

Recolonization of bigleaf maple branches by epiphytic bryophytes following experimental disturbance

Alexander R. Cobb, Nalini M. Nadkarni, Grant A. Ramsey, and Abraham J. Svoboda

Abstract: The dynamics of epiphytic bryophyte communities following natural and human disturbance have rarely been quantified. We describe the response of bryophyte communities on bigleaf maple trees (*Acer macrophyllum* Pursh) in Olympia, Washington, following their experimental removal. Approximately 8% of the exposed area was recolonized by bryophytes 1 year after clearing, and 27% after 3 years. Lateral encroachment from bryophytes on the sides of the 20-cm-long plots accounted for 75% of this recolonization, with growth from residual plant parts or aerially dispersed diaspores accounting for the remaining 25%. Though it was not possible to distinguish between the latter two sources of cover, the number of clear de novo colonization events over the course of the year was low (0.18 dm⁻²). Disturbance appeared to reduce bryophyte diversity at this successional stage, as alpha and gamma diversity remained low after 1 year and had not recovered after 3 years. Reflecting the preponderance of lateral encroachment as the mechanism for recolonization, disturbance size may significantly affect the time needed to recolonize disturbed branch substrates. In addition to contributing to ecologists' understanding of processes of succession, these experiments may help to develop sustainable practices for moss-harvesting in the Pacific Northwest.

Key words: succession, bryophytes, epiphytes, *Acer macrophyllum*, recolonization, canopy studies.

Résumé : On a rarement quantifié la dynamique des communautés épiphytes suite à des perturbations naturelles et humaines. Les auteurs décrivent la réaction de communautés de bryophytes venant sur des tiges d'érable grandifolié (*Acer macrophyllum* Pursh) en Olympie, état de Washington, suite à leur élimination expérimentale. Une année après l'élimination, environ 8 % des surfaces exposées se sont vu recolonisées, et 25 % après 3 ans. L'attachement latéral des bryophytes le long des parcelles de 20 cm compte pour 75 % de cette recolonisation, la croissance à partir de fragments végétaux résiduels ou de diaspores venues par la voie des aires expliquant les 25 % qui restent. Bien qu'il fut impossible de distinguer entre ces deux dernières sources de couverture, le nombre d'évènements de colonisation de novo évidents au cours de l'année est faible (0,18 dm⁻²). La perturbation semble réduire la diversité des bryophytes à ce stade de la succession, puisque les diversités alpha et gamma demeurent faibles après une année et ne se sont toujours pas rétablies après 3 ans. Reflétant la prépondérance de l'attachement latéral comme mécanisme de recolonisation, la dimension de la perturbation peut affecter significativement le temps nécessaire à la recolonisation des substrats raméaux perturbés. En plus de contribuer à la compréhension par les écologistes du processus de succession, ces expériences peuvent aider à développer des pratiques durables lors de la récolte des mousses dans le Pacific Northwest.

Mots clés : succession, bryophytes, épiphytes, *Acer macrophyllum*, recolonisation, études de la canopée.

[Traduit par la Rédaction]

Introduction

Epiphyte communities are subject to disturbance by wind, animals, branch breakage, and tree fall (Matelson et al. 1993). Some forest resource extraction practices (e.g., moss harvest-

ing in the Pacific Northwest of North America, Peck 1997a) and activities of recreational tree-climbers and canopy researchers can also disturb epiphyte communities. Although studies of terrestrial and riparian bryophytes implicate disturbance as a factor in maintaining diversity in those habitats (Kimmerer and Allen 1982; Jonsson and Esseen 1990), the role of disturbance in epiphytic bryophyte ecology has not been studied (Peck 1997a, but see Peck and McCune 1998). Canopy plant communities affect forest nutrient cycles (Pike 1971; Pike 1978; Nadkarni 1981, 1994), provide resources for arboreal animals (Nadkarni and Matelson 1988), and contribute to high biodiversity (Gentry and Dodson 1987), so understanding the processes that influence epiphyte colonization and growth will enhance our knowledge of forest ecosystems. Further, quantifying epiphyte community dynamics could al-

Received February 24, 2000. Published on the NRC Research Press website on December 23, 2000.

A.R. Cobb,^{1,2} N.M. Nadkarni, G.A. Ramsey, and A.J. Svoboda. The Evergreen State College, Olympia, WA 98505, U.S.A.

¹Corresponding author (e-mail: nadkarnn@elwha.evergreen.edu).

²Present address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, U.S.A.

low us to better assess and mitigate human-induced disturbances.

Although the abundance and community composition of epiphyte communities at a single point in time have been documented in many tropical and temperate studies (e.g., Stone 1989; Ingram and Nadkarni 1993; Peck et al. 1995), few studies have examined their dynamics directly. Researchers in temperate forests have inferred how succession proceeds by using chronosequences of forest stands (e.g., Dudgeon 1923) or tree branches (Pike 1978). Studies of recolonization following clearing of branch surfaces in the tropics indicate that the process can take more than a decade (Nadkarni 2000; D. Janzen, personal communication). However, the dearth of experimental studies on epiphyte colonization has prevented the construction of a quantitatively predictive model that can explain such observations (cf. Peck and McCune 1998). Static descriptive studies cannot distinguish between features of distribution that are consequences of the substrate's and community's age from those that are consequences of the microclimate at a location, because microclimate changes progressively as a tree grows.

In forest canopies, an appreciable variation in species distribution is frequently observed that is not apparently linked to large-scale resource gradients. This observation has led to the hypothesis that rarity and randomness in propagule supply allow the coexistence of ecologically similar species in the canopy (Wolf 1994; Benzing 1995). Similarly, many bryophytes appear to be generalists, which suggests that their diversity might be maintained by differences in reproductive niches or by stochastic factors affecting disturbance or success in establishment, rather than by sharply defined niches as expected under classical niche theory (During 1979; Lloret 1988; Slack 1990; Herben et al. 1991; Lloret 1994). Very few terrestrial studies have documented modes of bryophyte establishment in the field (Mishler and Newton 1988), but the rarity of observed events of colony establishment on bare substrates has been noted several times (Miles and Longton 1990; Kimmerer 1991). This suggests that factors affecting dispersal and establishment could be significant in determining distributions of bryophytes in the forest canopy, since the sparseness of substrates could make success still rarer there. There is evidence that epiphytic lichens in the Pacific Northwest are limited in recolonization by their capacity for dispersal (Sillett et al. 2000), and the same might be true of epiphytic bryophytes. Thus, documenting the dynamics of colonization and recolonization should help us understand patterns of the distribution of mature epiphytic plants and their associated biota.

In this study, we assessed the composition and abundance of epiphytic bryophytes on mature bigleaf maple trees (*Acer macrophyllum* Pursh [Aceraceae]). We then quantified the abundance, composition, and spatial distribution of recolonizing bryophytes 1 and 3 years after the experimental clearing (1997 and 1999). We interpreted the patterns of recolonization to derive an understanding of small-scale recolonization of epiphytic bryophytes during early stages of succession.

Study site

The study site was located on the campus of The Evergreen State College, Olympia, Washington (55-m elevation,

47°04'27"N, 122°58'26"W). The study area is mesic, open in structure, and flat, with well-drained alluvial soil. The site had been clear-cut in the early 1920s, producing an even-aged stand dominated by bigleaf maple trees. This species supports the most abundant epiphyte communities of all host trees in the region. The adjacent forest consists of second-growth mixed Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and red alder (*Alnus rubra*), which is typical of mixed conifer – hardwood forests in the coastal Douglas-fir/Western hemlock zone of the Pacific Northwest (Franklin and Dyrness 1988).

Epiphyte communities are fairly diverse and abundant for this age and composition of forest, covering branch surfaces in nearly contiguous mats co-dominated by mosses and liverworts. Epiphytes grow on nearly all trunk and branch surfaces; small amounts of "crown humus" accumulate on inner branches and branch bifurcations. Epiphyte communities are dominated by bryophytes, with foliose, fruticose, and crustose lichens present in the uppermost branches, and scattered individuals of the single vascular epiphyte in the region, licorice fern (*Polypodium glycyrrhiza*).

Materials and methods

Field sampling

In July 1996, we identified 76 cylindrats (20-cm-long plots encircling branches) in seven bigleaf maples in the study site. When possible, trees were selected to allow the location of 12 cylindrats, of a range of sizes and angles, more than 9 m above the ground. Each cylindrat was located on a separate branch. We recorded height above ground, diameter, and the vertical angle of the branch.

In July and August 1996, all live and dead epiphytes (excluding the few lichens and licorice ferns), residual plant parts, and crown humus were removed from each cylindrat by hand and with a firm toothbrush. This material will be referred to as the original sample. All material was bagged separately by cylindrat and taken to the laboratory for separation to species and assessment of abundance. Species were classified according to their relative abundance in each cylindrat and also according to the percentage of cylindrats in which they appeared. Species identifications were verified by J. Harpel and D. Norris; vouchers are at The Evergreen State College Herbarium.

The cylindrats were censused for recolonization from October to December 1997. One tree and several other branches were destroyed in a severe ice storm in December 1996, which reduced the sample size to 60 cylindrats; the sample was further reduced to 47 by storm damage prior to a second census in 1999. To quantify the abundance and composition of the bryophytes that occupied the cleared cylindrats 1 and 3 years after the experimental disturbance (herein, referred to as the recolonizing sample), we wrapped a clear acetate sheet around each cylindrat, over the recolonizing bryophytes. The sheets were aligned with an aluminum nail 6 cm outside each cylindrat. The area occupied by recolonizing bryophytes was then traced with a waterproof pen, using a separate acetate sheet for each species.

Classification of spatial patterns

We followed Peck's (1997b) application of Whittaker's (1972) classification to epiphyte diversity. Alpha (α) diversity is the number of species in a given area (in this study, the number of species in a single cylindrat); beta (β) diversity is a measure of the variation in species richness across areas (cylindrats; most easily estimated as the ratio γ/α); gamma diversity (γ) is the richness in species over a range of areas (here, the total species richness over all cylindrats).

We followed Frego's (1996) type classifications of gap recolonization in moss beds: a, encroachment (here, lateral elongation from the undisturbed bryophytes on either side of the cleared cylindrat); b, microscopic vegetative or sexual diaspores; c, larger vegetative fragments; and d, growth from residual particles.

Data analysis

Each acetate sheet tracing was scanned into a separate black and white computer image file (TIFF) using a 50% gray value threshold, transferred to 200×200 pixel files with Adobe Photoshop, converted to ASCII format using Idrisi (Geographic Information System software; 1997 data) or Lemkesoft Graphic Converter (1999 data), and analyzed as a matrix of binary data in Microsoft Excel. Portions of the resulting binary matrix were then summed to quantify cover distribution within different regions of each cylindrat. These regions were arranged in two ways: (i) relative to the ground (dorsal vs. ventral) and (ii) relative to the trunk (proximal vs. distal). To distinguish between encroachment and the other modes of recolonization, we also divided the cylindrats into proximal, middle, and distal thirds (Fig. 1). We refer to the middle third as the non-encroachment zone since no bryophytes reached this area by encroachment in the study period. Conversely, we called the distal and proximal thirds of the cylindrat the encroachment zone, since encroachment was confined to these areas (although recolonization by other—non-encroachment—methods also occurred there, see below). To estimate cover from non-encroachment recolonization in a whole cylindrat, we multiplied the total cover in the non-encroachment zone by a factor of three to account for non-encroachment methods in the proximal and distal thirds. Recolonization by encroachment was then estimated by subtracting the estimate for non-encroachment cover from the total cover in the cylindrat. Both of these estimates are subject to error since proximity to an intact bryophyte mat may affect both the frequency with which diaspores arrive and their likelihood of establishment.

Biomass and percent cover data (within cylindrats and their subdivisions) were log-transformed prior to parametric analysis, when possible. Following transformation, both variables showed normal distributions both overall and by species. Means for growth variables were also found using log transformation when possible. Means obtained through log-transformation are accompanied by a geometric-scale standard deviation, i.e., the mean is multiplied and divided by this deviation to give the limits that encompass 68% of the sample variation. The preponderance of zeroes prevented log-transformation, and hence parametric analysis, for comparing recolonization in regions within each cylindrat (i.e., dorsal vs. ventral, proximal vs. distal, encroachment vs. non-encroachment); the Wilcoxon paired-sample sign-rank test was used for this purpose. Statistics were run in Microsoft Excel. The 0.01 level of significance was adopted except where otherwise noted.

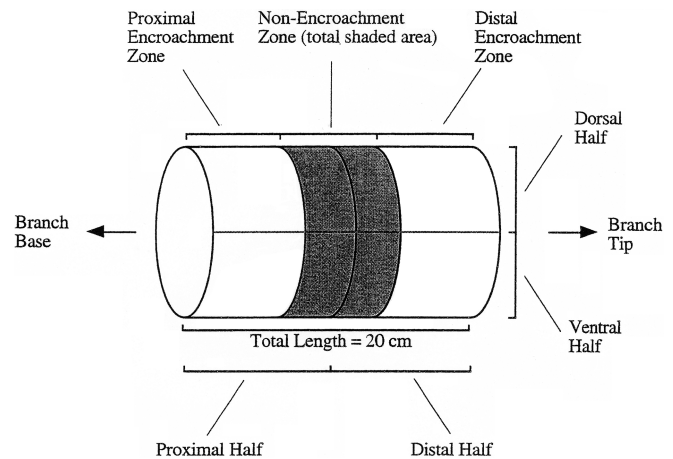
Results

Description of original and recolonizing samples

Cylindrat characteristics

Mean diameter of the cylindrats was 10.1 cm (4.2–31.1 cm, $\times/\div 1.54$). Our sample trees had few horizontal branches of large diameter; however, correlations among height, diameter, and angle were not significant. We investigated potential autocorrelation among cylindrats related to the proximity of samples within trees by carrying out nested analysis of variance (ANOVA) to compare within- versus between-tree variation. There was no significant tree effect for percent cover, biomass, or species richness for the original or recolonizing samples of bryophytes.

Fig. 1. Schematic of cylindrat illustrating subplot dimensions and terminology. All divisions include both sides of the cylindrat.



Community abundance and composition of original and recolonizing samples

The original sample had an overall biomass density (total sampled biomass/total sampled area) of $2.56 \text{ g}\cdot\text{dm}^{-2}$. After 1 year, the entire sampled area had an overall percent cover of 7.7%; after 3 years, 26.6% was covered. The 12 species of bryophytes found (Table 1) are typical of epiphytic bryophytes in forests of this type and successional stage (cf. Peck et al. 1995). Bryophyte abundance by cylindrat in both the original and recolonizing samples showed a significant positive relationship to the three measured substrate characteristics (diameter, height, and angle) taken together. In the original sample, there was a positive linear regression of log-transformed biomass on diameter and a negative linear regression of log-transformed biomass on height.

Relationships of substrate characteristics to epiphyte abundance and species composition

In contrast to the original epiphyte community, log percent cover in the recolonizing community showed a weak positive linear regression on diameter only (Table 2A). This contrasted with species distribution on an individual species basis. None of the most common species showed significant linear relationships with any of the measured substrate characteristics.

Alpha diversity was related to substrate characteristics in both the original and recolonizing samples. In the original sample, α diversity showed a strong positive relationship with branch diameter, a weak positive relationship with branch angle, and a strong negative relationship with cylindrat height. Recolonizing cylindrat richness showed a significant positive relationship with diameter, but not with angle or height (Table 2B).

Within-cylindrat distribution of recolonizing epiphytes

We discerned trends in recolonization by comparing cover in the proximal vs. distal and dorsal vs. ventral regions for each species (except where species had fewer than 6 replicates and could not be analyzed). Overall, there was greater total bryophyte cover in the proximal than in the distal halves of the cylindrats, with proximal cover accounting for roughly 58% of cylindrat cover. The two *Homalothecium* species were the only ones that showed this pattern, but were suf-

Table 1. Bryophyte names, abbreviations, abundance (biomass by species not recorded for original sample, mean percent cover for recensuses), frequencies (% of cylindrats), and frequency classes for original sample and recensuses.

| Species | Abbreviations | Frequency (%)* | | | % of total area | | Factor of increase |
|---------------------------------|---------------|----------------|------------|------------|-----------------|------|--------------------|
| | | 1996 | 1997 | 1999 | 1997 | 1999 | |
| All bryophytes | | | | | 7.7 | 26.6 | 3.4 |
| <i>Antitrichia curtipendula</i> | Ancu, ac | 8.5 (RAR) | 4.3 (RAR) | 4.3 (RAR) | 0.004 | 0.1 | 30.7 |
| <i>Claopodium crispifolium</i> | Clcr, cc | 8.5 (RAR) | 0 (ABS) | 0 (ABS) | 0 | 0 | 0 |
| <i>Homalothecium fulgescens</i> | Hofu, hf | 80.9 (ABU) | 85.1 (ABU) | 85.1 (ABU) | 3.5 | 13.1 | 3.7 |
| <i>Homalothecium nuttallii</i> | Honu, hn | 74.5 (ABU) | 51.1 (ABU) | 59.6 (ABU) | 1.9 | 4.7 | 2.5 |
| <i>Hypnum subimponens</i> | Hysu, hs | 14.9 (COM) | 8.5 (RAR) | 8.5 (RAR) | 0.02 | 0.1 | 4.4 |
| <i>Isothecium myosuroides</i> | Ismy, im | 17.0 (COM) | 29.8 (COM) | 17 (COM) | 0.1 | 0.3 | 3.7 |
| <i>Metaneckera menziesii</i> | Meme, mm | 2.1 (RAR) | 0 (ABS) | 4.3 (RAR) | 0.0 | 0.1 | Undefined |
| <i>Neckera douglassii</i> | Nedo, nd | 89.4 (ABU) | 70.2 (ABU) | 80.9 (ABU) | 0.4 | 3.4 | 7.6 |
| <i>Orthotrichum lyellii</i> | Orly, ol | 93.6 (ABU) | 48.9 (COM) | 53.2 (ABU) | 0.2 | 0.4 | 2.1 |
| <i>Porella navicularis</i> | Pona, pn | 95.7 (ABU) | 85.1 (ABU) | 83.0 (ABU) | 1.3 | 3.9 | 2.9 |
| <i>Porella roellii</i> | Porol, pr | 2.1 (RAR) | 4.3 (RAR) | 4.3 (RAR) | 0.1 | 0.1 | 2.5 |
| <i>Plagiomnium venustum</i> | Plve, pv | 19.1 (COM) | 19.1 (COM) | 17.0 (COM) | 0.2 | 0.4 | 2.1 |

Note: Total cylindrat area is 33 788 cm².

*Frequency classes are given in parenthesis. ABS, absent; RAR, rare (<10%); COM, common (10–50%); ABU, abundant (>50%).

Table 2. *R*-squared values and significance levels for relationships between substrate characteristics and (A) bryophyte abundance and (B) species richness of bryophytes in original and recolonizing samples.

| | Branch characteristics | | |
|-----------------------------|------------------------|------------|-----------|
| | Diameter | Height | Angle |
| A. Abundance. | | | |
| Original sample | 0.33** (+) | 0.25** (–) | 0.03 |
| Recolonizing sample | 0.07* (+) | 0.05 | 0.01 |
| B. Species richness. | | | |
| Original sample | 0.37** (+) | 0.23** (–) | 0.08* (+) |
| Recolonizing sample | 0.15** (+) | 0.01 | 0.01 |

Note: *, 0.05 level of significance; **, 0.01 level of significance; (+), positive relationship; (–), negative relationship. See Table 1 for bryophyte abbreviations.

ficiently distributed to impart the pattern to colonizing bryophytes when species is disregarded. Table 3 shows the remaining statistics. In 1999, the pattern no longer held, though the average proportion of the proximal to total cover remained similar for bryophytes without regard to species. In this recensus, *Homalothecium nuttallii* no longer showed the predominance of growth in the proximal region, and *Porella navicularis* showed a greater proportion (68%) of growth in the distal region.

On average, recolonization of dorsal surfaces significantly exceeded that of ventral surfaces in cylindrats, accounting for an average 63% of cover in both recensuses ($p < 0.001$). More regrowth occurred on the dorsal than on the ventral branch surfaces for *Homalothecium fulgescens*, *Isothecium myosuroides*, and *Plagiomnium venustum* in 1997; in 1999, *Orthotrichum lyellii* also showed this pattern (Table 4).

Dynamics of succession

Relationships between the original sample and the recolonizing sample

Gamma diversity decreased by two species in the recolonizing sample. The species that were absent in the 1997 sam-

ple (*Claopodium crispifolium* and *Metaneckera menziesii*) were rare in the original sample; of these, only *C. crispifolium* remained absent in 1999. *Hypnum subimponens* and *O. lyellii* declined by one class for the 1997 census (common to rare and abundant to common, respectively; Table 1) but had recovered in 1999. Mean α diversity had decreased from 5.2 to 4.1 species per cylindrat in 1997, and remained at this level in 1999 (paired *t* tests, $p < 0.001$).

However, β diversity increased slightly in the three consecutive samples, from 2.3 to 2.4 to 2.7. This resulted from the decreases in mean α diversity without a commensurate loss in γ diversity, and then from the increase in γ diversity in 1999. No significant change in the relative abundances of species in cylindrats occurred between the original sample and the 1997 census. Cylindrat species richness in the 1997 census was significantly related to species richness in the same cylindrat of the original sample (Spearman correlation, $R = 0.51$), i.e., a cylindrat with high species richness in the original sample tended to have high species richness in the recolonizing sample.

Modes of recolonization

Original and recolonizing samples included both tuft-forming (acrocarpous) and carpet-forming (pleurocarpous) bryophytes, all of which are capable of attaching directly to the bare bark substrate. Recolonization in the cleared cylindrats occurred primarily by encroachment from their margins. The majority of species under study were pleurocarps that were strongly attached to the bark substrate by rhizoids, and appeared to exhibit the “colonizer” life strategy (sensu During 1979), growing laterally rapidly but presumably requiring greater ambient humidity than acrocarpous (Lloret 1994). This strategy favors encroachment over dispersal and propagation (sensu Frego 1996).

Overall, encroachment accounted for 75.2% of recolonization (6.15% cover), with growth from residual particles, dispersed fragments, and (or) propagules accounting for the remaining 24.8% (2.06% cover). When estimated cover from encroachment was compared with that from propagules on a cylindrat-by-cylindrat basis, the encroachment estimate was

Table 3. Average percent covers \times/\div standard deviation by cylindrat for all bryophytes and by each species taken separately in the cylindrats where they occurred.

| Species | 1997 | | | 1999 | | |
|---------|----------|--------------------------------------|-------------|----------|--------------------------------------|-------------|
| | <i>n</i> | Mean % cover in inhabited cylindrats | Range | <i>n</i> | Mean % cover in inhabited cylindrats | Range |
| All | 60 | 5.72 \times/\div 1.84 | 0.48–21.14 | 47 | 20.20 \times/\div 2.37 | 1.42–72.38 |
| ac | 3 | 0.05 \times/\div 2.68 | 0.02–0.14 | 2 | 1.35 | 0.23–8.18 |
| hf | 51 | 1.54 \times/\div 6.81 | 0.001–20.30 | 40 | 7.86 \times/\div 4.11 | 0.24–65.78 |
| hn | 29 | 0.54 \times/\div 8.57 | 0–15.87 | 28 | 2.98 \times/\div 3.76 | 0.05–20.08 |
| hs | 5 | 0.07 \times/\div 9.96 | 0.001–0.56 | 4 | 0.37 \times/\div 2.89 | 0.08–0.80 |
| im | 17 | 0.14 \times/\div 3.55 | 0.003–0.68 | 8 | 1.17 \times/\div 2.13 | 0.35–3.07 |
| mm | 0 | 0 | 0 | 2 | 0.24 | 0.01–3.83 |
| nd | 41 | 0.27 \times/\div 4.89 | 0.01–3.54 | 38 | 1.41 \times/\div 6.05 | 0.005–44.59 |
| ol | 30 | 0.24 \times/\div 5.17 | 0.004–3.49 | 25 | 0.35 \times/\div 4.34 | 0.03–7.02 |
| pn | 53 | 1.09 \times/\div 3.22 | 0.02–7.88 | 39 | 2.05 \times/\div 4.46 | 0.09–37.65 |
| pr | 2 | 0.49 | 0.13–1.93 | 2 | 1.54 | 0.49–4.86 |
| pv | 12 | 0.33 \times/\div 3.91 | 0.05–5.11 | 8 | 0.74 \times/\div 6.11 | 0.03–10.05 |

Note: Means were obtained by log transformation of data and backtransformation of the mean. See Table 1 for bryophyte abbreviations.

Table 4. Average proportion of cylindrat cover accounted for by growth in the proximal or dorsal regions or estimated to result from encroachment for all bryophytes and for each species.

| Species | 1997 | | | | 1999 | | |
|---------|----------|--|---------|--------------|----------|--|---------|
| | <i>n</i> | Mean proportion of cylindrat cover via | | | <i>n</i> | Mean proportion of cylindrat cover via | |
| | | Proximal | Dorsal | Encroachment | | Proximal | Dorsal |
| All | 60 | 0.58*** | 0.63*** | 0.85* | 47 | 0.52 | 0.64*** |
| ac | 3 | 0.66 | 0.33 | 1.00 | 2 | 1.00 | 0.98 |
| hf | 51 | 0.66*** | 0.74*** | 0.77*** | 40 | 0.67*** | 0.69*** |
| hn | 29 | 0.59*** | 0.56 | 0.89*** | 28 | 0.66 | 0.44 |
| hs | 5 | 0.53 | 0.56 | 0.25 | 4 | 0.42 | 0.85 |
| im | 17 | 0.32 | 0.75* | 0.73* | 8 | 0.39 | 0.83* |
| mm | 0 | 0 | 0 | 0 | 2 | 0.50 | 0.50 |
| nd | 41 | 0.48 | 0.44 | 0.91** | 38 | 0.48 | 0.51 |
| ol | 30 | 0.52 | 0.54 | 0.88*** | 25 | 0.48 | 0.77** |
| pn | 53 | 0.48 | 0.53 | 0.86*** | 39 | 0.32** | 0.57 |
| pr | 2 | 0 | 0.31 | 1.00 | 2 | 0.74 | 0.31 |
| pv | 12 | 0.61 | 0.77* | 0.91** | 8 | 0.64 | 0.89** |

Note: Significance values determined by paired comparisons of proximal vs. distal, dorsal vs. ventral, and encroachment vs. non-encroachment growth using a Wilcoxon paired-sample test. See Table 1 for bryophyte abbreviations. ***, significant at the 0.001 level; **, significant at the 0.01 level; *, significant at the 0.05 level.

always the larger when analysis was made possible by sufficient sample size (Table 4).

The appearance of “newcomer” species (i.e., those not found in the original sample of the same cylindrat) was a relatively rare occurrence. No more than one new species appeared on the non-encroachment zone of any cylindrat, and no more than two on any whole cylindrat. The location of nearly all of the newcomer species was in the encroachment zone (Fig. 2). The total number of newcomer species in the non-encroachment zone relative to the total area of the zone was 0.18 events·dm⁻² of substrate area. In every case, the new arrival was *I. myosuroides*, a ubiquitous species that occurs on many substrate types, including rocks and other abiotic surfaces. Total cover from newcomer species in the non-encroachment zones was 0.013%.

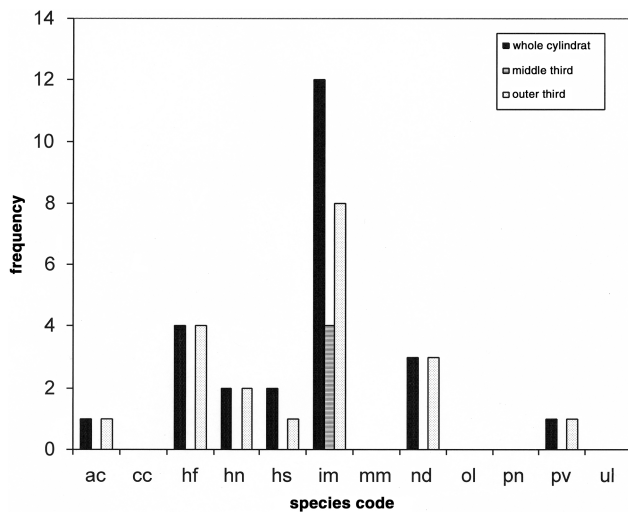
From these values, we can estimate minimum and maximum amounts of recolonization contributed by aerial recolonization relative to the total amount of recolonization. The maximum

value (24.8% of the total recolonizing cover) is equal to the percentage of recolonization from non-encroachment and assumes that none of the measured growth in the non-encroachment zone was from growth of residual fragments. The minimum value (0.15% of the total recolonizing cover), is equal to the percentage of total cover from newcomer species in the non-encroachment zone, and assumes that all recolonization by non-newcomers resulted from growth of residual fragments.

Discussion

The abundance of the epiphytes measured in the original sample lies within the range of previously reported values for epiphyte biomass on *A. macrophyllum* trees in the Pacific Northwest. As expected, it fell below the biomass of heavily loaded trees in old-growth temperate rainforests of the Olympic Peninsula (11.6 g·dm⁻², Nadkarni 1984) but above

Fig. 2. Frequency of occurrence of newcomer species (those present in the recolonizing sample that were not present in the original sample of a given cylindrat) by location within the different cylindrat zones. Species codes are given in Table 1.



that reported as “harvestable bryophytes” on trees in the Cascade Mountains ($157.4 \text{ g}\cdot\text{m}^{-1}$ or $1.457 \text{ g}\cdot\text{dm}^{-2}$ based on the mean surface area of stems; Peck 1997b). We found no comparable data on amount of colonization following perturbation of bryophytes on bigleaf maple trees.

Our findings on the relationships between both overall bryophyte abundance and diversity and substrate characteristics (diameter and relative height in tree) matched the associations reported in the literature (e.g., Trynoski and Glime 1982; McCune 1993; Peck 1997b). These relationships presumably result from the correlations between these variables and moisture availability gradients and substrate age (Hosokawa et al. 1964; Hoffman and Kazmierski 1969; Hoffman 1971; Studlar 1982).

Our results provide some evidence of specialization in reproductive or ecological niche at a smaller spatial scale. Specifically, some species appear to prefer dorsal branch surfaces, while other, often closely related and similarly abundant, species showed no such preference (Table 4). Another case was the predominance of encroachment from the proximal end of the cylindrat in some cases and from the distal end in others. Further study is needed to determine whether this is the consequence of differences in response to the disturbance, or to differences in distribution prior to the disturbance. The other case of apparent niche specialization was that of the branch tip specialists in the genus *Orthotrichum*, which are more often found higher in the canopy, where their superior capacity for water retention likely makes them better suited for establishment than the other, mostly pleurocarpous, species (Lloret 1994).

However, our results also provide evidence that capabilities for dispersal and establishment may be limiting for many of the species studied, such that the first few years of recolonization involve mostly recovery by remaining plants rather than species turnover owing to an abundance of newcomers. In this census, we could not distinguish among the three types of non-encroachment recolonization (growth from residual bryophytes, colonization by microscopic diaspores,

or colonization by larger plant fragments). However, the high conservation of original species in the non-encroachment zone (suggesting a residual or local source for recolonizing bryophytes) and the rarity of newcomer species in this zone ($0.18 \text{ events}\cdot\text{dm}^{-2}$ over 1 year, always *I. myosuroides*, Fig. 2) support the hypothesis that the successful establishment of colonizing epiphytic bryophytes in this system by aerial propagation or dispersal is infrequent. De novo aerial colonization must occur at some rate for new trees to be colonized or for new colonies to be formed, and clearly is a more important mechanism for some species, such as tuft-forming acrocarps. However, over time scales of a few years in the lower canopy, the mere presence of available substrate does not appear to be sufficient to allow increases in local diversity by aerial colonization.

These conclusions concur with recent research that suggests that rates of successful dispersal and colony establishment by spores or gemmae of many bryophytes are quite small in the field, reflecting infrequent sporophyte production and low establishment rates (van Tooren et al. 1990; Herben et al. 1991; Økland 1995; Frego 1996). Successful aerial dispersal is probably even more rare, and stochastic, in epiphytic than in terrestrial bryophytes owing to the additional requirement of interception and retention by an appropriate branch surface. According to a recent model addressing the possibility of dispersal limitation, very unlikely and highly variable establishment probabilities are required for a species to survive for many generations with a dispersal-limited distribution (Herben et al. 1991).

In terrestrial studies, colony establishment is often considered to be the domain of spores, owing to their greater distances of dispersal (Miles and Longton 1990; van Tooren et al. 1990; Herben et al. 1991; Økland 1995; Frego 1996), but further study is needed to clarify to what extent this principle applies to epiphytic bryophytes. Even a short horizontal displacement might carry the larger asexual diaspores far from the source plant on air currents, and their superior capacity for establishment on bare substrates (Kimmerer 1991) might make them well-suited for colony establishment on trees.

Many studies of bryophyte communities in other habitats (all terrestrial) have documented a generally large impact of disturbance on bryophyte ecology (e.g., Kimmerer and Allen 1982). However, our results do not suggest that disturbance is important in maintaining bryophyte diversity at least at this early successional stage. Furthermore, the substrates made available by disturbance did not appear to differ substantially from other uncolonized tree surfaces created by tree growth. Alpha diversity and gamma diversity both decreased slightly with disturbance, with no change in cylindrat species compositions.

Disturbances at a larger scale than those created in this study could be expected to lead to slower recovery of both biomass and species diversity, since recolonization of bare substrate by airborne diaspores or residual plant parts appears to be slow. This suggests that smaller human-induced disturbances (e.g., stripping more numerous small patches rather than a few large patches in harvesting for the florist trade) may be more easily mitigated. Long-term studies of epiphyte recolonization, as well as experimental studies of

epiphytic bryophyte reproductive ecology, are necessary to develop a useful understanding of these dynamic systems.

Acknowledgments

This project was initiated with Amy Shippy as a Partners in Science Program, funded by the Murdock Foundation. We thank Don Solick, Matt Denton, and Betsy Lyons for help in the field and the laboratory. The manuscript was much improved by comments from W.B. Schofield and Bruce McCune. Funds were provided by The Evergreen State College Faculty Sponsored Research, the National Science Foundation (Long-term Studies Program (DEB 96-15341), Database Activities Program (BIR 96-30316 and BIR 99-75510), and Ecology Program (DEB 99-74035)). Rip Heminway, James Gutholm, and the Computer Applications Laboratory provided excellent computer facilities. We thank Judith Harpel for moss identification and Dan Norris for liverwort identification.

References

- Benzing, D.H. 1995. Vascular epiphytes. *In* Forest canopies. Edited by M.D. Lowman and N.M. Nadkarni. Academic Press, San Diego, Calif. pp. 225–254.
- Dudgeon, W. 1923. Succession of epiphytes in the *Quercus incana* forest at Landour, western Himalayas. *J. Indian Bot. Soc.* **3**: 270–272.
- During, H.J. 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia*, **5**: 2–17.
- During, H.J., and van Tooren, B.F. 1986. Recent developments in bryophyte population ecology. *Trends Ecol. Evol.* **2**: 89–93.
- Franklin, J.F., and Dyrness, C.T. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Ore.
- Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. *Can. J. Bot.* **74**: 1937–1942.
- Gentry, A., and Dodson, C. 1987. The contribution of non-trees to tropical forest species richness. *Biotropica*, **19**: 145–156.
- Herben, R., Rydin, H., and Söderstrom, L. 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthotrichum lineare*: a spatial simulation model. *Oikos*, **60**: 215–221.
- Hoffman, G.R. 1971. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington II. Diversity of the vegetation. *Bryologist*, **74**: 413–427.
- Hoffman, G.R., and Kazmierzki, R.G. 1969. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. I. A description of the vegetation. *Bryologist*, **72**: 1–19.
- Hosokawa, T., Odani, N., and Tagawa, H. 1964. Causality of the distribution of corticolous species in the forests with special reference to the physioecological approach. *Bryologist*, **67**: 396–411.
- Ingram, S.W., and Nadkarni, N.M. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. *Biotropica*, **25**: 370–383.
- Jonsson, B.G., and Esseen, P.A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J. Ecol.* **78**: 924–936.
- Kimmerer, R.W. 1991. Reproductive ecology of *Tetraphis pellucida* II. Differential success of sexual and asexual propagules. *Bryologist*, **94**: 255–260.
- Kimmerer, R.W., and Allen, T.F.H. 1982. The role of disturbance in the pattern of a riparian bryophyte community. *Am. Midl. Nat.* **107**: 370–383.
- Lloret, F. 1988. Estrategias de vida y formas de vida en briófitos del pirineo oriental (España). *Cryptogam. Bryol. Lichenol.* **9**: 189–217.
- Lloret, F. 1994. Gap colonization by mosses on a forest floor: an experimental approach. *Lindbergia*, **19**: 122–128.
- Matelson, T.M., Nadkarni, N.M., and Longino, J.T. 1993. Longevity of fallen epiphytes in a neotropical montane forest. *Ecology*, **74**: 265–269.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga* – *Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, **96**: 405–411.
- Mishler, B.D., and Newton, A.E. 1988. Influences of mature plants and desiccation on germination of spores and gametophytic fragments of *Tortula*. *J. Bryol.* **15**: 327–342.
- Miles, C.J., and Longton, R.E. 1990. The role of spores in reproduction in mosses. *Bot. J. Linn. Soc.* **104**: 149–173.
- Nadkarni, N.M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science (Washington, D.C.)*, **213**: 1024–1025.
- Nadkarni, N.M. 1984. Biomass and mineral capital of epiphytes in an *Acer macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. *Can. J. Bot.* **62**: 2223–2228.
- Nadkarni, N.M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Am. Zool.* **34**: 70–78.
- Nadkarni, N.M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica*, **32**: 358–363.
- Nadkarni, N.M., and Matelson, T.J. 1988. Bird use of epiphyte resources in neotropical trees. *Condor*, **91**: 891–907.
- Økland, R.H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. *J. Ecol.* **83**: 697–712.
- Peck, J.E. 1997a. Commercial moss harvest in northwestern Oregon: describing the epiphyte communities. *Northwest Sci.* **71**: 186–195.
- Peck, J.E. 1997b. The association of commercially harvestable bryophytes and their host species in northwestern Oregon. *Bryologist*, **100**: 383–393.
- Peck, J.E. 1998. Commercial moss harvest in northwestern Oregon: biomass and accumulation of epiphytes. *Biol. Conserv.* **86**: 299–305.
- Peck, J.E., Hong, W.S., and McCune, B. 1995. Diversity of epiphytic bryophytes on three host tree species, thermal meadow, Hotsprings Island, Queen Charlotte Islands, Canada. *Bryologist*, **98**: 123–128.
- Pike, L.H. 1971. The role of epiphytic lichens and mosses in production and nutrient cycling in an oak forest. Ph.D. thesis, University of Oregon, Eugene, Ore.
- Pike, L.H. 1978. The importance of epiphytic lichens in mineral cycling. *Bryologist*, **81**: 247–257.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., and Ruchty, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* **10**: 789–799.
- Slack, N.G. 1990. Bryophytes and ecological niche theory. *Bot. J. Linn. Soc.* **104**: 187–213.
- Stone, D.F. 1989. Epiphyte succession of *Quercus garryana* branches in the Willamette Valley of Western Oregon. *Bryologist*, **92**: 81–94.
- Studlar, S. 1982. Succession of epiphytic bryophytes near Mountain Lake, Virginia. *Bryologist*, **85**: 51–63.
- Trynoski, S.E., and Glime, J.M. 1982. Direction and height of bryophytes on four species of northern trees. *Bryologist*, **85**: 281–300.

- Van Tooren, B.F., Odé, B., During, H.J., and Bobbink, R. 1990. Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. *Lindbergia*, **16**: 153–160.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*, **21**: 213–251.
- Wolf, J.H.D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, **112**: 15–28.