and the 12 independent variables for the 28 plots on northern Vancouver Island (Area 1) and the 27 plots on southern Vancouver Island (Area 2) are given in Appendix 2. Pearson correlation coefficients (Appendix 3) were calculated to determine which of the independent variables were related to SUMLICH and therefore merited further examination. Of the six variables expected to be important, only VETS was not significantly correlated (p<0.05) with the dependent variable. Of the six topographic variables, ASPECT was related to SUMLICH in Area 2 but not in Area 1.

Relationships between the number of lichen fragments in the plots and the significantly correlated independent variables are shown in Figures 5-8.

Lichen abundance in adjacent mature timber was positively correlated with lichen fragments in plots in both study areas (Fig. 5). The correlation was higher in Area 1 than in Area 2, probably because Area 2 had more plots that were distant from the mature timber, and were therefore less affected by the abundance of lichen in the mature timber. The three data points in the lower right corner of Figure 5B, for example, all represent plots that were more than 400 m from mature stands. The data point in the upper left corner of Figure 5B represents Plot 19, which was located 90 m from a stand of mature timber having relatively low lichen abundance (MLICH = 8), but only 200 m from a stand having much higher lichen abundance (MLICH = 21). It is likely that the latter stand had a major effect on the plot, and consequently its lichen abundance value was substituted in subsequent analyses.
FIGURE 5. Lichen fragments in plots (SUMLICH) and lichen abundance in adjacent mature timber (MLICH). Arrow indicates data points for Plot 19; see text. "2" denotes two data points at the same location.
FIGURE 6. Lichen fragments in plots (SUMLICH) and distance to nearest mature timber (DISTMT).
Maximum possible area of mature timber

FIGURE 7A. Lichen fragments in plots (SUMLICH) and area of mature timber (ha) within 500 m (HA500), 1000 m (HA1000), and 1500 m (HA1500) of plot centres, Study Area 1.
FIGURE 7B. Lichen fragments in plots (SUMLICH) and area of mature timber (ha) within 500 m (HA500), 1000 m (HA1000), and 1500 m (HA1500) of plot centres, Study Area 2.
FIGURE 8. Lichen fragments in plots (SUMLICH) and aspect (degrees).
"2" denotes two data points at the same location.
Because of the correlation between lichen abundance in the mature timber and lichen abundance in second growth, plots were identified according to whether their MLICH values came from the upper, middle or lower third of the data set (Fig. 6). In plots having high MLICH values, numbers of lichen fragments on twigs declined from high levels at 100-150 m from the stand edge, and levelled off at 300-400 m. Most plots having medium or low MLICH values were low in numbers of lichen fragments, even if they were near the mature timber. Beyond about 400 m, the number of lichen fragments in plots was uniformly low, regardless of MLICH values.

Figure 7 shows the relationship between lichen fragments in plots and the area of mature timber within various radii of the plots. In Area 1, HA1000 was correlated slightly more closely ($r=0.65$, $p=0.00$) with SUMLICH than were HA500 and HA1500 ($r=0.58$, $p=0.00$). In Area 2, only HA500 was strongly correlated ($r=0.64$, $p=0.00$) with SUMLICH. However, the effect of the single highest value of SUMLICH in each study area on the apparent relationships should be noted. In both areas, SUMLICH was more closely correlated with HA500 than with DISTMT.

Figure 7 also shows that the overall proportion of mature to immature timber around the plots was much higher in Area 1 than in Area 2.

Lichen fragments in plots in Area 2 tended to be most abundant on southeast to east aspects and least abundant on south to southwest aspects (Fig. 8). However, the apparent relationship depends heavily on two data points, and should not be regarded as conclusive.

Stepwise multiple regressions of the dependent variable SUMLICH on all independent variables produced
results that, although highly significant, had poor predictive value (Appendix 4).

4.1.3 Propagule types

Of the 1495 lichen thalli found on young twigs in Area 1, only one, a specimen of *Alectoria* sp., met the criteria given in Section 3.1.3 for thalli originating from a point source. Of the 1312 thalli found in Area 2, none met those criteria.

4.2 Genus Composition of Lichens in Young Stands

The samples from one of the trap plots were lost in shipping. Data are available for five trap plots (Plots 1, 3, 4, 15, and 23) in Area 1 and six trap plots (Plots 1, 2, 5, 6, 10, and 13) in Area 2.

In Area 1, 34 *Alectoria* fragments, 163 *Bryoria* fragments, and 1 *Usnea* fragment were found in the lichen traps. In Area 2, numbers of *Alectoria*, *Bryoria*, and *Usnea* were 38, 139, and 1, respectively.

The hypothesis that the proportion of *Bryoria* to *Alectoria* propagules occurring on twigs in second growth exceeded the proportion of *Bryoria* to *Alectoria* dispersed by air was rejected (Table 2). In Area 1, the proportion of *Bryoria* to *Alectoria* on twigs was smaller than the proportion in traps in all five trap plots, although the difference was statistically significant in only two cases. In Area 2, differences between the proportion of *Bryoria* in traps and on twigs showed no consistent trend, but were generally insignificant.

The proportion of *Bryoria* in the mature timber, based on the mature timber surveys, was much lower than average proportions of *Bryoria* in traps or on twigs (Fig. 9).
TABLE 2. Proportions of \textit{Bryoria} to \textit{Alectoria} in lichen traps and on twigs

<table>
<thead>
<tr>
<th>Plot</th>
<th>Traps</th>
<th>Twigs</th>
<th>Chi-square$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bryoria n(%)</td>
<td>Alectoria n(%)</td>
<td>Bryoria n(%)</td>
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</table>

<table>
<thead>
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<th>Area 1</th>
<th></th>
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$^a$ Test of hypothesis that the proportion \textit{Bryoria}:\textit{Alectoria} differs between twigs and traps. Chi-square $p > 0.05 = 3.84$.

$^b$ N too small for test.
Dispersal ----→ Colonization ----→

Study Area 1

% Bryoria

25% 83% 67%

+83%

Study Area 2

% Bryoria

16% 79% 77%

In mature timber In traps On twigs

Alectoria
Bryoria

FIGURE 9. Percent *Bryoria* in mature timber, in lichen traps, and on twigs.
Relationships between the proportion of *Bryoria* to *Alectoria* and distance to mature timber were unclear (Fig. 10). In Area 1, no relationship was found between DISTMT and the proportion of *Bryoria* in traps or on twigs. In Area 2, the proportion of *Bryoria* in traps, but not necessarily on twigs, appeared to increase with distance from mature timber. The percentage of *Bryoria* on twigs in all twig plots similarly appeared to increase with distance from mature timber in Area 2 but not in Area 1 (Fig. 11).
A. Study Area 1

B. Study Area 2

FIGURE 10. Percent *Bryoria* in traps and on twigs and distance to nearest mature timber (DISTMT).
FIGURE 11. Percent *Bryoria* on twigs in all plots and distance to nearest mature timber (DISTMT).
DISCUSSION

5.1 Factors Affecting Dispersal and Colonization of Lichens

The number of arboreal lichens establishing themselves in a given stand of young timber is a function of two complex sets of variables, one concerning the dispersal of propagules into the stand, and one concerning the suitability of the stand for colonization by those propagules. This study has focussed primarily on those variables affecting the arrival of lichen propagules at the stand of young timber.

It is reasonable to expect that lichen establishment in young stands is affected by the biomass and vertical distribution of lichens in the mature timber stands that are close enough to act as sources of propagules. Initial plans for this study excluded lichen abundance in mature timber as a variable to be measured, but observations early in the field season suggested that it would be critically important in explaining the variation in lichen abundance in young growth. Estimated lichen abundance in the mature timber was significantly related to lichen abundance in second growth, but the effect was only noticeable within about 400 m of the edge of the mature timber (Fig. 6). The relationship probably resulted primarily from the function of the mature timber as a dispersal source. However, it is also possible that levels of lichen abundance in the young stands and nearby mature timber stands were mutually correlated with site characteristics that allowed for good lichen growth.

The distribution pattern of the maximum values for lichen fragments on twigs (Fig. 6), which correspond approximately to the upper third of the mature forest survey ratings, closely resembles the generalized curve for organism dispersal

5 Stevenson, 1986.
described by Wolfenbarger (1975; reproduced by Stevenson 1985). The portion of the curve beyond 300-400 m, which tends to parallel the abscissa, is termed the regional zone by Wolfenbarger (1975); it derives primarily from the regional vegetation rather than from any local source. In contrast, the distribution pattern of the data points corresponding to the middle and lower third of the mature forest survey ratings is nearly flat. For lichen establishment to occur in young growth at levels above the regional level, two conditions are necessary: lichen abundance must be high in the adjacent mature timber, and the mature timber must be within 300-400 m of the young stand.

Figure 12 shows the data on lichen establishment in young growth, in relation to distance from mature timber in this study and two previous studies. The data from the Nimpkish Valley indicate that levels of establishment in the local zone (closest to the mature timber) may be higher than levels observed in this study. Most data points fall well below the curve formed by the maximum values. The scatter in the Nimpkish data is likely due to small sample sizes (18 twigs or fewer per data point), as all samples were taken from three closely matched transects. The scatter in the data points from the present study is attributed to environmental differences among plots. The combined data from all studies indicate that establishment rates decrease to about 50% of their maximum values within about 100 m of their source; remain at 10-15% of maximum at 300-400 m from their source; and are consistently less than 5% of maximum beyond 450 m.

As expected, lichen abundance in second-growth plots correlated with the amount of mature timber surrounding the plots. No one radius from the plot centres -- 500, 1000, or 1500 m -- emerged as a clearly superior predictor of lichen abundance. The data, in combination with the data shown in
FIGURE 12. Lichen fragments on 2-year-old twigs in second growth and distance from mature timber in three studies.
Figure 6, suggest that lichen abundance in second growth is most influenced by the distance to, and the amount of mature timber within, 500 m; more distant sources do not seem to affect lichen abundance significantly.

The present study was not designed to assess the possibility that lichen-bearing veterans and snags might affect lichen abundance in young stands. If they do, then retention of residuals may be a valuable management option. Few veterans and snags were tallied in second-growth stands in the present study, and most of those present bore little lichen. An adequate test of the effects of residuals on lichen abundance in second growth would require site selection and an experimental design specifically oriented to that objective.

Although distance to mature timber, amount of mature timber, and lichen abundance in the mature timber were significantly related to lichen abundance in second growth, the relatively low $r^2$ values of the regressions indicate that a considerable amount of the variation in the dependent variable is unexplained.

The most critical unexamined factor was probably a complex of variables determining air movements between dispersal sources and the young-growth plots. Topographic relationships between mature timber and plots were ignored in the study, but it is obvious that a mature timber stand located on a ridgetop is more effective as a source for long-distance dispersal of propagules than a mature timber stand in a depression. Because wind patterns in mountainous areas are complex, and the directions of the prevailing winds at the plot locations were unknown, no attempt was made to include wind direction as a variable. Weather patterns during the 2 years the sample twigs were growing were not monitored. Air movements, determined by topography and weather, were probably
the source of much of the unexplained variation in lichen abundance in the second growth.

The species composition and vertical distribution of lichens in the mature timber are other factors that undoubtedly affected lichen abundance in second-growth stands, but were not treated in this study. However, significant differences in dispersal rates among genera were demonstrated, and are discussed below (Section 5.3).

Once the lichen propagules have arrived at a site, the number that successfully establish themselves and begin growing depends on a variety of additional factors. This study was designed primarily to examine the factors affecting dispersal rather than colonization; site variables were held constant as much as possible. However, the differences that occurred in moisture regime, aspect, slope, tree growth rate, stocking, silvicultural treatments, and insect infestation among (and sometimes within) plots likely influenced colonization rates.

Of the topographic variables recorded in this study, only aspect was apparently related to lichen abundance in second growth. Figure 8 suggests that lichen abundance in young growth was greatest on the coolest aspect (east to southeast) and least on the warmest aspect (south to southwest). The pattern occurred only in Area 1, the warmer of the two study areas, and is consistent with field observations that, in open south-facing stands, more lichens were found in cool spots than in exposed areas. Similarly, Palmer (1987) reported that retention of inoculated lichen fragments was poor in the three plots in her Nimpkish Valley study area that had the warmest summer temperatures. Those observations contrast with the conclusions of Stevenson (1978), who found that lichen abundance increased with solar radiation in mature stands on northern Vancouver Island. In the warmer subzones of
Vancouver Island, microclimatic conditions in young stands on exposed south-facing slopes may be too warm or dry for optimum development of *Alectoria* and *Bryoria*, even though lichen development is good in the more moderate microclimate of the mature timber.

The two field investigators independently noted that lichens were rare on the longest twigs, despite their greater surface area. Trees with rapid growth rates, as indicated by twig length, leader length, and whorl separation, supported few lichens. However, the expected negative correlation between twig length and number of lichens on twigs was not found (Section 4.1.1).

The following reasons are suggested for the lack of correlation: First, the large number of twigs without any lichens, regardless of length, may have obscured the relationship. Second, the postulated relationship may exist only for long twigs, and not for those that are short or average in length. In the short to average length range, a positive correlation may exist because of differences in the surface area of twigs. Further investigation of a relationship between growth rates of trees and lichen establishment would require a different experimental design from that of this study.

Palmer (1986, 1987) demonstrated that twigs with few needles did not retain inoculated lichen fragments as well as twigs with normal foliar development. Those results are consistent with the observations made in the present study, as needle loss on young twigs is often associated with rapid growth (Palmer 1987).

The field investigators also noticed that twigs with smooth bark rarely supported lichens. When they did, the lichens were entangled among the needles and not attached by
holdfasts. The environmental conditions that result in rough rather than smooth bark on twigs merit investigation.

5.2 Propagule Types

In this study and in two previous studies (Stevenson 1985, Stevenson6), the colonization of 2-year-old twigs was overwhelmingly dominated by thallus fragments. If spores or soredia were established on the 2-year-old twigs, they had not yet developed into recognizable thalli. Thallus fragments are the propagules that are most important in the early colonization of a young stand. They are therefore the propagules that managers should work with to ensure the earliest possible establishment of the lichens in second growth.

5.3 Differences among Genera in Dispersal and Colonization

Results of the study indicate that Bryoria is relatively less abundant than Alectoria in mature stands, and more abundant than Alectoria in young stands. The change in proportions of the two genera occurs mainly at the dispersal stage, not at the colonization stage (Fig. 12).

Three possible explanations for those results are suggested. First, the Bryoria spp. occurring in the study area are generally more fine-bodied than the Alectoria spp. Their delicate structure may make them more susceptible to breakage. Because they are lighter per unit length, they may be expected to disperse farther (Niklas 1985).

Second, in mature stands on Vancouver Island, the relative abundance of Bryoria increases with height in the canopy (Stevenson 1978; S. Stevenson, unpubl. data). Observations of lichen abundance in this study were made in

6 Stevenson, 1986.
the upper mid-canopy, not on the uppermost branches (Fig. 4). Lichens on the uppermost branches are likely to contribute disproportionately to long-distance dispersal because their exposure to higher wind speeds increases the probability of liberation, and because their greater release height increases their dispersal range (Nicklas 1985). It is possible that the mature forest surveys slightly underestimated the proportion of *Bryoria* in the population from which most of the dispersal originated.

Third, *Bryoria* is more difficult to see than *Alectoria* because it is darker. Under some light conditions, it is difficult to distinguish *Bryoria* from shadows. Differential visibility of the two species may have resulted in an underestimation of *Bryoria* in the mature timber surveys.

It seems unlikely that the third explanation could account for the large differences in the proportions of the two genera that are shown in Figure 9. It is more likely that both the fine-bodied morphology of *Bryoria* and its characteristic location high in the canopy contribute to its superior dispersal ability.

No conclusions can be drawn about the dispersal ability of *Usnea* in the study area, because no quantitative observations of its abundance in the mature timber were made. Informal observations in both study areas indicate that it occurs sporadically, and much less abundantly than the other two genera. Only two *Usnea* fragments were found in lichen traps, one in each study area, and none were found established on trees. Apparently, managers need not be concerned with *Usnea* as a colonizing genus in young second growth.

The limited dispersal ability of some *Usnea* species has been reported elsewhere. Esseen (1985) questioned the effectiveness of thallus fragmentation as a dispersal method in *U. filipendula* and *U. subfloridana* because of their strong
central cords and their attachment by holdfasts. He also observed that *Alectoria sarmentosa* and most *Bryoria* spp. in Swedish *Picea abies* forests dispersed mainly by fragments up to a few centimetres long, whereas *U. longissima* fragments were up to some decimetres in length, and therefore less effective for long-distance dispersal.

Changes in genus composition of lichens at the colonization stage were minor compared to changes at the dispersal stage. In Area 2, *Bryoria* was present on twigs in approximately the same proportions that it was present in traps, although there was considerable variation in the proportions among plots (Table 2). It appears that no special selective pressure occurs at the colonization stage. Perhaps the relatively dry climate of southeastern Vancouver Island is equally suitable to colonization by the two genera in second growth. Those results correspond to the results obtained in the pilot study, also carried out in Area 2, in which the proportions of the two lichen genera on twigs and in traps were similar.

In Area 1, *Bryoria* was present on twigs in lower proportions than in traps. Those results suggest that in that study area, some sort of selective pressure favours *Alectoria* over *Bryoria* at the colonization stage. The selective pressure may be related to the cooler, moister climate of northern Vancouver Island. Although statistically significant in some plots, the difference in proportions of the two genera in traps and on twigs should not be considered conclusive without confirming evidence.
6 CONCLUSIONS AND RECOMMENDATIONS

6.1 Summary

The objectives of the study were: to determine the relationships between arboreal lichens occurring in second growth and a number of independent variables; to compare the genus composition of lichens dispersed by air and lichens established on twigs; and to identify the type of propagule that is most important in the colonization of second growth.

The lichen fragment data at the plot level best fitted the negative binomial distribution, and could not be satisfactorily normalized by transformation. Although some statistical analyses were reported, data interpretations were based primarily on graphical presentations.

Lichen colonization in second-growth stands depends on lichen abundance in the nearest mature timber, distance to the mature timber, and the area of the mature timber. Estimated lichen abundance in the mature timber was significantly related to that in second growth, but the effect was only noticeable within about 400 m of the edge of the mature timber. Numbers of lichen fragments in plots adjacent to mature timber with high lichen abundance declined from high values at 100-150 m from the stand edge, and levelled off at 300-400 m. Plots adjacent to mature timber with medium or low lichen levels were low in numbers of lichen fragments, even if they were near the mature timber. The combined data from this and other studies indicate that colonization rates of lichen fragments in second growth decrease to about 50% of their maximum values within about 100 m of their source, remain at 10-15% of maximum at 300-400 m, and are consistently less than 5% of maximum beyond 450 m.

A considerable amount of the variation in lichen colonization in second-growth stands could not be explained by
the parameters measured in this study. Air movements between mature timber and second-growth plots were probably a major source of the unexplained variation in the data.

Although the study was designed primarily to examine the factors affecting dispersal rather than colonization of lichen propagules, observations suggest that some sites may be too warm or dry for optimum development of Alectoria and Bryoria spp. in second growth, and that rapidly growing trees support fewer lichens than trees with slow or average growth rates.

Results of the study confirm previous observations that the colonization of young twigs was overwhelmingly dominated by thallus fragments rather than by thalli originating from spores or soredia. Bryoria was relatively less abundant than Alectoria in mature stands, and more abundant than Alectoria in young stands. The change in proportions of the two genera occurred mainly during the process of dispersal, not during colonization. Usnea was sporadically present in mature timber, but was extremely rare in lichen traps and absent on twigs. Of the three genera studied, Bryoria appears to be the most effective at dispersal.

6.2 Management Implications

A strategy for enhancing the development of arboreal lichens in second-growth forests must be based on an understanding of the factors that ordinarily limit lichen abundance in young stands. This study has examined the role of dispersal in limiting the abundance of Alectoria, Bryoria, and Usnea spp. in 10- to 15-year-old stands. The study was not intended to provide information about the long-term relationships between mature timber and lichen abundance in second growth. Ideally, managers would like to know how dispersal-related factors affect overall lichen abundance in
stands that are old enough to begin producing lichen forage, such as stands in the 40- to 60-year-old age range.

The long-term effects on stands of that age were not studied for several reasons: First, the independent variables related to the neighbouring mature timber stands, such as distance to mature timber, are unstable over time. Second, trees in that age range are difficult to sample efficiently for lichens. Finally, variations in stand structure are likely to introduce even more confounding factors at that age than at the shrub-seedling stage. The study does not indicate the extent to which dispersal has limited lichen abundance in 40- to 60-year-old stands, but it does provide information about the relative effectiveness of dispersal in relation to characteristics of mature timber. The results are relevant to young stands up to the time that dispersal of lichens from within the young stand becomes a significant factor.

Earlier observations of the relatively great abundance of *Bryoria* in second growth raised the question of whether that genus was more successful than *Alectoria* at the dispersal or colonization stage. If *Bryoria* was a better colonizer than *Alectoria*, then high proportions of *Bryoria* should probably be selected for inoculation. This study has shown that *Alectoria* is at least as successful as *Bryoria* at the colonization stage, suggesting that there is no advantage in favouring *Bryoria* for inoculation. The relative ability of the two genera to develop over time in growing stands remains unknown. Until that information is available, the most prudent strategy is to include both genera in the material for inoculation.

If it is assumed that dispersal limitations affect lichen development in young growth, as seems likely, then the following inferences regarding management may be made from this study:
1. Reliance on natural dispersal as a source of propagules for the establishment of abundant Alectoria and Bryoria spp. should be restricted to young-growth stands within 350 m of mature timber that supports above-average lichen loads.

2. If enhancement of lichen abundance is a management objective for young-growth stands greater than 350 m from lichen-rich mature timber, then artificial dispersal of lichen fragments should be attempted. Alectoria and Bryoria are about equally successful as colonizers, and both genera should be included in inoculation plans.

3. Where the creation of lichen-bearing winter ranges in second growth is a management objective, the effective limit of 350 m for lichen dispersal above background levels should be considered by managers preparing harvesting plans.

Management of second-growth stands to enhance lichen abundance must be based on other factors in addition to dispersal. Substrate and microclimatic considerations may restrict the kinds of stands that are selected for lichen enhancement. Frequent thinnings may be prescribed to maintain a suitable microclimate for the lichens. Late in stand development, thinning techniques that result in standing dead trees may be used to increase litterfall rates. Overall
strategies for enhancing lichen abundance in second-growth
winter ranges are discussed by Stevenson and Palmer7.

6.3 Research Recommendations

This study has left many unanswered questions about
dispersal and establishment of arboreal forage lichens in
second-growth stands. The research recommendations that
follow focus on the questions that have the most significant
implications for management.

The pattern of fragment dispersal observed, and the
differences in magnitude of lichen establishment between the
local and regional zones, are compatible with the untested
hypothesis that lichen dispersal limits the production of
lichen forage in some second-growth stands. Artificial
application of lichen fragments may be a practical management
tool in young-growth stands that are distant from mature
timber. Methods for inoculating young stands with lichens are
being developed (Palmer 1986, 1987). Continued
experimentation with the technology and effectiveness of
artificial introduction of forage lichens is recommended.

Managers need to know what site characteristics offer the
optimum conditions for enhancing lichen development. For
example, the hypothesis suggested in Section 5.1 that lichens
are less successful in establishing themselves on rapidly
growing trees than on slowly growing trees should be tested,
as should the possibility that some sites are too warm and dry
for successful establishment.

enhancement with programs for winter range creation. Report
prepared for MacMillan Bloedel, Ltd. and B.C. Min. For.
Lands, Victoria, B.C. Silvifauna Research, Prince George,
B.C. Unpubl. draft.
Managers also need to know at what stage in stand development dispersal most affects future levels of lichen production. An understanding of the pattern of lichen development in natural stands would help managers determine the optimum age for the artificial introduction of lichen fragments, and the optimum ages for stand management activities regardless of whether or not artificial dispersal was included in the management plan.

Of the unanswered questions associated with natural dispersal, two are especially important to managers. First, is the retention of lichen-bearing residuals a practical method for increasing dispersal of lichens into second growth? The results of this study suggest that residuals would have to support high lichen loads to be effective as sources of propagules. Second, what characteristics (such as size and topographic position) must a block of mature timber have to increase levels of lichen establishment significantly in adjacent second growth?

The management strategies recommended in Section 6.2 depend on the ability of field staff to recognize stands that are high in lichen abundance. New inventory techniques proposed by Stevenson and Palmer¹ should be tested in the field.

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LITERATURE CITED


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APPENDIX 5. Personnel contacted

W. Bergerud, Ministry of Forests and Lands, Victoria, B.C.
B. Chapman, MacMillan Bloedel Ltd., Chemainus, B.C.
D. Eastman, Ministry of Environment and Parks, Victoria, B.C.
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B. Gibson, Crown Forest Industries Ltd, Campbell River, B.C.
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S. Lorimer, Crown Forest Industries, Nanaimo Lakes, B.C.
R. McLaughlin, MacMillan Bloedel Ltd., Nanaimo, B.C.
B. Nyberg, Ministry of Forests and Lands, Vancouver, B.C.
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K. Palmer, Larkspur Biological Consultants, Sidney, B.C.
L. Stordeur, Ministry of Forests and Lands, Victoria, B.C.
C. Van Oosten, MacMillan Bloedel Ltd., Sayward, B.C.
G. Whalley, MacMillan Bloedel Ltd., Sayward, B.C.