

Riparian Bryophytes of the H. J. Andrews Experimental Forest in the Western Cascades, Oregon

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Abstract. *The knowledge of the distribution and habitat demands for bryophytes in the Pacific Northwest is scarce, and few published quantitative accounts of the flora are present. The present paper includes habitat description, elevational range, substrate preference, and frequency estimates for more than 130 riparian mosses and liverworts found in old-growth Pseudotsuga-Tsuga forests of the H. J. Andrews Experimental Forest, Oregon. The data are based on 360 samples distributed among 42 sites covering 1st to 5th order streams and 420 to 1250 m. TWINSPAN analysis resulted in 6 sample groups, representing samples from different elevations, geomorphic surfaces, and stream sizes. The most common mosses are Eurhynchium oregonum, Isoetecium stoloniferum, Hypnum circinale, and Dicranum fuscescens. Among the hepatics Scapania bolanderi, Cephalozia lunulifolia, and Porella navicularis are the most abundant species. Most species are rare at both site and sample plot level, and this is especially true for acrocarps where more than one-third of the observed species occurred in only one or two sites or land samples. Four of the occurring species (i.e., Antitrichia curtispindula, Buxbaumia piperi, Douinia ovata, and Ptilidium californicum) are listed for special management and/or regional surveys.*

Bryophytes constitute an important and conspicuous component of old-growth forests in the Pacific Northwest (Lesica et al. 1991; McCune 1993; Schofield 1988); however, few studies on the abundance and distribution of mosses and liverworts have been conducted. The epiphytic flora, composed of bryophytes and lichens, of old-growth Douglas-fir has been shown to be species rich and influences nutrient dynamics and overall production in old-growth stands (Pike et al. 1975, 1977). Besides these studies, however, there has been until now no published account of factors influencing the distribution of individual species within old-growth forests (see however Peck et al. 1995; Schofield 1976). Despite this lack of study, many bryophytes are considered to be dependent of old-growth conditions (FEMAT 1993; Söderström 1988). Thus, effective management of the bryophyte flora, which is an important forest product of the region (Peck 1990; Schlosser et al. 1992) and a significant part of forest biodiversity, is constrained by lack of knowledge.

Riparian zones are thought of as key elements in the forested landscape, and preservation of these is a major goal of forest management (FEMAT 1993). Of the mosses and liverworts considered as vulnerable in the Pacific Northwest (USDA 1994), many occur in riparian areas. This association is dependent on many factors, but the occurrence of

a wide range of different substrates, disturbance patterns, and a moist microclimate are important contributors to the diversity in these zones (Glime & Vitt 1987; Vitt et al. 1986). The present paper reports habitats and frequencies of species found in riparian areas of old-growth *Pseudotsuga-Tsuga* forests in the western Cascades of Oregon. A general treatment of the bryophyte community patterns will be published elsewhere.

METHODS

Study area.—The H. J. Andrews Experimental Forest is located in the western part of the Cascade Mountain Range about 80 km east of Eugene, Oregon. The 6,400 ha area comprises the entire Lookout Creek watershed which is characterized by well defined drainage, steep slopes, and sharp ridges. Lookout Creek is a tributary to the Blue River in the MacKenzie River system. The upper portion of the watershed is divided into three major streams — Lookout Creek, Mack Creek, and McRae Creek. Most of the forests are within the *Tsuga heterophylla* zone (*sensu* Franklin & Dyrness 1973) with large old-growth trees of *Pseudotsuga menziesii* (Mirbel) Franco., *Tsuga heterophylla* (Raf.) Sarg., and *Thuja plicata* Donn. dominating the tree layer. At higher elevations (>1,100 m), forest stands belonging to the *Abies amabilis* zone occur. The climate is maritime, with mild winters and dry summers. Annual precipitation is approximately 2,300 mm, of which >70% occurs from November to March. Extensive snowpacks are common at higher elevations (>1,000 m), while lower elevations usually remain free of snow except for brief periods. The mean annual temperature at 420 m is 8.5°C ranging from a monthly mean of 0.6°C in January to 17.8°C in July. At 1,300 m the values are approximately 2°C lower (Bierlmaier & McKee 1989).

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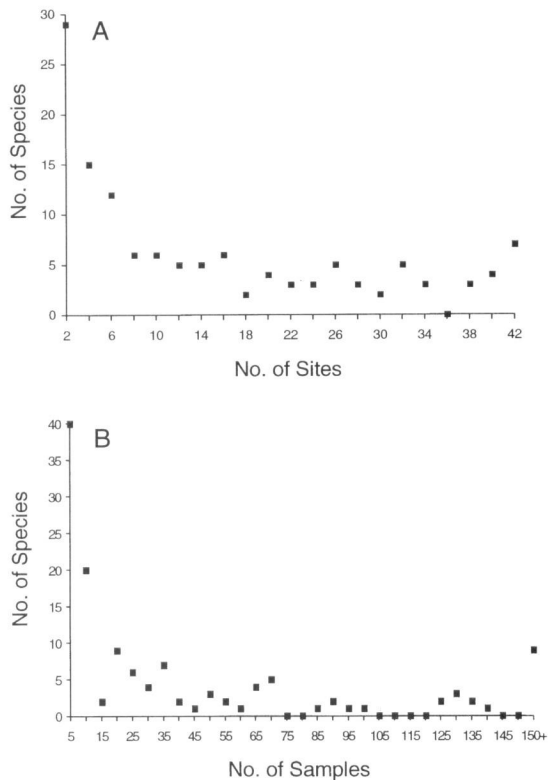


FIGURE 1. Species occurrence patterns, presented as number of species plotted against the number of sites (A) or samples (B) in which a species was found.

The vascular flora is species rich, with almost 500 species known from the forest (Franklin & Dyrness 1971). The distribution of forest types corresponds to major gradients in moisture and temperature, and the occurrence of many shrubs and herbs can be associated with these gradients (Zobel et al. 1976). Preliminary data indicate that the bryophyte communities also show significant changes between different elevations and forest types (Jonsson et al. in prep; Peck et al. 1995).

Sampling.—Quantitative data on the frequency and abundance of riparian bryophytes were collected from 42 sample sites within the Lookout Creek watershed. Sample sites ranged from 420 m to 1,250 m elevation and stream size from 1st to 5th order streams. At each site, a transect beginning in the centre of the stream channel was established. Five 2 × 4 m contiguous sample plots (hereafter referred to as plots) were located along the first 10 meters. In 1st order streams the hillslope was always reached in 10 m. In all other streams, 5 additional plots were placed every 8th meter up to 50 meters giving a total of 10 sample points per transect. A total of 360 8-m² plots was sampled.

In all of the sample plots, abundance of substrates, cover of vegetation layers, and bryophytes were noted as percent. In addition to the quantitative variables, each quadrat was assigned to a specific geomorphic surface: stream channel (with constant water), active channel (dry during short periods of low flow), flood plain (flooded annually), transition slope (steep bank separating the flood plain from stream terraces or hillslopes), stream terrace (flat level

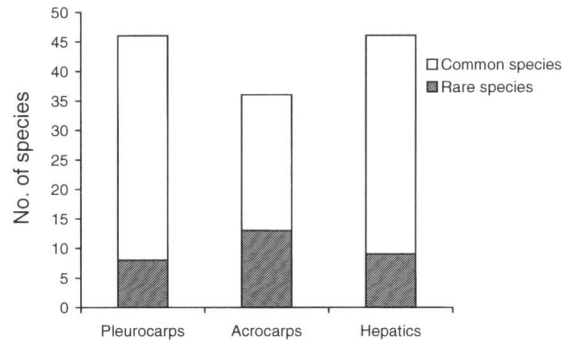


FIGURE 2. Number of species divided by species group in the study. Rare species in this case are those occurring in less than 3 sites (out of 42) and/or less than three samples (out of 360).

area with history of flooding), toeslope (lowest part of hillslope), and hillslope (areas above highest flood level).

The herbarium OSC, (including collections from the former UO and the private herbarium of Jack Lyford) was checked for additional species. Voucher specimens have been deposited in OSC and UME.

TWINSPAN analysis.—The bryophyte abundance data from each quadrat were subjected to the polythetic divisive hierarchical program TWINSPAN (Hill 1979). Although the reliability of the approach is questionable under certain conditions (Belbin & McDonald 1993; van Groenewoud 1992), it represents an objective approach of grouping samples for exploratory purposes. TWINSPAN's default options were used with the exception that rare species (fewer than 10 occurrences) were excluded from the analysis.

RESULTS AND DISCUSSION

A total of 131 taxa was found in the 360 plots, representing slightly less than 3,000 m² of sampled area. All major bryophyte groups were represented except *Sphagnum*. Many of the species were, however, infrequent both at site and sample plot level (Fig. 1). Of all species, one-third occurred in less than 10% of the sites and more than two-thirds in less than 10% of the sample plots. This pattern was most pronounced among acrocarps where more than one-third of the species occurred in only one or two samples and/or only one or two sites (Fig. 2). The large proportion of rare species seems to be a general feature in bryophyte communities, as this pattern occurs in many contrasting habitats and regions (e.g. Englund et al. 1996; Jonsson & Esseen 1990; Slack et al. 1980; Vitt & Belland 1995).

TWINSPAN analysis.—The analysis resulted in 6 sample groups (Table 1) that could be biologically interpreted (Fig 3). The species richness per sample varied significantly (one-way ANOVA: $F = 19.8$, $df = 5$, $p < 0.001$) between the groups (Fig. 4). The richest groups were low elevation terraces and medium-sized streams. Many of the samples in these groups occur in areas with intermediate levels

TABLE 1. Sample groups derived from TWINSpan analysis of riparian bryophyte community data ($n = 360$). Species characteristics for each group and other abundant species are given.

Groups	Characteristic species	Other abundant species
1) High elevation hillslopes (36 samples)	<i>Rhytidiopsis robusta</i> <i>Ptilidium californicum</i> <i>Isopterygium elegans</i>	<i>Isothecium stoloniferum</i> <i>Hypnum circinale</i> <i>Eurhynchium oregonum</i> <i>Dicranum fuscescens</i>
2) Low elevation hillslopes (203 samples)	<i>Eurhynchium oregonum</i> <i>Scapania bolanderi</i> <i>Dicranum fuscescens</i> <i>Dicranum howellii</i> <i>Porella navicularis</i> <i>Hylocomium splendens</i> <i>Rhytidiadelphus triquetrus</i>	<i>Cephalozia lunulifolia</i> <i>Hypnum circinale</i> <i>Antitrichia curtispindula</i> <i>Neckera douglasii</i> <i>Isothecium stoloniferum</i> <i>Rhizomnium glabrescens</i>
3) Low elevation terraces (61 samples)	<i>Rhytidiadelphus loreus</i> <i>Plagiomnium insigne</i> <i>Leucolepis acanthoneuron</i> <i>Eurhynchium praelongum</i> var. <i>stokesii</i>	<i>Isothecium stoloniferum</i> <i>Porella navicularis</i> <i>Rhizomnium glabrescens</i> <i>Rhytidiadelphus triquetrus</i> <i>Eurhynchium oregonum</i> <i>Brachythecium frigidum</i>
4) Medium sized streams (20 samples)	<i>Chiloscyphus polyanthos</i> <i>Scleropodium obtusifolium</i> <i>Racomitrium varium</i> <i>Racomitrium aciculare</i> <i>Scapania undulata</i>	<i>Hypnum circinale</i> <i>Isothecium stoloniferum</i> <i>Eurhynchium praelongum</i> var. <i>stokesii</i> <i>Eurhynchium oregonum</i>
5) High elevation streams (8 samples)	<i>Brachythecium frigidum</i> <i>Claopodium bolanderi</i>	<i>Hypnum circinale</i> <i>Plagiomnium insigne</i>
6) Low elevation streams (32 samples)	<i>Hygrohypnum ochraceum</i> <i>Scleropodium obtusifolium</i> <i>Chiloscyphus polyanthos</i>	<i>Scapania undulata</i> <i>Eurhynchium praelongum</i> var. <i>stokesii</i> <i>Brachythecium frigidum</i>

of disturbance from flooding and erosion. Consequently, both species typical of stable conditions and species of more disturbed habitats coexist. There was also a difference in the frequency of dif-

ferent bryophyte groups as pleurocarpic species were less common (decrease of 30%) and acrocarps and hepatics more common (increase of 50% and 33%, respectively) in the three stream groups (Fig.

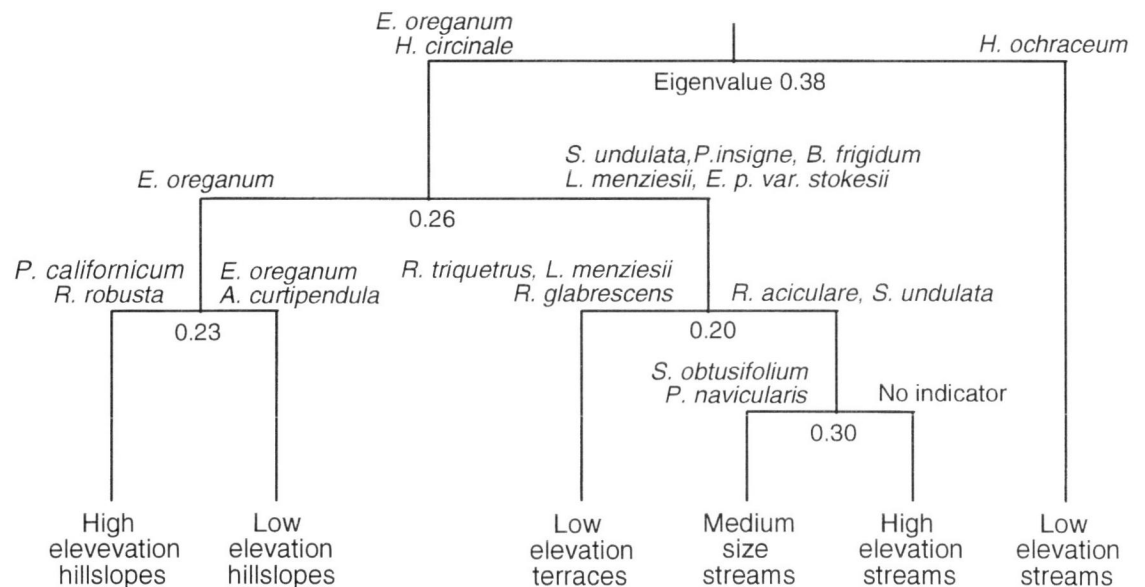


FIGURE 3. TWINSpan dendrogram of sample groups. Indicator species and eigenvalues are given for sample divisions.

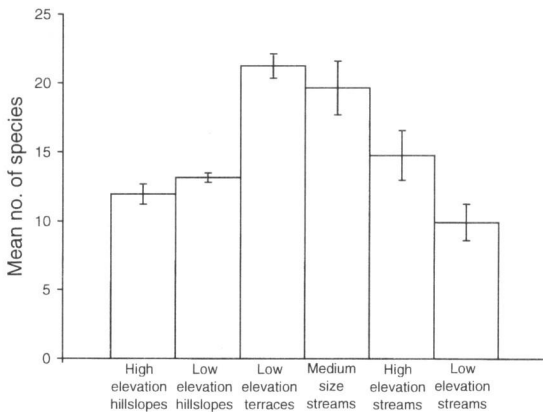


FIGURE 4. Mean number of species per sample (with SE bars) in the six TWINSpan sample groups.

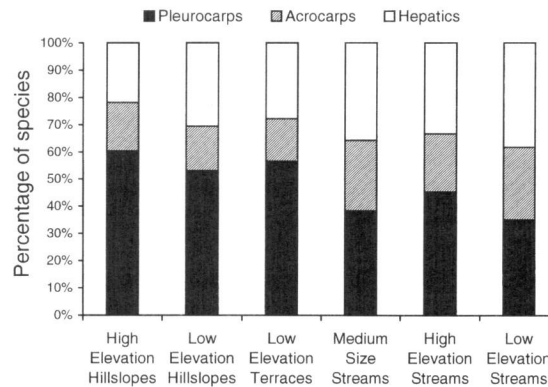


FIGURE 5. Relative percentage of species groups in the six TWINSpan sample groups.

5). This implies a structural difference in the bryophyte vegetation in addition to changes in species composition. Vitt et al. (1986) found somewhat contradictory evidence, indicating that hepatics were more common than pleurocarpic mosses on bank habitats as compared to stream habitats. However, their study did not include samples above the stream bank. Thus, the present results applies to larger scale changes — from terrestrial forested habitats to stream channels.

There is, however, a great deal of overlap between the sample groups and they should not be considered as phytosociological entities, but rather as one way of summarizing the present data into manageable units for discussion. Particularly the substrate aspects are not well represented as the analyzed quadrats (2 × 4 m) included many different microhabitats. A further division of the sample groups should probably be based on specific species-substrate associations.

1) *High elevation hillslopes*.—In addition to hillslopes, some terraces and transition slope samples are represented, but only two occur lower than 800 m. These include the vast majority of the high elevation hillslope samples. They are generally low in diversity and are dominated by terrestrial species, epiphytes, and epixylic species.

2) *Low elevation hillslopes*.—This is the largest group, comprising 56% of all samples. There is a strong dominance of terrestrial species, with a large component of epiphytic and epixylic species. The analysis suggested that further division of this group should be based mainly on abundance of coarse woody debris. Diversity is variable and related to amount of decaying wood.

3) *Low elevation stream terraces*.—This is a species rich group. A further division would include a separation of the samples with high abundance of wood. All types of species were well represented.

4) *Medium size stream channels*.—This includes stream channels, active channels, and floodplains. The aquatic flora is well developed, but there is low abundance of wood and epixylic species. The diversity is high in this group and all types of species are well represented, although terrestrial species are not as important.

5) *High elevation small streams*.—This includes sites where hillslope conditions dominate, even close to the stream. There is low diversity and a lack of aquatic species. All types of species are poorly represented.

6) *Low elevation large streams*.—These sites are more or less constantly flooded and are dominated by aquatic species. They show low diversity. Species demanding mesic conditions are fairly common and some epixylic and epiphytic species are usually present.

ANNOTATED SPECIES LIST

The following list compiles habitat information based on the quantitative data collected, but also includes my personal impression and interpretation on the occurrence of the species. The data are specific for the studied sites, but may serve as an indication of the general habitat demands of the species within the western Cascades and to some extent for riparian zones in the Coastal Mountain Range. The following four frequency classes are used in the list: *very common*—occurring in more than 25% of all samples; *common*—10–25%; *scattered*—1–10%; *rare*—<1%. The abundance is also classified to four groups: *very abundant*—>1% cover across all samples; *abundant*—0.1–1% cover; *fairly abundant*—0.01–0.1% cover; *low abundant*—<0.01% cover.

MOSSES

Antitrichia curtipendula (Hedw.) Brid.—Very common and abundant epiphyte with stray occurrences on logs and

boulders. Also commonly occurring on fallen twigs and branches on the forest floor. The second-most abundant epiphyte after *Isothecium stoloniferum*. 420–1,150 m, with a tendency to be more abundant at low elevations.

Atrichum selwynii Aust.—Scattered and fairly abundant on exposed soil, often on erosion zones in transition slopes. 460–1,150 m.

Aulacomium androgynum (Hedw.) Schwaegr.—Scattered and fairly abundant on highly decayed wood and soil. Mainly occurring from the floodplains up to stream terraces. 420–940 m.

Blindia acuta (Hedw.) Bruch & Schimp.—Rare, in low abundance on wet boulders close to streams. Two occurrences in Mack Ck. at 750 and 780 m.

Brachythecium frigidum (C. Müll.) Besch.—Common and abundant species characteristic for floodplains, where it grows on the ground and among stones along the entire elevation range, 420–1,250 m, but more abundant at higher elevations. Partly replaced by *Leucolepis acanthoneuron* at lower elevations.

Brachythecium hylotapetum B. Hig. & N. Hig.—Scattered and fairly abundant on the forest floor in stream terraces and on hillslopes. 580–1,150 m, with major occurrences at mid elevations (700–1,000 m).

Brachythecium leibergii Grout—Rare, in low abundance on needle litter. A single occurrence on a toeslope in Lookout Ck. at 1,100 m.

Brachythecium oedipodium (Mitt.) Jaeg.—Scattered, in low abundance on debris on transition slopes and hillslopes. 420–940 m.

Brachythecium velutinum (Hedw.) Schimp.—Scattered and fairly abundant, mainly growing on litter on hillslopes. 570–1,250 m, but most abundant at elevations above 900 m.

Bryoerythrophyllum recurvirostre (Hedw.) Chen—Scattered and fairly abundant on exposed soil in floodplains and transition slopes. 460–850 m, i.e. mainly a low elevation species.

Bryum pseudotriquetrum (Hedw.) G.M.S.—Rare and low abundant species of wet habitats. Two occurrences at 460 and 540 m in fairly large streams.

Bryum sp.—Scattered and low abundant mainly on soil. Leaf characters suggest *B. capillare* Hedw., but sterile conditions and small material makes identification unreliable and could represent more than one species. 460–940 m.

Buxbaumia piperi Best—Rare and low abundant species occurring only on highly decayed wood. Apparently restricted to wood with cubic brown rot in these stands. Three occurrences with a single or a couple of capsules in each case. Potentially overlooked related to small size and extremely scattered occurrence. On hillslopes by tributaries to Lookout Ck. at 570 m and 1,150 m and at Mack Ck. 850 m.

Claopodium bolanderi Best, *Claopodium crispifolium* (Hook.) Ren. & Card.—Both species common and abundant on decaying wood, stem bases, and boulders. No separation of substrates seems to be present as suggested by Lawton (1971). Instead, they show strong elevation separation, with *C. crispifolium* dominating below 800 m and *C. bolanderi* above. Both species, however, occur over the entire elevational range.

Claopodium whippleanum (Sull.) Ren. & Card.—Scattered and fairly abundant on exposed soil under a wide range of conditions. 420–1,250 m.

Dichodontium pellucidum (Hedw.) Schimp.—Scattered and fairly abundant on boulders and stones in and close to streams of all sizes. 430–1,250 m.

Dicranoweisia cirrata (Hedw.) Lindb.—Rare, in low

abundance on decaying wood. Two occurrences on transition slope and stream terraces at 540 and 580 m in Lookout Ck.

Dicranum fuscescens Turn.—Very common and very abundant species on decaying wood and coniferous stem bases at a wide range of conditions. 420–1,250 m. Some specimens might belong to var. *flexicaule* (Brid.) Wils., however no serious attempt was made to distinguish between the two varieties.

Dicranum howellii Ren. & Card.—Very common and abundant on large logs and on the forest floor. Primarily at lower elevations and less common close to the streams. 420–1,100 m. The presence of the closely related *D. scoparium* Hedw. has not been possible to verify. Many specimens were fertile and the character of the perichetal leaves consistently agrees with *D. howellii*.

Dicranum tauricum Sapeh.—Very common, but only fairly abundant on decaying wood under a wide range of conditions. A few occurrences on stem bases of large conifers. 460–1,250 m.

Ditrichum montanum Leib.—Rare, in low abundance on exposed soil. One occurrence on a hillslope by McRae Ck. at 940 m.

Eurhynchium oregonum (Sull.) Jaeg.—Very common and very abundant species on drier ground and on tops of large logs. The most abundant species in the study with an average cover of almost 16%; occurring in 89% of all samples. It is, however, less dominant at elevations >1,000 m where it is replaced by *Rhytidiopsis robusta* as the dominant forest floor species. 420–1,250 m.

Eurhynchium praelongum var. *stokesii* (Turn.) Dix.—Very common and very abundant species on moist ground. Characteristic for higher portions of the lowest geomorphic surfaces, and often dominant on boulders and cobbles just above the water level. 420–1,250 m.

Fissidens bryoides Hedw.—Scattered and low abundance on moist exposed soil in shaded conditions. Occurs all the way up to the hillslope as long as substrate requirements are fulfilled. Probably a low elevation species, 420–630 m.

Fissidens ventricosus Lesq.—Scattered and fairly abundant on stones and boulders in permanent streams. A low elevation species, most abundant in small streams. 420–850 m.

Fontinalis neomexicana Sull. & Lesq.—Scattered and fairly abundant species growing attached to stones in streams. Shows strong affinity to small to medium streams at middle elevations (600–1,000 m). Some poorly developed specimens were difficult to clearly identify however, the lack of good material of *F. antipyrretica* indicates the absence of the latter.

Heterocladium dimorphum (Brid.) Schimp.—Rare, in low abundance on exposed soil. One hillslope occurrence at 1,150 m at Lookout Ck.

Heterocladium macounii Best—Scattered and fairly abundant on exposed soil under a wide range of conditions. 580–1,150 m.

Heterocladium procurrans (Mitt.) Jaeg.—Scattered and of low abundance on boulders and soil, mainly occurring on hillslopes. 470–820 m.

Homalothecium fulgescens (C. Müll.) Lawt.—Scattered and low abundance epiphyte of deciduous trees and thus most common on floodplains and terraces. Potentially a low elevation species, 420–760 m.

Homalothecium nuttallii (Wils.) Jaeg.—Common and abundant epiphyte on deciduous trees, with its major occurrence on stream terraces at low elevations. 420–940 m.

Hookeria lucens (Hedw.) Sm.—Scattered, in low abundance on moist soil and decaying wood. Most abundant on transition slope at low elevations. 420–780 m. Appears

to be much more common in similar habitats in the Coastal Mountain Range.

Hygrohypnum duriusculum (De Not.) Jamieson.—Rare, in low abundance on boulders in streams. One single occurrence in Lookout Ck. at 1,030 m.

Hygrohypnum ochraceum (Wils.) Loeske.—Common and abundant on stones and boulders in streams. Mainly abundant in larger streams. 420–1,250 m. The dominant type in the studied streams has non-falcate leaves and more or less complanate shoots. The occurrence of this type has been noted as typically occurring deeper in water than the common form with falcate leaves (Slack & Glime 1985). Too few samples of the common type occurred to evaluate their water depth distribution in the present study.

Hylacomium splendens (Hedw.) Schimp.—Very common and very abundant on the forest floor and on the tops of logs. Less abundant at the lowest geomorphic surfaces and at elevations above 800 m. 420–1,150 m.

Hypnum circinale Hook.—Very common and very abundant on logs and coniferous stem bases under all conditions. 420–1,250 m.

Hypnum subimponens Lesq.—Common and abundant on boulders and logs. Most abundant along larger streams, but occurring on all geomorphic surfaces. 420–1,140 m.

Isopterygiopsis pulchella (Hedw.) Iwats.—Rare, in low abundance on organic debris. One occurrence in Lookout Ck. on a stream terrace at 850 m.

Isothecium cristatum (Hampe) Robins.—Rare, in low abundance mainly on boulders. Only two occurrences along Mack Ck. at 780 and 850 m. Although commonly epiphytic only seen on boulders within the studied area.

Isothecium stoloniferum Brid.—Very common and very abundant epiphyte. Also occurring on boulders, fallen twigs, and branches, as well as on large logs, sometimes on the ground. The most abundant epiphyte and the second-most common species with an average cover of 5%; occurring in 87% of all samples. Truly ubiquitous, occurring at all elevations and stream sizes. 420–1,250 m. Notable for its wide range of growth forms from more or less pinnately and densely branched shoots through loose wefts to pendent stoloniferous shoots.

Leucolepis acanthoneuron (Schwaegr.) Lindb.—Very common and very abundant on moist ground, sometimes on highly decayed logs and large boulders. Characteristic species for floodplains at low elevations. 420–1,140 m. It is partly replaced by *Brachythecium frigidum* at higher elevations.

Metaneckera menziesii (Hook.) Steere.—Rare and low abundant epiphyte on deciduous tree stems. Only two occurrences at 520 m in Lookout Ck. and at 750 m in Mack Ck.

Mnium cf. ambiguum H. Müll.—Rare and low abundance on moist soil. One occurrence on floodplain at 850 m along Mack Ck. Presence of this species in North America is questioned (Anderson et al. 1990). The present specimen is not well developed and the identification is tentative.

Mnium spinulosum Bruch & Schimp.—Scattered and fairly abundant on logs and soil covered boulders on hillslopes. 760–1,250 m and apparently somewhat restricted to higher elevations.

Neckera douglasii Hook.—Very common and abundant epiphyte on both conifers and deciduous trees. Most abundant on stream terraces along larger streams at low elevations. 420–940 m.

Orthotrichum affine Brid.—Rare and low abundant epiphyte on deciduous trees. Only one occurrence on a stream terrace by Lookout Ck. at 420 m.

Orthotrichum lyellii Hook. & Tayl.—Rare and low

abundant epiphyte in deciduous trees. Only one occurrence along Lookout Ck. at 570 m.

Orthotrichum rivulare Turn.—Scattered and low abundant species occurring on twigs and boulders close to streams. Only at low elevations along Lookout Ck. 420–580 m.

Orthotrichum speciosum Nees.—Common and fairly abundant epiphyte on twigs and branches of deciduous trees. Most abundant on stream terraces and lower geomorphic surfaces. The only common *Orthotrichum* in the study area and the only one occurring at higher elevations. 420–1,150 m.

Philonotis fontana (Hedw.) Brid.—Rare, in low abundance on moist soil. Only two occurrences at low geomorphic surfaces, 540 m in Lookout Ck. and 630 m in McRae Ck. The specimens from the sample plots were tiny and it is difficult to have opinions on what variety they belong to. I have seen specimens from several other riparian areas in the studied forest corresponding to var. *falcata* (Hook.) Brid.

Plagiomnium insigne (Mitt.) T. Kop.—Very common and abundant species growing on moist ground, primarily in transition slopes and stream terraces at all elevations and stream sizes. 420–1,250 m.

Plagiomnium rostratum (Schrad.) T. Kop.—Scattered and fairly abundant on wet soil. Mainly on low geomorphic surfaces and at lower elevations. 420–850 m.

Plagiothecium cavifolium (Brid.) Iwats.—Rare and low abundant on exposed soil and litter. All occurrences from one site along Lookout Ck. at 1,150 m. At that particular site fairly common and abundant, with several occurrences from the stream channel and along the entire hillslope.

Plagiothecium curvifolium Limpr.—Frequency and abundance uncertain. This taxon is by some considered to be within the variation of *P. laetum*. However, several specimens with characters typical of *P. curvifolium* (larger size, leaf apices turned towards the ground, long curved capsules, and broad leaf decurrences) were observed.

Plagiothecium denticulatum (Hedw.) Schimp.—Rare, in low abundance on exposed soil and boulders. Only four occurrences along Lookout Ck. 420–760 m.

Plagiothecium laetum Schimp.—Common and fairly abundant on highly decayed wood and sometimes on exposed humus rich soil. 460–1,250 m. The most common *Plagiothecium* in the area.

Plagiothecium undulatum (Hedw.) Schimp.—Scattered and fairly abundant species occurring mainly on the ground on terraces and hillslopes. 480–770 m and typical for lower elevation hillslopes. Appears to be much more common in similar habitats in the Coastal Mountain Range.

Pohlia cruda (Hedw.) Lindb.—Rare, in low abundance on dry but shaded soil. Only one occurrence in McRae Ck. at 940 m on a transition slope.

Pohlia nutans (Hedw.) Lindb.—Rare and low abundance species of disturbed sites. Only one occurrence in McRae Ck. at 580 m on a stream terrace. The rarity of this usually weedy and common species is striking and indicative of the low degree of human disturbance in the area.

Polytrichum lyallii (Mitt.) Kindb.—Rare and low abundance species growing on ground. Only three occurrences of a few shoots from a wide elevation range, 430–1,150 m.

Polytrichum juniperinum Hedw.—Scattered and fairly abundant species growing on disturbed soil. 470–940 m and apparently a low elevation species most common on transition slopes. Apparently *P. commune* Hedw. is rare or absent in the area, no specimens of this species were

present in OSC, UO, or J. H. Lyford private herbarium, and I have not been able to locate it in the field.

Porotrichum bigelovii (Sull.) Kindb.—Scattered and fairly abundant epiphyte, strongly restricted to thin branches of deciduous shrubs, such as *Acer circinatum*. 460–850 m and apparently a low elevation species.

Pseudoleskea stenophylla Ren. & Card.—Scattered and fairly abundant epiphyte, strongly restricted to thin branches of deciduous shrubs, such as *Acer circinatum*. 560–1,250 m, however only common above 1,000 m.

Pseudotaxiphyllum elegans (Brid.) Iwats.—Common and abundant on exposed soil, highly decayed wood, and litter in shaded situations. Typical for transition slopes and most abundant along smaller streams at high elevations. 460–1,150 m.

Pterigyantrum filiforme Hedw.—Rare and low abundant epilithic species. One occurrence on a boulder in a transition slope in Lookout Ck. at 850 m.

Racomitrium aciculare (Hedw.) Brid.—Common and abundant species characteristic of wet rocks and boulders in or close to streams. 460–1,250 m. Common in streams of all elevations and sizes.

Racomitrium canescens (Hedw.) Brid. *s. lat.*—Rare but fairly abundant on top of large boulders. Only occurring at three sites, but when present abundant and forming extensive patches in floodplains. 520–580 m.

Racomitrium heterostichum (Hedw.) Brid. *s. str.*—Rare but fairly abundant on dry boulders on terraces and hillslopes. Only occurring at two sites but abundant at these, Lookout Ck. at 540 m and McRae Ck. 940 m. The *R. heterostichum* group is species rich in the region (Frisvoll 1988), however, only *R. heterostichum s. str.* and *R. occidentale* were found.

Racomitrium occidentale (Ren & Card.) Ren. & Card.—Rare and low abundance species on boulders, mainly on hillslopes. Only four occurrences along McRae Ck. and Lookout Ck. all at high elevations, 1,140–1,250 m.

Racomitrium varium (Mitt.) Jaeg.—Common and abundant species on boulders and rocks. Strongly associated with floodplains. 460–1,140 m. The most common species of *Racomitrium* in the study area.

Rhizomnium glabrescens (Kindb.) T. Kop.—Very common and very abundant species mainly occurring on decaying wood but to some extent on the forest floor. Occurs at all elevations, stream sizes, and geomorphic surfaces. 420–1,250 m.

Rhizomnium magnifolium (Horik.) T. Kop.—Scattered and fairly abundant species on moist soil at low geomorphic surfaces. 470–850 m and probably a low elevation species.

Rhytidiadelphus loreus (Hedw.) Warnst.—Common and abundant species growing on the forest floor and on top of large logs. No particular affinity to elevation, stream size, or geomorphic surface. 470–1,100 m.

Rhytidiadelphus triquetrus (Hedw.) Warnst.—Very common and very abundant forest floor species. Strongly associated with low elevation and higher geomorphic surfaces. 420–1,100 m.

Rhytidiopsis robusta (Hook.) Broth.—Common and very abundant forest floor species sometimes occurring on large logs. Restricted to high elevation sites (above 1000 m) where it dominates on the forest floor and replaces *Eurhynchium oregonum*, *Hylocomium splendens*, and *Rhytidiadelphus triquetrus*. 560–1,250 m.

Roellia roellii (Broth.) Andr.—Scattered, in low abundance on the forest floor, mainly on hillslopes. Usually only a few shoots at each site. 630–1,250 m, mostly above 1000 m.

Schistidium rivulare (Brid.) Podp.—Rare, in low abun-

dance on boulders in and close to streams. Only two occurrences at 520 m in Lookout Ck. and at 940 m in McRae Ck.

Scleropodium obtusifolium (Jaeg.) Kindb.—Common and abundant on boulders and rocks in and close to stream channels. Most common in larger streams and the most abundant aquatic species in the study. 420–1,140 m.

Scleropodium tourettii (Brid.) L. Koch v. *colpophyllum* (Sull.) Lawt.—Scattered and fairly common on stones and boulders in or close to streams. 420–1,140 m. The occurrence of this taxon associated with wet conditions close to streams differs from the description given by Lawton (1971). In the study area it showed almost the same habitat demands as *S. obtusifolium*, however not as common.

Scouleria aquatica Hook.—Scattered but low abundant species on boulders in or close to streams. 620–1,140 m and somewhat more abundant at higher elevations.

Tetraphis pellucida Hedw.—Scattered and fairly abundant on decaying wood. Restricted to cubic brown rot and occurring at primarily low elevations. 480–820 m.

Thamnobryum neckeroides (Hook.) Lawt.—Rare, in low abundance on boulders. Only four occurrences, all at fairly high elevations, 750–1,150 m.

Trachybryum megaptilum (Sull.) Schof.—Scattered but abundant forest floor species. Most abundant on and characteristic for hillslopes above 800 m. 470–1,250 m.

HEPATIC

Anastrophyllum sp.—Rare, in low abundance on boulders by streams. Only one occurrence of this unidentified species at 630 m in McRae Ck. The specimen clearly belongs to *Anastrophyllum*, but does not seem to fit any described species of western U.S.A.

Asterella sp.—Rare, in low abundance on exposed soil in transition slope. One occurrence at 540 m in a 3rd order tributary to Lookout Ck. The tiny and sterile specimen could not be properly identified to species.

Blepharostoma arachnoideum M. A. Howe—Rare, in low abundance on decayed wood above the water level but in or close to small streams. Three occurrences of this tiny hepatic in Lookout Ck.: the main channel at 1,100 m, a 1st order tributary at 430 m, and a 2nd order tributary (Shorter Ck.) at 820 m.

Blepharostoma trichophyllum (L.) Dum.—Very common and abundant on decaying wood, occasionally growing on shaded, moist portions of boulders. At 420–1,250 m.

Calypogeia azurea Stotler & Crotz—Rare and low abundant species on highly decayed wood. All five occurrences in 1st and 2nd order streams and in a narrow elevational range, at 760–850 m.

Calypogeia fissa (L.) Raddi, *Calypogeia muelleriana* (Schiffn.) K. Müll.—Common and fairly abundant on decaying wood and exposed humus rich soil. Occurring on all geomorphic surfaces and over the entire elevation gradient, 430–1,150 m. Both species are present; however, the presence of many tiny and poorly developed specimens made a clear distinction between the two species impossible.

Cephalozia bicuspidata (L.) Dum.—Scattered but fairly abundant on decaying wood and on moist exposed soil. At 480–1,250 m and occurring on all geomorphic surfaces. My impression is that this species is more abundant on wood in similar situations in the Coast Range where it to some extent replaces *C. lunulifolia*.

Cephalozia lunulifolia (Dum.) Dum.—Very common and abundant species on decaying wood of all types. Although present over the entire elevational gradient it is less abundant below 600 m. At 420–1,250 m.

Cephaloziella divaricata (Sm.) Schiffn.—Rare, in low abundance on decaying wood. Four occurrences on wood in fairly dry conditions and at higher elevations. At 760–1,250 m.

Cephaloziella rubella (Nees) Warnst.—Scattered and low abundant species on decaying wood mainly on floodplains and on transition slopes. Apparently mainly a low elevation species, 460–900 m.

Chiloscyphus bidentata (L.) Engel & Schust., *Chiloscyphus cuspidatus* (Nees) Engel & Schust.—Scattered and low abundance on decaying wood. Mainly occurring on floodplains, transition slopes, and stream terraces. Mainly a low elevation species, only found once above 850 m. At 470–1,140 m. Both species are present, but as sexual condition is needed for accurate identification, many sterile specimens could not be identified to species.

Chiloscyphus pallescens (Hoffm.) Dum.—Rare, in low abundance on wet ground and sometimes on logs close to streams. At 460–1,140 m. Some uncertainties are encountered in separating sterile specimens of this taxon from *C. polyanthos* as the number of oil bodies per cell seems variable; however, both taxa do occur in the study area.

Chiloscyphus polyanthos (L.) Corda—Common and abundant, usually submerged on boulders and rocks in streams. Together with *Scapania undulata*, the most common aquatic hepatics. Tends to be more common in large streams. At 420–1,250 m.

Chiloscyphus profundus (Nees) Engel & Schust.—Very common and fairly abundant on wood of many types. Most abundant on hillslopes close to smaller streams. At 430–1,250 m.

Conocephalum conicum (L.) Lindb.—Scattered but abundant species characteristic of moist ground on higher portions of active channels and floodplains. Most abundant at higher elevations. 430–1,150 m.

Douinia ovata (Dicks.) Buch.—Scattered, in low abundance on decaying wood and fallen branches in the forest floor. Occurs at lower elevation on hillslopes and terraces. 420–760 m. This species is apparently typical of the lower side of branches in the tree canopy (Sillett 1995); branches were not sampled in the present study and the occurrences may represent marginal habitats for the species.

Frullania bolanderi Aust.—Rare and low abundance epiphyte on stems of deciduous trees. One occurrence along Lookout Ck. at 580 m on *Acer macrophyllum* on stream terrace. Potentially overlooked; its small size and colour blend with the maple bark.

Frullania californica M.A. Howe—Scattered and low abundance epiphyte on deciduous tree stems. Mainly on *Alnus rubra* on low elevation stream terraces. At 420–820 m. Easily overlooked; superficially resembling *F. nisquallensis*.

Frullania nisquallensis Sull.—Common and fairly abundant epiphyte on stems of deciduous trees in terraces and on hillslopes. Mainly on *Alnus rubra* at low elevations. The most common *Frullania*. At 420–1,100 m.

Geocalyx graveolens (Schrad.) Nees—Common and fairly abundant on decaying logs close to streams. A characteristic epixyl on the lower sides of large wet logs at lower elevations. At 420–850 m.

Gymnocolea inflata (Huds.) Dum.—Rare, in low abundance on wet ground. One occurrence in McRae Ck. at 1250 m. Identification based on poorly developed and sterile material.

Jamesoniella autumnalis (DC.) Steph.—Rare, in low abundance on moist humus in stream terrace. One occurrence at 940 m. at McRae Ck. Identification based on poorly developed and sterile material.

Jungermannia exsertifolia ssp. *cordifolia* (Dum.)

Vana—Scattered and fairly abundant on submerged rocks and boulders in streams. Most abundant at high elevations. At 460–1,150 m. Usually with a distinctive 'carrot-like' smell.

Jungermannia leiantha Grolle—Scattered and low abundant species on decaying logs close to streams. Low elevation species with similar habitat demands as *Geocalyx graveolens*. At 430–820 m.

Jungermannia pumila With.—Rare, in low abundance on submerged rocks and boulders in streams. Similar habitat to *J. exsertifolia* ssp. *cordifolia*, but much smaller in size and with less pronounced smell. At 470–1,030 m.

Lepidozia reptans (L.) Dum.—Common and abundant on decaying wood and bases of large conifer stems. At all elevations and geomorphic surfaces. At 460–1,150 m.

Lophozia incisa (Schrad.) Dum.—Scattered, in low abundance on decaying logs and sometimes at bases of large conifers. Absent at higher elevations, 520–820 m.

Lophozia longiflora (Nees) Schiffn.—Scattered, in low abundance on decaying logs. Primarily occurring on hillslopes at higher elevations. At 850–1,250 m.

Marchantia polymorpha L.—Rare, in low abundance on moist exposed soil. Only one occurrence in an old dry stream channel at Lookout Ck., 520 m. This species is otherwise typical of artificially disturbed sites.

Marsupella emarginata (Erhr.) Dum.—Rare, in low abundance on boulders close to streams. Four occurrences from floodplains and transition slopes, at 460–1,030 m.

Pellia neesiana (Gott.) Limpr.—Rare, in low abundance on moist exposed soil close to streams. At 620–1,150 m. All fertile specimens were dioicous, however, a sterile specimen could potentially belong to *P. epiphylla* (L.) Corda.

Plagiochila asplenoides (L.) Dum.—Rare, in low abundance on moist ground. Only one specimen could clearly be placed in this species. On a stream terrace along McRae Ck. at 620 m.

Plagiochila porelloides (Nees) Lindenb.—Common and fairly abundant, mainly growing on soil covered boulders close to streams. At 460–1,150 m. Some large specimens might belong to *P. asplenoides*.

Porella cordaeana (Hueb.) Moore—Scattered, in low abundance on moist soil and boulders close to streams. Primarily at higher elevations. At 520–1,150 m. No specimen was found on tree stems in the studied area.

Porella navicularis (Lehm. & Lindenb.) Pfeiff.—Very common and abundant epiphyte on both branches and stems of conifers and deciduous trees. The most common epiphytic hepatic. Occurs on all geomorphic surfaces but most abundant at lower elevations. At 420–1,150 m.

Ptilidium californicum (Aust.) Underw.—Very common and abundant epiphyte and wood species. Typical on small conifers on higher geomorphic surfaces and a pronounced high elevation species. At 480–1,250 m.

Radula bolanderi Gott., *Radula complanata* (L.) Dum.—Common and fairly abundant epiphytes on stems and branches of both conifers and deciduous trees. I have the impression that *R. bolanderi* is somewhat more common on conifers and at higher elevations than *R. complanata*. Both species range from 420 to 1,150 m.

Riccardia latifrons (Lindb.) Lindb.—Scattered and fairly abundant on decaying wood and sometimes on wet soil. Very common on the ends of cut logs. At 460–1,100 m.

Riccardia multifida (L.) S. Gray—Scattered and fairly abundant on decaying wood and moist soil and pebbles. On average usually closer to streams than *R. latifrons*. At 430–1,100 m.

Riccardia palmata (Hedw.) Carruth.—Rare, in low

abundance on decaying logs. Only one occurrence on wood in the active channel along Lookout Ck. at 760 m.

Scapania americana K. Muell.—Scattered and fairly abundant on disturbed ground mainly close to streams. More common in smaller streams. At 430–1,150 m.

Scapania bolanderi Aust.—Very common and very abundant on logs and conifer stem bases. The most abundant hepatic in the study area, occurring at all elevations, stream sizes, and geomorphic surfaces. At 420–1,250 m.

Scapania umbrosa (Schröd.) Dum.—Very common and fairly abundant on decaying logs. Often mixed with *S. bolanderi* but usually closer to the stream and apparently demanding moister wood. At 420–1,250 m.

Scapania undulata (L.) Dum.—Common and abundant on wet and submerged rocks and boulders in streams. More common at high elevations. At 430–1,250 m. Only specimens in or close to water were found of this otherwise wide-ranging and polymorphic species.

ADDITIONAL SPECIES REPORTED FROM H. J. ANDREWS EXPERIMENTAL FOREST

Although not necessarily occurring in riparian areas, the following species have been found within the experimental forest. For each species, collector, year, specimen number, herbarium reference, and literature reference are given when available.

Mosses.—*Antitrichia californica* Sull.—Tracey, osc B23; Pike et al. 1975. *Bryum capillare* Hedw.—Pike et al. 1975. *Ceratodon purpureus* (Hedw.) Brid.—Sherwood 86, osc B654. *Dendroalsia abietina* (Hook.) Britt.—Christy 7218 osc B2316; Pike et al. 1975. *Funaria hygrometrica* Hedw.—Lyford, 1975 Lyford private herb. 70. *Oligotrichum aligerum* Mitt.—Jonsson 462A/94. *Orthotrichum consimile* Mitt.—Pike et al. 1975. *Plagiommium venustum* (Mitt.) T. Kop.—Tracy osc B16; Sawbridge 72171, osc B1119; Pike et al. 1975. *Scleropodium cespitans* (C. Müll.) L. Koch.—Lyford, 1976 Lyford private herb. 609. *Ulota megalospora* Vent.—Jonsson 172/94.

Hepatics.—*Anthoceros punctatus* L.—Sherwood osc B668. *Anthoceros* sp.—Wagner 1474, uo 104098. *Cephaloziella turneri* (Hook.) K. Muell.—Pike 3463, osc B947. *Diplophyllum obtusifolium* (Hook.) Dum.—Jonsson 461C/94; Wagner 1831, uo 108022. *Diplophyllum taxifolium* (Wahlenb.) Dum.—Pike et al. 1975. *Gyrothya underwoodiana* M. A. Howe—Jonsson 172/94; Wagner 1831, uo 108022. *Lophozia bicrenata* (Schmid.) Dum.—Jonsson 461C/94. *Nardia scalaris* S. Gray.—Jonsson 461D/94. *Porella roellii* Steph.—Wagner 1812, uo 108332.

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