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# Bryophytes in old-growth forests of western Massachusetts<sup>1</sup>

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COOPER-ELLIS, SARAH (Department of Biological Sciences, Smith College, Northampton, Massachusetts 01366). Bryophytes in old-growth forests of Western Massachusetts. *Bull. Torrey Bot. Soc.* 125:117–132. 1998—Old-growth forests constitute rare habitat that may support rare bryophytes (mosses and liverworts) or provide refugia for populations once more widely distributed. This study was undertaken to determine what differences, if any, can be found between the bryophyte flora of old-growth and nearby second-growth forest sites matched for elevation, slope, aspect, and forest type. Bryophytes were censused on trees, logs, rocks and exposed soil in four western Massachusetts old-growth stands and in four second-growth stands. Ninety-one bryophyte species were identified; the majority of species were sparsely distributed. Several species either occurred only in old-growth or were most abundant in old-growth, although no species was strictly associated with old-growth. The total number of species on trees in old-growth is nearly twice that of species on trees in second-growth, and *Acer saccharum* in old-growth hosted more bryophyte species than *Acer saccharum* of same diameter in second-growth. Abundances of substrate available for bryophyte colonization were similar in old-growth and second-growth. Although old-growth and second-growth plots had similar bryophyte floras, there may be important differences in habitat provided by these forest types, and some less common species may be slow to recolonize cleared areas.

Key words: Bryophytes, old-growth.

“Old-growth” forest has been of increasing interest in recent years as researchers attempt to understand the dynamics of the few temperate forest ecosystems that have been relatively untouched by humans. As conservation biologists recognize the importance of rare habitats such as those represented by old, undisturbed forest ecosystems, the need for documentation of poorly known organisms such as bryophytes within these habitats becomes more apparent.

Bryophytes evolve and speciate slowly and are thought to occupy microhabitats more conservative over geologic time than the macrohabitats influencing vascular plants (Mishler 1988). Because of these differences, bryophytes may provide important information about climate and habitat change. Species diversity of bryophytes is high in temperate forests (Andrus 1990), although abundances may be greater in other biome types. Dispersal of many bryophyte species is limited, and gene flow between populations is often restricted (Wyatt 1982). Although old-growth forests may contain critical source populations, little is known about the re-

lationship between forest disturbance history and bryophyte species diversity.

Attempts to define old-growth forest have generated considerable discussion in the ecological literature about the nature of forest ecosystem processes and the importance of human influences on shaping forest ecosystems. The terms “virgin” and “primeval” have generally been applied to forests in eastern North America that have not been subject to the intensive management practices of European settlers, including timber harvesting, cultivation, and grazing of livestock (Cronon 1983). The resulting regional deforestations profoundly changed environmental conditions at ground level, warming and drying the soil, and the composition of forests that regenerated after these disturbances reflected these changes as well as species-specific responses to disturbance (Cronon 1983). Because of these broad-scale human-induced changes as well as more subtle forces such as suppression of fire, introduction of pathogens, and changes in air quality resulting from industrialization, it would be difficult to characterize any forest area in the eastern United States as virgin or primeval. Nonetheless, while old-growth forests are not necessarily typical of the forest landscape existing before European settlement, they represent our best examples of mature forest ecosystems that have developed over a long period of time free of large-scale disturbance.

Recent efforts have attempted to determine the extent of forest area remaining in the eastern

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United States that might be considered old-growth (Nowacki and Trianosky 1993). Estimates of remaining old-growth forest in the Northeast vary, with the most extensive stands probably in the Adirondacks of New York (Leopold et al. 1988). Maine, New Hampshire and Vermont also have areas that may qualify as old-growth (Maine Critical Areas Program 1983; Carbonneau 1986; Cogbill pers. comm.). In Massachusetts, fourteen sites containing 143.2 hectares of old-growth forest had been identified by 1994, representing less than 0.1% of the forested area of the region (Dunwiddie 1991). Old-growth criteria proposed by Dunwiddie (1991) based on Cogbill (1982) serve as a reasonable working definition for old-growth throughout the Northeast.

According to Dunwiddie (1991), old-growth forest must have:

- 1) A minimum size homogeneous area (at least 4–5 ha) to continuously support a forest stand.
- 2) Dominant trees of an age >50% of the maximum age for those species, with at least some individuals approaching the average life expectancy for the species on each site.
- 3) Minimal evidence of human influence, or other catastrophic disturbance of the stand, and
- 4) Evidence of regeneration, especially of late-successional species, resulting in a relatively stable forest composition.

The fragments of old-growth forest that remain in Massachusetts are relatively inaccessible and include some of the most rugged terrain found in the state.

Although studies in Europe and the western United States have examined bryophyte floras of old-growth forests and found that there are species that appear to prefer older forests (Edwards 1986; Gustafsson et al. 1992; Norris 1987; Lesica et al. 1991), the composition of bryophyte floras in forests of different ages in northeastern North America, particularly in New England, are poorly known. I undertook this study with the following goals:

- 1) to characterize the bryophyte flora of old-growth forests in western Massachusetts.
- 2) to identify species that are restricted to old-growth forests or that achieve maximum abundance in old-growth forests.
- 3) to compare the bryophyte species composition in old-growth and second-growth forests

that have similar environmental characteristics.

- 4) to determine bryophyte substrate availability in old-growth versus second-growth stands.
- 5) to identify species associated with each substrate type.
- 6) to determine the degree to which availability of suitable substrate or environmental variables such as slope, aspect, and cover of vascular plants within individual sites determine species composition of bryophyte communities in forests.

**Materials and Methods.** **SITE SELECTION.** In 1992, Dunwiddie established 26 permanent 0.1 ha circular plots at 13 old-growth sites in western Massachusetts (Dunwiddie 1991, 1993). The number of plots at each site ranged from one to four. I selected seven of Dunwiddie's plots from four sites for detailed study on the basis of accessibility and dominance of hardwood trees in the overstory, since it appeared that the hardwood stands supported a richer bryophyte flora than conifer-dominated stands. Dunwiddie (1993) characterized five of these seven plots as sugar maple-beech-yellow birch and the remaining two as hemlock-yellow birch on the basis of guidelines of the Society of American Foresters (1940).

Second-growth stands were chosen adjacent to the old-growth sites to match the old-growth stands as closely as possible in elevation, slope, aspect, and forest type. All second-growth stands shared the following site characteristics:

- 1) A minimum size of 4–5 ha,
- 2) Dominant trees with diameters between 25 cm and 60 cm, and heights between 10 m and 20 m,
- 3) Plot boundaries at least 100 m from roads, powerlines, brooks or clearings,
- 4) Evidence of human influence in the immediate area,
- 5) Overstory trees including the same species found in old-growth sites,
- 6) Early-successional species also in the overstory or in the immediate surrounding area.

**SITE DESCRIPTIONS.** The four sampled sites occur in the northwest corner of Massachusetts. Table 1 lists sites and plots established by Dunwiddie and the second-growth plots chosen to compare with each of Dunwiddie's sites. Terminology for the old-growth sites and plots follows Dunwiddie (1993). Sampled old-growth plots and the corresponding second-growth plots

Table 1. Sites and 0.1 ha plots within each site studied. Old growth terminology follows Dunwiddie (1993). Second growth sites were chosen adjacent to old growth sites and contained one plot each. Old growth tree ages, densities and basal areas from Dunwiddie (1993). Second growth densities and basal areas from Urich (1994).

Site:	Cold River				Dunbar Brook				Fife Brook				Mt. Greylock	
	Old		Second		Old		Second		Old		Second		Old	Second
	CR1	CR2	CRSG	DB1	DB2	DBSG	FB1	FB2	FBSG	GK1	GKSG			
Elevation (m)	308	413	275	392	468	360	500	497	540	611	590			
Aspect (degrees)	360	30	32	58	46	12	190	190	195	340	335			
Slope (degrees)	32	45	25	28	26	30	17	10	10	45	22			
Forest type <sup>b</sup>	AS-FG-BA	TC-BA	BP-AS	AS-FG-BA	TC-BA	FG-BA	AS-FG-BA	AS-FG-BA	AS-BA	AS-FG-BA	AS-QR			
Height (m)	24-36	24-36	20	24-36	24-36	18	24-36	24-36	16	24-36	no data			
Tree ages (years)	154; 202	221; 272	no data	165; 219	321; 403	no data	158; 223	121; 247	no data	221; 222	no data			
Density (trees/ha)	190	330	599	370	320	460	390	320	776	370	481			
Basal area (m <sup>2</sup> /ha)	27.8	25.9	25.26	26.3	44.7	48.9	36	39.1	27.7	30.1	31.3			

<sup>a</sup> CR1 = Cold River Plot 1, CR2 = Cold River Plot 2, CRSG = Cold River Second Growth, DB1 = Dunbar Brook Plot 1, DB2 = Dunbar Brook Plot 2, DBSG = Dunbar Brook Second Growth, FB1 = Fife Brook Plot 1, FB2 = Fife Brook Second-Growth, GK2 = Mt. Greylock Plot 2, GKSG = Greylock Second-Growth.

<sup>b</sup> AS = *Acer saccharum*, BA = *Betula alleghaniensis*, BP = *B. papyrifera*, FA = *Fagus grandifolia*, QR = *Quercus rubra*, TC = *Tsuga canadensis*.

occur at four sites, Fife Brook and Dunbar Brook in the upper Deerfield River watershed, Cold River A in the Cold River watershed, and Greylock-Money Brook in the Mt. Greylock State Reservation, at elevations ranging from 300 m to 660 m. Soils are well-drained sandy loams formed in glacial till derived primarily from gneiss and schist, with pockets of moisture seepage. Climate of the region is continental with July temperatures averaging ~22°C and January temperatures ~-5°C (Freeman and Natusi 1994). Annual precipitation averages approximately 110 cm distributed fairly evenly throughout the year. Old-growth stands range in extent from 7.6 ha to 13.1 ha. Cold River (CR), Dunbar Brook (DB), and Greylock (GK) sites face northeast to northwest on slopes of 26-45 degrees, while the Fife Brook site occurs on a southwest-facing slope of 10-20 degrees. Dominant trees are *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Fraxinus americana* and *Tsuga canadensis*. Tree heights range from 24 m to 36 m. Most of the sites contain large boulders and uneven topography. Works Progress Administration Land Utilization maps indicate that all sites except for Fife Brook second-growth (FBSG) were forested in the early 1930's. FBSG was an open hayfield at that time.

FIELD SAMPLING. In order to determine the amount of available bryophyte substrate, the proportion of the plot area covered by decaying wood, rocks, and exposed soil was estimated using a line-intercept method (Mueller-Dombois and Ellenberg 1974). The circular plot centers were marked, and plots were divided into quarters by establishing four 17.84 m cardinal radii from the plot center with meter tapes. The length along each radius of each intersected unit of rock, piece of decaying wood, or exposed soil patch greater than 5 cm diameter was recorded. Tree surface available for bryophyte colonization was not measured.

The plots occurred on steep and uneven terrain, and substrate suitable for bryophytes was relatively sparse and unevenly distributed. Therefore random sampling would have been neither feasible nor efficient (see McCune and Lesica 1992 for a discussion of "the trade-off between species capture and quantitative accuracy" in sampling bryophytes). However, in order to ensure that sampled bryophyte stands were distributed throughout the plot and that their selection was systematic, the following methods were used. On each plot, eight sam-

pling points were established, one at 6 m and one at 12 m from the plot center along the four cardinal radii. In each quarter of the plot moving clockwise from each radius, the tree, rock, log, and soil patch nearest to the 6 m and 12 m points which supported bryophytes was sampled. No substrate was sampled twice (i.e., if it was the closest substrate patch to both the 6 m and 12 m points.)

Flexible grid quadrats (10 cm × 20 cm) were located on substrates as follows:

*Trees.* Four quadrats were sampled on each tree. Quadrats were centered on the north and south faces of the trunk of the tree at breast height and on the north and south faces of the base of the tree. Trees with bryophytes were identified and their diameters recorded.

*Decaying Wood.* One quadrat was centered on the upper surface of the log or stump on the patch of bryophytes closest to the sampling line. Logs that were large enough to support bryophytes on their sides were sampled with an additional quadrat.

*Rocks.* One quadrat was centered on the upper surface of each rock. Rocks that were large enough to support bryophytes on their sides were sampled with an additional quadrat.

*Soil.* One quadrat was centered on each soil patch.

When no tree, decaying wood, rock, or soil patch with bryophytes was found within the area available to be sampled from a sampling point, this was recorded as no suitable substrate. For each quadrat, percent cover of each bryophyte species was visually estimated within 12 cover classes as follows: 0–1%, 1–5%, 5–15%, 15–25%, 25–35%, 35–45%, 45–55%, 55–65%, 65–75%, 75–85%, 85–95%, 95–100%. In addition, reconnaissance of the entire plot was made in order to determine a complete list of bryophytes present. A specimen of each bryophyte species encountered in the sampling and during whole plot reconnaissance was collected for laboratory identification.

Identification of bryophytes follows Crum and Anderson (1981) for mosses and Crum (1991) for liverworts. Nomenclature follows the List of the Mosses of North America North of Mexico (Anderson et al. 1990) for mosses and Crum (1991) for liverworts. Although mature perianths of both *Porella platyphylla* and *Porella platyphylloidea* were found during sampling, for the purposes of ecological comparisons, all *Porella* specimens are treated as one taxonomic unit. Voucher specimens were deposited at the

Farlow Herbarium, Harvard University, Cambridge, Massachusetts.

**ANALYSIS.** Means of substrate abundances for old-growth and second-growth plots were compared with a Kruskal-Wallis non-parametric one-way ANOVA (SYSTAT6.0). I considered differences among means large enough for meaningful comparison if  $p$ -values were  $<0.1$ .

Species richness was measured in the following ways:

- 1) Total number of species on each plot.
- 2) Average number of species per quadrat for the plot: All occurrences of all species in all quadrats on the plot ÷ total number of quadrats on the plot.
- 3) Average number of species per quadrat on substrate  $y$ : All occurrences of all species in all quadrats on substrate  $y$  ÷ total number of quadrats on substrate  $y$ .

Means of species richness per plot on each substrate type in old-growth versus second-growth were tested by a Kruskal-Wallis test with a significance level of  $P < 0.1$ .

To determine whether some species are associated with either old-growth or second-growth forest, a subset of 19 bryophyte species was selected for comparison on the basis of the following measures of importance: only species occurring on at least three plots in either old-growth or second-growth, and ranking among the five most important species on at least one plot (importance = absolute frequency + absolute cover) were included. Mean importance values for old- and second-growth plots were tested by the Kruskal-Wallis test and resulting  $P$ -values were adjusted for multiple comparisons with a sequential Bonferroni test (Rice 1989). I considered effect size among means large enough for meaningful discussion if  $P$ -values were  $<0.1$ .

Sorensen's Coefficient of floristic similarity between species composition of old-growth and second-growth sites was calculated in the following way:

$$S = 2a/(2a + b + c),$$

where  $a$  = the number of species present in both old-growth and second-growth,  $b$  = the number of species present in second-growth and absent in old-growth,  $c$  = the number of species present in old-growth and absent in second-growth, and  $d$  = the number of species absent in both old-growth and second-growth (Sørensen 1948).

Lists of species occurring on each substrate in

old and second-growth were compiled for comparison of richness and substrate-specificity of floras in old and second-growth.

The relationship between diameters and species of host trees and number of bryophyte species supported was analyzed by plotting tree species and diameters against bryophyte species numbers in old and second-growth plots. Because *Acer saccharum* trees of comparable diameters appeared to support higher numbers of bryophyte species in old than in second-growth, an analysis of covariance was conducted using MINITAB Release 8 (1992) in which the number of species of bryophytes found on sampled trees was modeled as a linear function of the diameter of the trees on which they grew and as a categorical indicator for location of trees in old-versus second-growth forest. The data set included only trees with diameters between 10.5 and 40.5 cm.

Differences between the means of total amount of bryophyte cover on trees in old and second-growth were compared by the Kruskal-Wallis test with a critical level for significance of  $P < 0.1$ .

United States Department of Agriculture 1937 Works Progress Administration Land Utilization maps were consulted to determine land use categories designated for each site in the late 1930s.

**Results.** SUBSTRATE ABUNDANCE. Substrate abundances varied widely among plots but never represented more than 25% of any plot area (Table 2). Mean percentages of decaying wood were similar in old- and second-growth plots, although DB1 (old-growth) and DBSG had much higher percentages of dead wood than other plots, and both old- and second-growth contained plots with extremely low percentages of decaying wood. GK2 had the highest combined substrate values of all plots but less decaying wood than all but one other plot. The range of percentages of exposed soil was greater on old-growth plots than on second growth plots. The plots with the highest percentages of exposed soil, GK2 and CR2, represented the steepest plots in which the greatest extent of soil erosion takes place. Similarly, the amount of rock ranged much more widely on old-growth plots than on second-growth plots due to the presence of rock outcrops and exceptionally large boulders on some old-growth plots.

Table 2. Mean percentages of old-growth and second-growth plots occupied by decaying wood ("Wood"), rock and soil, with standard errors and  $P$ -values from a one-way nonparametric ANOVA (SYSTAT 6.0).

	Old-growth										2ND-growth				P	
	CR1	CR2	DB1	DB2	FB1	FB2	GK2	Mean	SE	CRSG	DBSG	FBSG	GKSG	Mean		SE
Wood	3.56	4.44	7.47	3.52	4.76	3.74	1.51	4.14	1.72	2.94	8.55	0.46	5.34	4.32	0.68	1.00
Rock	17.43	6.03	7.85	5.83	2.16	0.31	11.45	7.29	0.86	3.32	0.91	4.76	1.72	2.68	2.18	0.13
Soil	1.85	5.49	2.84	1.40	0.52	1.26	11.74	3.59	0.5	2.63	2.27	0.49	2.45	1.96	1.49	0.71

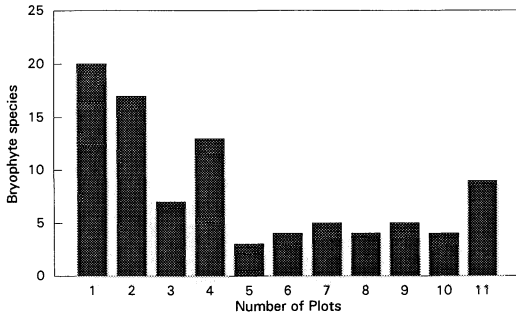


Fig. 1. Constancy of bryophyte species on the eleven plots, showing percentages of species occurring on each number of plots.

**SPECIES DISTRIBUTION.** Seventy-four moss and 17 liverwort species were identified (Appendix 1, Table 1). The majority of bryophyte species occurred infrequently (Fig. 1). Nearly 40% of species occurred on only one or two plots. Ten moss and three liverwort species were found only during whole-plot reconnaissance. Nineteen moss and five liverwort species occurred only on old-growth plots. Seven of these occurred at more than one site: the mosses *Brachythecium populeum*, *Dicranum fuscescens*, *Haplohymenium triste*, *Hypnum curvifolium*, *Lindbergia brachyptera*, and *Cyrto-hypnum minutulum*, and the liverwort *Scapania nemorea*. Five moss and two liverwort species occurred only on second-growth plots but only one of these, *Polytrichum*

*ohioense*, occurred at more than one site. These species may be more abundant in either old- or second-growth forest, however the number of plots examined and the infrequency of species occurrences precluded establishing statistical significance. Sorensen's Coefficient of similarity is  $S = 0.792$ , where 1 is complete identity between old-growth and second-growth, and 0 is no species in common.

Table 3 presents mean importance values for species that were more abundant on either old or second-growth plots. After adjusting for multiple comparisons, none of the species tested showed statistically different abundance in old-growth and second-growth plots. However, the Kruskal-Wallis test is conservative, especially when  $P$ -values were adjusted to avoid making a type one error. In addition, sample sizes were inevitably small because there are few old-growth hardwood sites. Although importance values tested do not meet criteria for statistical significance, they suggest that several species are more abundant in either old-growth or second-growth (*Anomodon attenuatus*, *Frullania eboracensis*, *Hypnum pallescens*, *Leskeella nervosa*, and *Plagiothecium cavifolium*).

**SPECIES RICHNESS.** Species richness was greater on tree trunks and tree bases in old-growth than in second-growth (Table 4). Tree trunks supported far fewer species than did tree bases.

Table 3. Mean importance of most abundant species in old-growth and second-growth plots. Species occur on at least half of old or second-growth plots, and are among the five most important species on at least one plot. Importance values are absolute frequency plus absolute cover.

Species	Old growth (N = 7)		2 <sup>ND</sup> growth (N = 4)		Kruskal-Wallis <i>P</i>	Bonferroni adjusted <i>P</i>
	Mean	SEM	Mean	SEM		
<i>Amblystegium varium</i>	7.92	2.38	4.11	3.00	0.30	0.96
<i>Anomodon attenuatus</i>	7.44	3.36	1.22	1.17	0.06	0.64
<i>Brachythecium acuminatum</i>	5.41	1.29	2.09	0.92	0.21	0.93
<i>Brachythecium reflexum</i>	5.08	2.42	5.55	2.19	0.45	0.98
<i>Bryhnia novae-angliae</i>	3.55	1.35	1.33	1.33	0.32	0.96
<i>Callicladium haldanianum</i>	4.85	0.92	9.79	3.2	0.19	0.93
<i>Dicranella heteromalla</i>	3.9	1.37	2.96	1.73	0.45	0.98
<i>Dicranum fulvum</i>	9.74	1.23	9.03	1.23	0.71	0.98
<i>Frullania eboracensis</i>	8.01	1.68	2.5	1.36	0.03	0.43
<i>Herzogiella striatella</i>	3.94	2.66	2.88	2.28	0.62	0.98
<i>Hypnum pallescens</i>	17.74	4.47	29.81	1.32	0.06	0.64
<i>Leskeella nervosa</i>	5.23	1.63	0.46	0.46	0.07	0.68
<i>Lophocolea heterophylla</i>	5.24	1.09	7.71	1.06	0.19	0.93
<i>Plagiomnium ciliare</i>	6.23	2.04	1.53	0.96	0.12	0.84
<i>Plagiomnium cuspidatum</i>	9.94	4.36	2.99	1.13	0.45	0.98
<i>Plagiothecium cavifolium</i>	10.36	3.26	2.21	0.36	0.04	0.50
<i>Plagiothecium laetum</i>	4.9	1.55	4.88	2.69	1.00	1.00
<i>Platygyrium repens</i>	12.53	3.27	17.33	6.16	0.57	0.98
<i>Thuidium delicatulum</i>	6.08	1.89	2.52	1.96	0.19	0.93

Table 4. Species richness. Means of species numbers per plot for old-growth and second-growth on each substrate type. *P*-values are from a Kruskal-Wallis one-way ANOVA (SYSTAT 6.0). Critical level for significance is  $P < 0.1$ .

	Old growth			2 <sup>ND</sup> growth			<i>P</i>
	Mean	SE	Range	Mean	SE	Range	
Tree trunk	4	0.62	1-6	2	0.71	0-3	0.055*
Tree base	13.4	0.81	10-16	8.8	1.71	4-12	0.022*
Dead wood	11.6	1.04	9-17	11.8	1.58	8-15	0.847
Rock	11.6	1.74	8-20	10.5	1.44	8-13	0.697
Soil	7.6	0.78	4-10	9	1.78	5-12	0.505

Tree trunks averaged twice as many species in old-growth than in second-growth, and this difference was significant at a level of  $P = 0.055$  (Table 4). Similarly, tree bases supported more bryophyte species in old-growth than second-growth. Although species richness on dead wood, rocks, and soil in old and second-growth were similar, the maximum number of species on rocks in an old-growth plot (DB1 = 20) exceeded the maximum number of species found on rocks in a second-growth plot (FBSG = 8).

**SPECIES-SUBSTRATE RELATIONSHIPS.** A total of 38 species were found on trees in old-growth (Table 5) as compared to 22 species found on trees in second-growth. The difference between these numbers may reflect higher numbers of plots sampled in old-growth than in second-growth. However, species richness per plot on trees was also higher in old-growth, and other substrate types supported similar numbers of species in old-growth and second-growth (Table 5). Nine species occurred on tree trunks in old-growth, and tree trunks hosted one species not found on the base of trees (*Orthotrichum sordidum*). Only three species occurred on tree trunks in second-growth. All species found on the trunk also occurred on the base in second-growth, and *Orthotrichum sordidum* did not occur at all in second-growth sampling, although it was found on a log in whole-plot reconnaissance of one second-growth plot. Ten species appeared to be associated with trees, i.e. they were found on trees only or on trees on at least three times as many plots as on any other substrate type (Table 5). An additional seven species appeared to be associated with trees and logs by these same criteria.

Numbers of species found on dead wood were slightly higher in old-growth than in second-growth. Seven species appeared to be associated with dead wood by the criteria stated above. The number of species found on rocks in old-growth and second-growth was identical, however, thir-

teen species were found on rocks in old-growth but not in second-growth, and thirteen species were found on rocks in second-growth but not in old-growth. Only four species showed an association to rocks. The number of species found on soil in old-growth was nearly identical to the number found on soil in second-growth, with seven found on soil in old-growth but not in second-growth, and nine found on soil in second-growth but not in old-growth. Five species occurred almost exclusively on soil. Seven species were generalists found on all four substrate types.

Bryophytes were sampled on five species of trees in old-growth and seven species in second-growth. *Acer saccharum* hosted nearly twice as many bryophyte species as any other species of host tree sampled. Trees sampled for bryophytes on old-growth plots had higher average diameters than those on second-growth plots. Only *Acer saccharum* was sampled in great enough numbers in both old-growth and second-growth to allow for comparison between trees of comparable diameters.

The model obtained from the analysis of covariance for number of bryophyte species as a function of *Acer saccharum* tree diameter and old-growth versus second-growth was:

$$\text{NO. OF SPECIES} = 0.425 + 0.0738 \\ \text{DIAMETER} + 1.41 \text{ OLD-GROWTH}$$

Both diameter and old-growth were significant predictor variables ( $R = 0.43$ ;  $P = 0.002$ ). The coefficient for DIAMETER can be interpreted to mean that for each one-centimeter increase in tree diameter, we would expect to find an additional .0738 species for trees in forests of the same age, or about one additional species for each increase in diameter of 10 centimeters. The coefficient of OLD-GROWTH means that we expect to find, on average, 1.41 more species on trees in old-growth forests than in second-growth forests when the tree diameters are the



Table 5. Species grouped by substrate affinities with numbers of old-growth and second-growth plots on which each occurs on each substrate. Species associated with a particular substrate occur only on that substrate and on more than one plot, or on at least three times as many plots on the associated substrate as on any other substrate. Groups are presented roughly in order of strength of association using the following criteria: 1) species occurs only on associated substrate and on at least 3 plots; 2) species occurs on at least three times as many plots on the associated substrate as on plots on any other substrate. Generalists occur on at least two plots on each substrate.

Species	Trees		Logs		Rocks		Soil	
	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>
<b>Trees</b>								
<i>Leskeela nervosa</i>	5	1						
<i>Metzgeria furcata</i>	4	2						
<i>Porella platyphylloidea</i>	2	1						
<i>Frullania eboracensis</i>	7	3	1					
<i>Ulotia crispa</i>	5	3	1	1				
<i>Radula complanata</i>	5						1	
<i>Anomodon attenuatus</i>	7				1	1		
<i>Amblystegium serpens</i>	1	1	1					
<i>Pterigynandrum filiforme</i>	2					1		
<i>Cyrto-hypnum minutulum</i>	2		1					
<b>Trees and logs</b>								
<i>Platygyrium repens</i>	6	4	3	3				
<i>Orthotrichum sordidum</i>	2		1					
<i>Lindbergia brachyptera</i>	1		1					
<i>Brachythecium digastrum</i>	1		1					
<i>Amblystegium varium</i>	5	2	3	2			1	
<i>Dicranum montanum</i>	2	3	2	2				1
<i>Brachythecium acuminatum</i>	5	1	6	3	1			
<b>Logs</b>								
<i>Brachythecium oxycladon</i>			2	1				
<i>Nowellia curvifolia</i>			2	1				
<i>Hypnum imponens</i>			4	1		1		
<i>Hypnum fertile</i>			2	3		1		
<i>Campylium hispidulum</i>	1		2	2				
<i>Dicranum flagellare</i>			1	1				
<i>Hypnum curvifolium</i>			2					
<b>Rocks</b>								
<i>Dicranum fulvum</i>					6	4	1	
<i>Paraleucobryum longifolium</i>	1	1			4	3		
<i>Grimmia apocarpa</i> var. <i>gracilis</i>					2			
<i>Trichostomum tenuirostre</i>					1	1		
<b>Soil</b>								
<i>Atrichum undulatum</i>							6	4
<i>Calypogeia fissa</i>							2	1
<i>Dicranella heteromalla</i>					2		6	2
<i>Atrichum angustatum</i>							2	
<i>Pohlia nutans</i>								2
<b>Generalists</b>								
<i>Hypnum pallescens</i>	5	4	6	4	7	4	1	2
<i>Plagiomnium cuspidatum</i>	4		5	3	2	1	3	
<i>Callicladium haldanianum</i>		3	4	3	4	3	2	2
<i>Lophocolea heterophylla</i>	4	2	6	4	3	2	2	1
<i>Plagiothecium cavifolium</i>	2		2	1	6	1	5	1
<i>Plagiothecium laetum</i>	3	2		2	6	1	4	2
<i>Plagiomnium ciliare</i>	1	1	3		5	1	3	1
<b>No pattern</b>								
<i>Brachythecium curtum</i>		1		1		1	1	1
<i>Brachythecium reflexum</i>	4	2	1	1	2	1		1
<i>Brachythecium rutabulum</i>	3	1	1	2	3	2		1
<i>Brotherella recurvans</i>			3		2		1	1
<i>Bryhnia novae-angliae</i>			2		3	1	2	1

Table 5. Continued.

Species	Trees		Logs		Rocks		Soil	
	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>	Old	2 <sup>ND</sup>
<i>Entodon cladorrhizans</i>			1			1		
<i>Eurhynchium pulchellum</i>	1				1			1
<i>Herzogiella striatella</i>	1	1	2		1		1	2
<i>Homalia trichomanoides</i>	1				1			
<i>Homomallium adnatum</i>	1	1			2			
<i>Isopterygium elegans</i>				1	2	1	2	3
<i>Jamesoniella autumnalis</i>	1		2		2	1		1
<i>Plagiochila porelloides</i>	1				2			1
<i>Plagiomnium medium</i>			1		1			
<i>Polytrichum formosum</i>					1		1	
<i>Polytrichum ohioense</i>				1		1		2
<i>Steerecleus serrulatus</i>		1		1		1	1	1
<i>Tetraphis pellucida</i>			1	1			2	1
<i>Thuidium delicatulum</i>	1		3	1	4	1	1	1
Only 1 occurrence								
<i>Bazzania trilobata</i>					1			
<i>Blepharostoma trichophyllum</i>						1		
<i>Brachythecium campestre</i>				1				
<i>Brachythecium populeum</i>	1							
<i>Brachythecium velutinum</i>								1
<i>Dicranum fuscescens</i>	1							
<i>Dicranum viride</i>	1							
<i>Fissidens cristatus</i>						1		
<i>Hedwigia ciliata</i>						1		
<i>Leucobryum glaucum</i>							1	
<i>Mnium stellare</i>						1		
<i>Pellia</i> sp.							1	
<i>Pylaisiella intricata</i>	1							
<i>Rhizomnium punctatum</i>						1		
<i>Scapania nemorea</i>					1			
<i>Ulota hutchinsiae</i>					1			
Totals	38	22	34	26	31	31	24	26

same. An analysis of the model's residuals suggested that the assumptions underlying linear model theory were satisfied in these data. The number of bryophyte species on *Acer saccharum* trees of varying diameters is indicated in Figure 2.

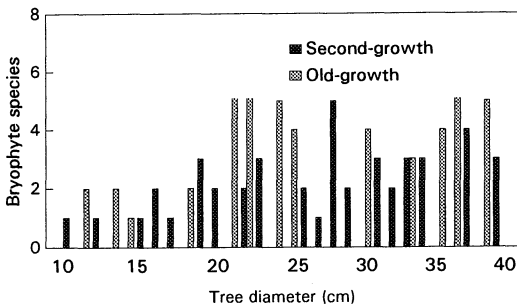


Fig. 2. Numbers of bryophyte species on sugar maples of varying diameters in old-growth and second-growth forest.

COVER. Mean total bryophyte cover in quadrats on tree trunks was generally low, and represented only  $\sim 1/10$  the cover found on tree bases. There were no significant differences between abundance of cover in old versus second-growth (Table 6).

**Discussion.** The majority of bryophyte species recorded are relatively infrequent, occurring on less than half the plots sampled. The bryophyte floras of old-growth and second-growth plots were found to be generally similar, with many more species occurring in both old-growth and second-growth than in only one or the other and a Sorensen's coefficient of floristic similarity approaching 80%. Among species that occurred on at least 50% of sampled plots, none were restricted to old-growth, and no species achieved statistically different mean importance in old-versus second-growth after adjusting for multiple comparisons. However, there are some im-

Table 6. Mean percentages of quadrat area per plot covered by bryophytes on each substrate sampled. *P*-values are from a Kruskal-Wallis one-way ANOVA (SYSTAT 6.0).

	Old growth			Second growth			<i>P</i>
	Mean	SEM	Range	Mean	SEM	Range	
Tree trunks	3.57	0.90	0.19–8.07	1.51	1.13	0–4.85	0.257
Tree bases	32.00	4.91	16.04–56.98	26.81	4.43	14.22–34.96	0.571
Logs	45.26	3.90	41.58–57.25	39.91	7.66	30.40–61.39	0.345
Rocks	64.73	2.35	57.80–74.78	63.39	4.41	52.77–73.85	0.571
Soil	44.39	7.07	23.26–66.08	31.54	9.00	7.01–50.20	0.257

portant differences in epiphytic species. A significantly higher number of species was found on trees in old-growth than on trees in second-growth, and several species apparently favor one forest type. Most of the species that are abundant or frequent in old-growth are epiphytes.

**SUBSTRATE.** No differences were found between amounts of substrate available for bryophyte colonization in old- and second-growth plots. Although several old-growth plots contained large amounts of rock, wood, or bare soil, high variability among plots resulted in means that were similar to means of substrate abundance in second-growth plots. This finding contrasts with much of the literature on old-growth that relies on quantity of dead wood as one structural characteristic differentiating old-growth from second-growth (Whitney 1987, Franklin and Spies 1991). Amount of surface area of dead wood may have been similar in old-growth and second-growth because the second-growth plots selected were "natural" stands rather than intensively managed woodlots. Since species richness is similar on logs, rocks, and soil in old-growth and second-growth, and since many species that are specific to these substrates are not more abundant in old-growth or second-growth, substrate quantity does not appear to explain any of the differences between old-growth and second-growth bryophyte floras. Since no attempt was made to quantify surface area of trees available for colonization, the question of whether differences in tree area available for colonization explains the higher number of epiphyte species in old-growth can not be addressed. However, since identical areas were sampled on trees in old- and second-growth, and placement of quadrats was strictly systematic, it seems unlikely that differences caused by amount of bark available for colonization would influence the quantitative sampling.

Differences were found between the epiphytic floras of old-growth and second-growth stands

in this study. Trees in second-growth forests hosted a very limited flora, even when their diameters equalled those of trees in old-growth forests that supported twice as many species. The majority of species with trends of greater abundance in old-growth are epiphytes. Five of the seven species that occurred only in old-growth and at more than one plot are strict epiphytes or occur on trees and logs, and the four species that appear to be more abundant in old-growth (although statistical significance was not established) include three strict epiphytes. Six epiphytes only occurring in old-growth were among the thirteen species that were found during whole-plot reconnaissance but not in quantitative sampling. Epiphytic species of interest include some that have been identified as typical of undisturbed forests in other studies (e.g. *Anomodon attenuatus* [Nichols 1913]; *Brachythecium populeum* [Nichols 1913, Rose 1992]; *Haplohymenium triste* [Nichols 1913]; *Homalia trichomanoides* [Rose 1992, Gustaffsson et al. 1992]).

**MICROCLIMATE.** Bark characteristics such as hydrogen ion concentration, roughness, and moisture-holding capacity are known to influence distribution of epiphytic bryophytes (Billings and Drew 1938). Slack (1976) found that epiphyte associations on host trees of the same age and species changed with differences in humidity, light, and topographical conditions. For example, *Tsuga canadensis*, which hosts very few bryophyte species in the northeastern United States, supports a richer flora in the southern Blue Ridge of the Appalachians where rainfall is higher and all tree species support higher numbers of epiphytes (Slack 1976). Hale (1955) described the gradual shifting of the optimal range of many bryophyte species from bases of trees up trunks along a gradient in forests from pioneer to late-successional forests. Similarly, McCune (1993), Peck et al. (1995) and others have described a moisture gradient associated

with tree position and forest age that affects composition of epiphyte communities including bryophytes, and Sillett (1995) found differences between epiphytes in old-growth forest interiors and those on the edges of clearcuts in western Oregon.

The fact that trees generally host more bryophyte species as they increase in diameter does not explain all observed differences in the richness of bryophyte flora between old-growth and second-growth. Trees of the same species and with equal diameters supported fewer species in second-growth plots than old-growth plots. Evidently, differences in epiphyte species composition reflect an interplay of factors involving bark characteristics and climate that together determine substrate suitability. It is important to note that trees of the same diameter can be of different ages depending on growing conditions. Old-growth trees may be generally older than trees of comparable diameter in second-growth, increasing the probability of their being colonized by bryophytes.

Microclimatic conditions unique to old-growth forest may be critical to creating substrate suitable for sensitive bryophyte species. The presence of large moist logs in Swedish virgin forests with a high and even humidity was found by Gustafsson and Hallingbäck (1988) to be essential for several rare species. These authors found that "suitable substrate" included not only the presence of logs of a particular size, but also conditions of steady high humidity and protection from the desiccating effects of wind and high light intensities. Although, as discussed above, logs do not appear to be responsible for differences between old-growth and second-growth bryophyte floras in this study, high humidity and protection from desiccation may explain differences in epiphytic floras in forests of western Massachusetts.

Important structural differences between old-growth and second-growth plots are the higher density of trees in second-growth and the substantially greater height of the canopy in old-growth. Densities and heights of trees influence the angle and intensity of light reaching bryophyte substrates and may be important in determining bryophyte species composition on plots. However, most species that occur in forests are not thought to be limited solely by light availability. Zonation on tree trunks is thought to be determined by increasing light intensity and decreasing atmospheric humidity towards the crown (Hosokawa et al. 1964). Species with the

highest light requirements, such as *Ulota crispa*, occur as high on the trunks of trees as the crown, while species that can not tolerate the desiccation accompanying high light levels are found on tree bases and on the forest floor. None of the species that occurred only or primarily in old-growth in this study were exclusively on tree trunks, and when these species did occur on second-growth plots, they were on tree bases or forest floor substrates. This suggests that moisture rather than light may limit these species.

**DISTURBANCE INTENSITY.** Edwards (1986) studied the occurrence of desiccation-sensitive bryophyte species in Welsh forests that had undergone some level of disturbance. She found that desiccation-sensitive species normally occurred under moist and shaded conditions and that species occurrence was more restricted to optimal substrate conditions in which forest canopy had been absent or open for an extended period rather than at sites where regeneration of the forest canopy was rapid. Only in optimal locations, including sites where open water in the form of brooks, rivers, waterfalls, and seeps was close by and where coarse-grained rock was available, could these desiccation-sensitive species survive prolonged canopy disturbance. Hence, an abundance of desiccation-sensitive species would suggest very little disturbance at a site.

Rose (1992) pointed out the importance of length of continuity of habitat for species with slow colonizing ability and the negative effects of exposure to desiccating winds and air pollution on epiphytic bryophytes and lichens. Rose's list of "ancient woodland bryophytes of lowland England" includes several species such as *Brachythecium populeum*, *Homalia trichomanoides*, and *Radula complanata* that occurred primarily or exclusively in old-growth in this study. Gustafsson et al. (1992) identified habitat factors important to desiccation-sensitive bryophytes and found that species such as *Homalia trichomanoides* were positively associated with stands of broad-leaved deciduous trees containing large old trees and many woody species on sloping terrain surrounded by other broadleaved deciduous stands. Desiccation-sensitive bryophytes were scarce near the edge of the forest. These studies emphasize the importance of intact, "permanent" forest habitat to continued populations of desiccation-sensitive bryophyte species. Differences in climate among study areas make it difficult to generalize from these

studies. However, it is interesting that particular species appear to be responding to similar gradients despite variation in geography and climate.

The present study also suggests that quality of potential bryophyte habitat may be affected by the intensity of disturbance. FBSG had fewer sampled species than any other second-growth plot with particularly low species richness on trees. United States Department of Agriculture Works Progress Administration land-use maps indicate that this plot was in an open hay-field in the late 1930s, and that all other plots in the study area have been forested for at least sixty years. Low species richness on FBSG may result from the absence of forest canopy from this plot within the last sixty years.

Both Nichols (1913) and Hale (1955) characterized regenerated forest sites as less mesophytic and more xeric than virgin or climax forest sites. Nichols (1913), describing a virgin forest in northwestern Connecticut observed: "No one feature better suggests the intense mesophytism of this forest than the character and distribution of the bryophytes. Not only do these commonly form a rich covering over the surface of the ground, on roots, logs, stumps and boulders, but they also plaster the bases of trees, extending up their trunks to a height of 24 meters. Maple, birch, and beech particularly are thus covered, while, as a rule, hemlock is singularly immune from epiphytes of any description." Nichols's description of the bryophytic vegetation in virgin forest resembles the bryophytic vegetation now found in the Southern Appalachian Cove forests, which receive roughly twice as much rainfall (Schmitt and Slack 1990).

This description contrasts sharply with the generally sparse bryophyte cover of forests in the Berkshires, despite the general similarity in climate and forest type, raising the possibility of habitat degradation due to air pollution as well as forest fragmentation. Fragmentation of forest habitat might affect bryophytes in several ways, including limiting dispersal possibilities, increased exposure to air pollution, and modification of microclimates from conditions of higher and more even humidity that allowed a more luxuriant bryophytic vegetation to current conditions in which extensive mats of bryophytes are rare. Bryophytes themselves may modify the microclimate of the forest floor by absorption and slow release of moisture (Tan 1987). Hence bryophyte cover in old-growth areas could play

an important role in providing conditions which would allow more sensitive species to persist.

**DISPERSAL.** In several instances, evidence of the distribution of individual species from the present study may suggest why some species have not yet recolonized second-growth forests even after the canopy has closed and where suitable substrate exists. *Radula complanata*, the third most abundant species on trees at CR1 (higher cover there than on any other old-growth plot), occurs on second growth only at CRSG. *Leskeella nervosa* is responsible for nearly 90% of the cover on trunks at GK2, and shows higher cover on tree trunks there than on any other old-growth plot (though absolute cover on tree bases is equal or higher on two other old-growth plots). *Leskeella nervosa* occurs on second growth only at GKSG. *Plagiomnium cuspidatum* is more abundant on DB1 and DB2 than on any other old-growth plots. While *P. cuspidatum* occurs on other second growth plots, it occurs with much higher absolute and relative cover on DBSG than on any other second-growth plot. Powerlines surround the stand containing FBSG on three sides, creating edges and isolating the stand from source populations. Species richness, particularly on trees, was lower on FBSG than on any other plot. Although these findings are not conclusive, they do suggest that dispersal may limit recolonization of forested stands that have been disturbed and that are isolated from source populations, preventing these stands from acquiring the full suite of bryophyte species that previously occurred there. Similar interpretations have been invoked to explain patterns of vascular plant distributions in primary forests versus forests that have been cleared for agriculture (Matlack 1994; Peterken and Game 1984; Whitney and Foster 1988).

Crum (1972) explored the limitations to long-distance dispersal of bryophytes and concluded that long-distance dispersals rarely explain species migration patterns. Wyatt's (1992) study of genetic diversity between populations of *Plagiomnium* also supports the idea that dispersal, and thus gene flow, is limiting for some species. A substantial number of bryophyte species seldom or never produce sporophytes (Mishler 1988), and habitat fragmentation reducing colonization opportunities and gene flow between populations have been shown to play a role in the decline of several bryophyte species (Andersson and Hytteborn 1991; Wyatt 1992).

Dispersal of spores over long distances prob-

ably contributes little to patterns of bryophyte distribution, particularly in enclosed forest surroundings where spores are primarily produced close to the forest floor and where moist obstacles in the form of trees, boulders, and logs intercept their progress. When vigorous source populations exist close by, recolonization is more likely, and species more common in old-growth that occur in some second-growth sites may be "recent" arrivals that have established on the most favorable microsites and have not yet colonized other sites.

**ADDITIONAL ANTHROPOGENIC EFFECTS.** Massachusetts old-growth forests presumably represent some of the best existing bryophyte habitat in the state. However, they contain surprisingly few occurrences of the epiphytic species such as *Anomodon rostratus*, *Anomodon rugelii*, *Neckera pennata*, *Haplohymenium triste*, and *Homalia trichomanoides* which are often important in such sites (Nichols 1913; Billings and Drew 1938; Hale 1952; Culberson 1955; Studlar 1982; Schmitt and Slack 1990; Rose 1992). Declines of these and other species in Europe (Söderström 1992) and Canada (LeBlanc and Sloover 1970) have been attributed to air pollution and habitat fragmentation. The bryophyte flora of old-growth relicts of the northeastern United States may also reflect changes in species composition and abundance due to air quality and deforestation and may thus be substantially different from the bryophyte flora of northeastern forests before and even well after the European settlement of the area in the 1600s.

Although it is generally acknowledged that land-use history has important effects on the ecology of forest stands, differences in plant composition between old-growth and second-growth stands have been difficult to establish (Whitney and Foster 1988, Schoonmaker and McKee 1988, Halpern 1988). Several factors limit our ability to evaluate and make comparisons between old- and second-growth sites, including the severely limited extent of old-growth forest remaining in the Northeast, the occurrence of old-growth on topographically and geologically distinct sites (i.e. steep, uneven topography, with an abundance of boulders), as well as the varying degrees and types of disturbance that have affected both old- and second-growth forest. Indeed, remaining old-growth stands, since they occupy primarily areas that could not be farmed or logged, are variable and difficult to characterize. Differences in species compo-

sition between old-growth and second-growth may consequently be difficult to measure and relatively subtle. The most fruitful direction for future research into the uniqueness of old-growth habitat may be to study the nature and variability of various types of second-growth forest.

Nevertheless, old-growth appears to provide optimal habitat for some species, and some species may have been eliminated from areas that were cleared. Preservation of remaining old-growth stands within larger tracts of developing forest may thus be critical to bryophyte species conservation.

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### Appendix

Complete bryophyte species list with authorities, showing number of old-growth and second-growth plots on which each species occurs.

	Old growth (N = 7)	2 <sup>ND</sup> growth (N = 4)
<b>Mosses</b>		
<i>Amblystegium serpens</i> var. <i>juratzkanum</i> (Schimp.) Rau & Herv.	1	1
<i>A. varium</i> (Hedw.) Lindb.	6	3
<i>Anomodon attenuatus</i> (Hedw.) Hüb.	7	3
<i>A. rostratus</i> (Hedw.) Schimp.	1	0
<i>Atrichum angustatum</i> (Brid.) Bruch & Schimp in B.S.G.	2	0
<i>A. undulatum</i> (Hedw.) P. Beauv.	7	4
<i>Brachythecium acuminatum</i> (Hedw.) Aust.	7	0
<i>B. campestre</i> (C. Mull.) Schimp in B.S.G.	0	1
<i>B. digastrum</i> C. Mull. & Kindb. in Mac. & Kindb.	1	0
<i>B. oedipodium</i> (Mitt.) Jaeg.	1	3
<i>B. oxycladon</i> (Brid.) Jaeg.	3	1
<i>B. populeum</i> (Hedw.) Schimp in B.S.G.	2	0
<i>B. reflexum</i> (Starke in Web. & Mohr), Schimp in B.S.G.	4	4
<i>B. rutabulum</i> (Hedw.) Schimp in B.S.G.	5	3
<i>B. salebrosum</i> (Web. & Mohr) Schimp in B.S.G.	1	0
<i>B. velutinum</i> (Hedw.) Schimp in B.S.G.	0	1
<i>Brotherella recurvans</i> (Michx.) Fleisch.	4	1
<i>Bryhnia novae-angliae</i> (Sull. & Lesq. in Sull.) Grout	5	1
<i>Bryohaplocladium microphyllum</i> (Hedw.) Wat. & Iwats.	2	0
<i>B. virginianum</i> (Brid.) Wat. & Iwats	1	0
<i>Callicladium haldanianum</i> (Grev.) Crum	7	4
<i>Campylium hispidulum</i> (Brid.) Mitt.	5	3
<i>Cyrto-hypnum minutulum</i> (Hedw.) Buck & Crum	4	0
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	6	3
<i>Dicranum flagellare</i> Hedw.	1	2
<i>D. fulvum</i> Hook.	7	4
<i>D. fuscescens</i> Turn.	2	0
<i>D. montanum</i> Hedw.	5	4
<i>D. scoparium</i> Hedw.	0	1
<i>D. viride</i> (Sull. & Lesq. in Sull.) Lindb.	1	0
<i>Diphyscium foliosum</i> (Hedw.) Mohr.	2	1
<i>Entodon cladorrhizans</i> (Hedw.) C. Müll.	1	1
<i>Eurhynchium pulchellum</i> (Hedw.) Jenn.	3	1
<i>Fissidens dubius</i> P. Beauv.	1	1
<i>Haplohymenium triste</i> (Ces. in De Not.) Kindb.	2	0
<i>Hedwigia ciliata</i> (Hedw.) P. Beauv.	2	1
<i>Herzogiella striatella</i> (Brid.) Iwats.	3	3
<i>Homalia trichomanoides</i> (Hedw.) Schimp in B.S.G.	3	1
<i>Homomallium adnatum</i> (Hedw.) Broth.	5	2
<i>Hypnum curvifolium</i> Hedw.	2	0
<i>H. fertile</i> Sendtn.	2	3
<i>H. imponens</i> Hedw.	5	3
<i>H. pallescens</i> (Hedw.) P. Beauv.	7	4
<i>Leskeella nervosa</i> (Brid.) Loeske	5	1
<i>Leucobryum glaucum</i> (Hedw.) Ångstr. in Fries	2	1
<i>Lindbergia brachyptera</i> (Mitt.) Kindb.	2	0
<i>Mnium stellare</i> Hedw.	2	1
<i>M. thomsonii</i> Schimp.	1	0
<i>Neckera pennata</i> Hedw.	1	0



**Appendix**  
Continued.

	Old growth (N = 7)	2 <sup>ND</sup> growth (N = 4)
<i>Orthotrichum sordidum</i> Sull. & Lesq. in Aust	3	1
<i>Oxystegus tebyuristrus</i> (Hook & Tayl.) A.J.E. Sm.		
<i>Paraleucobryum longifolium</i> (Hedw.) Loeske	5	4
<i>Plagiomnium ciliare</i> (C. Müll.) T. Kop.	5	2
<i>P. cuspidatum</i> (Hedw.) T. Kop.	6	4
<i>P. medium</i> (Bruch & Schimp. in B.S.G.) T. Kop. var. <i>medium</i>	1	0
<i>Plagiothecium cavifolium</i> (Brid.) Iwats.	7	4
<i>P. laetum</i> Schimp in B.S.G.	6	4
<i>Platygyrium repens</i> (Brid.) Schimp in B.S.G.	7	4
<i>Pohlia cruda</i> (Hedw.) Lindb.	1	0
<i>P. nutans</i> (Hedw.) Lindb.	0	1
<i>Polytrichum formosum</i> Hedw.	3	1
<i>P. ohioense</i> Ren. & Card.	0	2
<i>Pseudotaxiphyllum elegans</i> (Brid.) Iwats.	4	3
<i>Pterigynandrum filiforme</i> Hedw.	3	1
<i>Pylaisiella intricata</i> (Hedw.) Grout	1	0
<i>Rawella scita</i> (P. Beauv.) Reim.		
<i>Rhizomnium punctatum</i> (Hedw.) T. Kop.	3	1
<i>Schistidium apocarpum</i> (Hedw.) Bruch & Schimp. in B.S.G.	3	1
<i>Steerecleus serrulatus</i> (Hedw.) Robins.	2	2
<i>Tetraphis pellucida</i> Hedw.	4	3
<i>Thuidium delicatulum</i> (Hedw.) Schimp in B.S.G.	7	4
<i>Ulota crispa</i> (Hedw.) Brid.	6	3
<i>U. hutchinsiae</i> (Sm.) Hamm.	2	1
Liverworts		
<i>Bazzania trilobata</i> (L.) S. Gray	1	1
<i>Blepharostoma trichophyllum</i> (L.) Dum.	0	1
<i>Calypogeia fissa</i> (L.) Raddi	2	1
<i>Cephalozia</i> sp.	1	0
<i>Diplophyllum apiculatum</i> (Evans) Steph.	1	0
<i>Frullania asagrayana</i> Mont.	1	0
<i>F. eboracensis</i> Gottsche	7	3
<i>Jamesoniella autumnalis</i> (DC.) Steph.	3	2
<i>Lophocolea heterophylla</i> (Schrud.) Dum.	7	4
<i>Metzgeria furcata</i> (L.) Dum. var. <i>furcata</i>	4	1
<i>Nowellia curvifolia</i> (Dicks.) Mitt.	2	2
<i>Pellia</i> sp.	1	1
<i>Plagiochila porelloides</i> (Torr.) Lindenb.	3	1
<i>Porella platyphylla</i> (L.) Pfeiff.	1	0
<i>P. platyphylloidea</i> (Schwein.) Lindb.	5	2
<i>Radula complanata</i> (L.) Dum.	5	2
<i>Scapania nemorea</i> (L.) Grolle	2	0