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Autecology of Mosses in Coniferous Forests in the Central Western Cascades of Oregon

Abstract

Forest mosses contribute to nutrient cycling, provide food and nesting materials to small animals, and serve as biological indicators. In addition, the harvest of moss as a special forest product has grown in recent years in the Pacific Northwest. To quantify certain ecological characteristics of moss species, we examined substrate and forest community affinities in the central western Cascades of Oregon. Cover and frequency of individual species were measured on the forest floor, logs, and tree bases in *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Abies amabilis* Dougl. ex Forbes forest communities. Thirty moss species were found, representing 21 genera and 13 families. Common substrates for individual moss species were identified on the basis of frequency values. Mosses comprise a substantial portion of the vegetative biological diversity in forest ecosystems in the Cascades. A better understanding of moss autecology will assist resource managers in protecting this important source of diversity.

Introduction

Understanding the patterns of distribution and abundance of individual species is necessary for understanding ecosystem structure and function and for ensuring proper management. In forests, mosses are a critical component of nutrient cycling, serving as sinks that capture and then leach nutrients back into the ecosystem (Turner and Long 1975, Rieley et al. 1979). Mosses and other bryophytes provide food and nest material to invertebrates and vertebrates (Forest Ecosystem Management Assessment Team (FEMAT) 1993). Furthermore, mosses serve as indicators of environmental change in forest communities (Schofield 1988, Vitt 1990) and have economic value as forest products used in the floral industry (Peck 1990, Schlosser et al. 1992). To augment understanding of the ecology of individual species, we examined mosses on the forest floor, on the upper surface of downed logs, and on tree bases in forest stands in the central western Cascades of Oregon on and near the H. J. Andrews Experimental Forest.

For the most part, information on suitable substrates for moss species in the Pacific Northwest is limited to floristic works (Steele 1978), taxonomic keys (Schofield 1969, Lawton 1971, Flowers 1973, Schofield 1976), and anecdotal accounts in field guides (Vitt et al. 1988). This study quantifies local distribution patterns and substrate affinities to a greater extent than previous studies in the same geographic area (e.g., Pike et al. 1975, Hawk et al. 1978, Binkley and Graham 1981). Several habitats and their associated species were not included in our study (e.g., cliffs, sides of logs, tree limbs, tree canopies; see Pike et al. 1975). Nomenclature follows Anderson et al. (1990).

Study Area

Observations were made in 15 permanent 0.25-ha forest study areas in and near the H. J. Andrews Experimental Forest (Hawk et al. 1978, Franklin and Van Pelt 1990) near Blue River, Oregon, in the western Cascades. These sites were chosen to span the range of the environmental gradient discussed by Zobel et al. (1976), extending from warm and dry to cold and wet sites. Four of the 15 sites were mature forest, 130 to 150 years old, and the other 11 sites were old-growth forest, more than 400 years old.

Vegetation of the warm and dry sites (elevations 510 to 1060 m) was dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with oceanspray (*Holodiscus discolor* (Pursh) Maxim.) in the understory. On the driest intermediate sites on the environmental gradient, vegetation was dominated by Douglas-fir. On less dry intermediate sites, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was also present, and the wettest intermediate sites also had Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) co-dominants. All intermediate sites were between 490 and 950 m elevation; vine maple (*Acer circinatum* Pursh), western swordfern (*Polystichum munitum* (Kaulf.) Presl), Oregon oxalis (*Oxalis oregana* Nutt.), and twinflower (*Linnaea borealis* L.) were common understory species. Vegetation of the cold and wet sites (1020 to 1570 m) was dominated by Pacific silver fir with Alaska huckleberry (*Vaccinium alaskaense* Howell) and bunchberry (*Cornus canadensis* L.) or coolwort (*Tiarella trifoliata* L. var. *unifoliata* (Hook.) Kurtz.) in the understory.

Methods

Sampling took place from June to August, 1991. Cover was estimated visually to the nearest 1% (within a 20- by 50-cm Daubenmire (1959) frame) for each species on 30 microplots on the forest floor, 30 on logs, and 15 on tree bases at each of the 15 sites. The Daubenmire frame was systematically placed on the forest floor (with logs and rocks avoided) every 5 m along three parallel transects within a 50-m^2 plot. Frames were also placed on downed logs that had just begun to lose some of their bark; logs were chosen so that decay was as uniform as possible. Because bryophyte communities on the tops and sides of logs differ, only the upper surface was sampled. Finally, frames were placed to lean against the bases of overstory trees (with the 20-cm side down); the north side of trees was arbitrarily chosen for consistency. Cover was then averaged by species and substrate for all microplots within a site. Pearson correlation coefficients were used to assess the relationship between elevation and total cover of each species in each stand. Constancy was computed as the percentage of sites in which a species occurred out of the 15 sites examined.

Frequency on each substrate at each site was computed as the percentage of microplots containing the species divided by the total number of microplots for the substrate and site. Species substrate affinities were assigned only when average cover across all sites was greater than 1%. Substrate affinities are shown for species that occur on one substrate at least twice as often as on the next most common substrate. These substrate rankings were based on the species' frequency on that substrate across all sites.

Vouchers were deposited in the Oregon State University Herbarium, Corvallis, Oregon.

Results

We encountered 13 families, 21 genera, and 30 species of mosses (Table 1). Some species were quite widespread and abundant, while others were more narrowly distributed and rare (Table 2). Species in Table 2 are listed in order of their correlation coefficients with elevation, starting with species with low cover at high elevations. *Isothecium myosuroides, Hypnum circinale, Polytrichum juniperinum,* and *Eurhynchium oreganum* all had strong negative correlations with elevation. *Plagiothecium laetum* and *Roellia roellii*, however, showed the opposite tendency, with strong positive correlations with elevation.

Hypnum circinale and *Dicranum fuscescens* occurred across the entire elevational range, on all sites sampled, and on all three substrates. *Dicranum tauricum, Rhizomnium glabrescens, Rhytidiadelphus triquetrus*, and *Plagiothecium laetum* also had broad elevational ranges and occurred on all substrates, but they were absent from some sites. Despite their broad elevational ranges, *Aulacomnium androgynum* and *Atrichum selwynii* occurred on few sites and not all substrates.

Isothecium myosuroides, Eurhynchium oreganum, and *Dicranum scoparium* were found at most sites of low to moderate elevation and occurred on all substrates. *Homalothecium megaptilum, Rhytidiopsis robusta, Antitrichia curtipendula, Hylocomium splendens*, and *Rhytidiadelphus loreus* occurred on logs and the forest floor at low to moderate elevations and were less frequently encountered. *Claopodium crispifolium* did not occur above 830 m but was found on all three substrates.

Polytrichum juniperinum, Polytrichadelphus lyallii, Eurhynchium praelongum, and *Claopodium whippleanum* each were encountered on only two sites at relatively low elevation and occurred primarily on the forest floor. *Scleropodium touretеii, Racomitrium heterostichum, Metaneckera menziesii, Plagiothecium undulatum, R. canescens, R. aciculare, Plagiomnium insigne, Leucolepis menziesii,* and *Roellia roellii* each occurred in only one site and were rare where they did occur.

TABLE 1. Mosses on the forest floor, logs, and tree bases in coniferous forests of the central western Cascades of Oregon.

Species name, authority	Family	Growth form[1]
Aulacomnium androgynum (Hedw.) Schwaegr.	Aulacomniaceae	A
Eurhynchium oreganum (Sull.) Jaeg.	Brachytheciaceae	P
Eurhynchium praelongum (Hedw.) B.S.G.	Brachytheciaceae	P
Homalothecium megaptilum (Sull.) Schof.	Brachytheciaceae	P
Isothecium myosuroides Brid.	Brachytheciaceae	P
Scleropodium touretеii (Brid.) L. Koch	Brachytheciaceae	P
Roellia roellii (Broth.) Andr. in Crum	Bryaceae	A
Dicranum fuscescens Turn.	Dicranaceae	A
Dicranum scoparium Hedw.	Dicranaceae	A
Dicranum tauricum Sapehin.	Dicranaceae	A
Racomitrium aciculare (Hedw.) Brid.	Grimmiaceae	A
Racomitrium canescens (Hedw.) Brid.	Grimmiaceae	A
Racomitrium heterostichum (Hedw.) Brid.	Grimmiaceae	A
Hylocomium splendens (Hedw.) B.S.G.	Hylocomiaceae	P
Rhytidiadelphus loreus (Hedw.) Warnst.	Hylocomiaceae	P
Rhytidiadelphus triquetrus (Hedw.) Warnst.	Hylocomiaceae	P
Hypnum circinale Hook.	Hypnaceae	P
Plagiothecium laetum B.S.G.	Hypnaceae	P
Plagiothecium undulatum (Hedw.) B.S.G.	Hypnaceae	P
Claopodium crispifolium (Hook.) Ren. & Card.	Leskaeceae	P
Claopodium whippleanum (Sull.) Ren. & Card.	Leskaeceae	P
Antitrichia curtipendula (Hedw.) Brid.	Leucodontaceae	P
Leucolepis menziesii (Hook.) Steere	Mniaceae	A
Plagiomnium insigne (Mitt.) T. Kop.	Mniaceae	P
Rhizomnium glabrescens (Kindb.) T. Kop.	Mniaceae	A
Metaneckera menziesii (Hook.) Steere	Neckeraceae	P
Atrichum selwynii Aust.	Polytrichaceae	A
Polytrichadelphus lyallii Mitt.	Polytrichaceae	A
Polytrichum juniperinum Hedw.	Polytrichaceae	A
Rhytidiopsis robusta (Hook.) Broth.	Rhytidiaceae	P

[1]Growth form (Lawton 1971):

A = Acrocarp (erect plant with terminal capsules)

P = Pleurocarp (spreading plant with capsules on lateral branches)

Fifteen of the 30 species were abundant enough that substrate affinities could be assessed (Table 2). Species exhibiting affinities for the forest floor included *Polytrichum juniperinum, Eurhynchium praelongum, Homalothecium megaptilum,* and *Aulacomnium androgynum. Rhytidiopsis robusta,*

TABLE 2. Habitat and substrate distributions, listed in order of increasing correlation with elevation.

Species name	Elev. (m) Min.	Elev. (m) Max.	Correlation with elevation	Constancy (%)	Frequency class by substrate Floor	Log	Tree	Substrate affinity
Isothecium myosuroides	490	1060	-.4974	73	3	1	4	Generalist
Hypnum circinale	490	1570	-.4855	100	3	4	5	Trees (Logs)
Polytrichum juniperinum	510	680	-.4623	13	2	1	0	Floor
Eurhynchium oreganum	490	1060	-.4551	80	5	4	4	Generalist
Polytrichadelphus lyallii	510	680	-.3777	13	1	1	0	
Dicranum fuscescens	490	1570	-.3282	100	4	4	5	Trees
Claopodium crispifolium	510	830	-.2429	27	2	2	1	
Eurhynchium praelongum	490	510	-.2087	13	2	1	1	Floor
Homalothecium megaptilum	510	1060	-.2066	33	3	1	0	Floor
Scleropodium touretei	510	510	-.1959	7	1	0	0	
Rhytidiopsis robusta	490	1020	-.1793	33	1	2	0	Logs
Racomitrium heterostichum	670	670	-.1690	7	0	1	0	
Antitrichia curtipendula	520	830	-.1396	20	1	1	0	
Metaneckera menziesii	720	720	-.1311	7	1	1	1	
Hylocomium splendens	490	670	-.1299	33	2	1	0	
Dicranum scoparium	490	950	-.1092	53	2	2	3	Generalist
Dicranum tauricum	510	1570	-.1001	73	2	3	2	Logs
Aulacomnium androgynum	510	1570	-.0913	27	2	1	0	Floor
Rhizomnium glabrescens	490	1440	-.0773	47	2	3	2	Logs
Plagiothecium undulatum	830	830	-.0476	7	1	1	0	
Rhytidiadelphus loreus	490	830	-.0476	13	1	1	0	
Racomitrium canescens	680	680	.0000	7	1	0	0	
Racomitrium aciculare	950	950	.0146	7	1	1	0	
Rhytidiadelphus triquetrus	490	1570	.0291	73	3	3	2	Generalist
Plagiomnium insigne	950	950	.0435	7	0	1	0	
Claopodium whippleanum	670	830	.1194	13	1	0	0	
Leucolepis menziesii	1060	1060	.1270	7	0	1	0	
Atrichum selwynii	510	1570	.2681	13	1	0	0	
Roellia roellii	950	950	.4155	7	1	1	0	
Plagiothecium laetum	490	1570	.6438	60	3	3	2	Generalist

Frequency codes: 0 = 0%
1 = 0.1–1.0
2 = 1.1–5.0
3 = 5.1–10.0
4 = 10.1–50.0
5 = 50.1–100.0

Dicranum tauricum, and *Rhizomnium glabrescens* showed an affinity for logs. *Dicranum fuscescens* occurred most commonly on tree bases. *Hypnum circinale* occurred on tree bases nearly twice as often as on logs and occurred on the forest floor less than one-tenth as often as on tree bases. Those species listed as generalists had similar frequencies for each of the three substrates.

Discussion

Basic ecological information for mosses is one requirement for ecologically sustainable forest management (FEMAT 1993). Currently, however, moss ecology is poorly understood. In part, this is because of the tremendous variability among moss species and their flexibility as poikilohydric cryptogams. Thus the habits and habitats of some species may vary from one geographic region to the next, and possibly from one microsite to the next.

Ecological observations from farther north in the Pacific Northwest indicate patterns that differ from those found for some of the same species in this study. On the Olympic Peninsula, *Hypnum circinale* and *Dicranum fuscescens* attain their greatest abundance in relatively mesic areas (Hoffman and Kazmierski 1969). In this study these species were almost equally abundant in warm and dry and cold and wet sites. Differences in sampling protocols may have contributed to this discrepancy; tree bases up to 4 m were sampled in the Olympic Peninsula study, which allowed the authors to observe that, as Szczawinski (1953) proposed, bryophytes in mesic areas are displaced further up the trunks of trees than in more xeric areas. Our sampling only extended up tree bases to 50 cm, which appears to be too small a gradient to show this phenomenon.

In British Columbia, *Dicranum tauricum* occurs on logs and *Plagiomnium insigne* on moist earth and tree bases (Schofield 1976). However, we found *D. tauricum* on all three substrates (although primarily on logs) and *P. insigne* only on logs. In addition, we found *Polytrichadelphus lyallii* on the forest floor and logs in low-elevation stands. Lawton (1971) reports this species as occuring on soil at high elevations (1200 m to 3300 m and higher).

In our area, Lawton (1971) reported elevational zonation for four of the moss species we encountered. Our findings agree with these regional descriptions. We found *Claopodium crispifolium*, *Plagiomnium insigne*, and *Plagiothecium laetum* within the elevational ranges described by Lawton (1971), but *Dicranum fuscescens* occurred at all elevations up to and including our highest site at 1570 m, 570 m higher than Lawton (1971) describes. This is in keeping with the findings of Bellolio-Trucco and Ireland (1990), who reported *D. fuscescens* to be very widespread in Quebec with populations occurring over a broad geographic area as well as on varying substrates. This species, along with *Hypnum circinale*, showed a strong affinity for tree bases and was very abundant in our stands. Other studies of tree base habitats in the Pacific Northwest have also found these species to be among the most frequently encountered (Hawk et al. 1978, Hoffman and Kazmierski 1969).

Higher-elevation stands had a lower abundance of *Isothecium myosuroides, Hypnum circinale, Polytrichum juniperinum,* and *Eurhynchium oreganum*. The absence of *P. juniperinum* at higher elevations is inconsistent with the reported phenotypic plasticity of this species; in other areas it is known to adapt to the altered climatic conditions along elevational gradients (Bazzaz et al. 1970). The other three species are present on all substrates in most stands. Their distributions may reflect an extension to higher-elevation stands of the "similar gradient hypothesis" proposed by McCune (1993). High-elevation *Abies* stands are structurally different from lower-elevation *Pseudotsuga* and *Tsuga* forests, with lower canopies and smaller-diameter trees (Franklin 1988). This structure can be considered comparable to that of young *Pseudotsuga* forests, which have a lower biomass of bryophytic epiphytes than older, more structurally complex stands (McCune 1993). However, the reduction in moss abundance in higher-elevation stands may also be a function of reduced temperatures, greater snowpacks, and less free water during the growth season, as well as other factors that were not measured in this study.

Two species, however, showed strong positive associations with elevation. *Roellia roellii* was present in only one stand and thus did not change in abundance with increasing elevation. This species, which occurred at 950 m elevation, has been noted previously in stands of approximately 1000 m (D. Norris, D. Wagner, pers. comm.). *Plagiothecium laetum*, found on all substrates in all stands, showed a marked increase in abundance with increasing elevation. This distribution supports its description in Lawton (1971) as a very variable species occurring on a wide range of habitats, and in particular in high-elevation (>700 m) coniferous forests.

Several species that most commonly occur as epiphytes were found well established on the forest floor (*Isothecium myosuroides, Claopodium crispifolium, Antitrichia curtipendula, Metaneckera menziesii*). Although it is impossible to determine whether these populations began their development while epiphytic, all were clearly established on the forest floor and apparently thriving. The reestablishment of these epiphytes on the forest floor is common throughout the Pacific Northwest and has been previously noted by Lawton (1971) and Schofield (1976).

Six of the species in this study were identified by FEMAT (1993) as "closely associated with late-successional or old-growth forests" and described as dependent on particular habitats within such forests. *Hypnum circinale* and *Dicranum fuscescens* were most common on tree bases in this study, consistent with the FEMAT report. Similarly, *Rhizomnium glabrescens* was most common on logs, although it was not found exclusively on decaying wood as stated in the report. We found *Rhytidiopsis robusta*, on the other hand, to be most common on logs, whereas the FEMAT report described it as a species of shaded duff and humic soil. Two other species included in the FEMAT report, *Plagiothecium undulatum* and *Roellia roellii*, were each encountered in only one of our sites.

The classification of substrate affinities is intended to serve as a general guide for species distributions in our area. Classifications of this sort are useful when habitats and substrates are managed for specific goals such as promoting biodiversity. Other studies in the central western Cascades of Oregon indicate that additional moss species occur on the substrates we sampled. These include *Dicranoweisia cirrata* and *Barbula* sp. on tree bases (Pike et al. 1975), and *Claopodium bolanderi* and *Mnium* sp. (Hawk et al. 1978) on the forest floor. However, *C. bolanderi* and *C. crispifolium* are difficult to distinguish in the field. Thus it is possible that both species were present and only one was recognized by each set of researchers. Further, Hawk et al. (1978) may have classified *Plagiomnium insigne* as *Mnium* sp.

Generalizations about moss species distributions are best made and utilized on a regional basis where geographic and climatic variables are relatively consistent. Although it would be difficult to manage for individual moss species, given their broad distributions and the paucity of ecological data, information on moss groups associated with certain habitats or forest communities allows managers to operate on a larger scale. With the increased harvest of moss as a forest product in western Oregon, ecological information of this kind should facilitate sustainable management. Understanding moss species distribution patterns may allow managers to regulate for groups of species and to anticipate which species will be targeted by the floral industry. Both ecosystem science and sustainable management of forest mosses will be furthered if the ecology of western forest mosses and the impact of harvest on these mosses and the forest ecosystem are investigated.

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