Corticolous bryophytes in managed Douglas-fir forests: habitat differentiation and responses to thinning and fertilization

Sean C. Thomas, Denise A. Liguori, and Charles B. Halpern

Abstract: Corticolous bryophytes, that is, mosses and liverworts that inhabit tree trunks, represent an important component of plant diversity in temperate ecosystems, but little is known of their ecology in managed forests. In this study, we quantified community composition and habitat differentiation of corticolous bryophytes in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations subjected to experimental thinning and fertilization treatments. Twenty-four bryophyte species were recorded in a sample of 480, 225 cm^2 quadrats on 60 tree trunks. All moss species and obligately epiphytic liverworts (those with a primary habitat preference for tree trunks) showed highest cover values on south and west exposures. In contrast, facultatively epiphytic liverworts occurred only at the tree base, and mainly on north and west exposures. Pairwise correlations among species cover values were nearly always positive, and cover of the most abundant species, *Isothecium myosuroides*, was also positively correlated with local species richness of other bryophyte taxa. These patterns suggest that competitive interactions among bryophyte species are not strong in this community. There was little evidence for fertilization or thinning effects on total bryophyte cover or species richness. However, analyses of community composition and species-specific responses indicated significant negative effects of thinning on some bryophyte species. Observed patterns of habitat differentiation, interspecific associations, and treatment responses suggest that stand hydrology and microclimate are of primary importance in determining the distribution and abundance of corticolous bryophytes in managed forests.

Key words: corticolous bryophytes, liverworts, mosses, nitrogen fertilization, plant diversity, silvicultural thinning.

Résumé : Les bryophytes corticoles, i.e., mousses et hépatiques qui vivent sur le tronc des arbres, constituent une importante composante de la diversité végétale dans les écosystèmes tempérés, mais on connaît peu de choses sur leur écologie dans les forêts aménagées. Les auteurs ont quantifié la composition et la différenciation de l'habitat des bryophytes corticoles dans des plantations de sapin Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) soumises à la fertilisation et à l'éclaircie expérimentales. On retrouve 24 espèces de bryophytes dans un échantillon de 480 quadrats, mesurant 225 cm^2, sur 60 tronc d'arbres. Toutes les espèces de mousse et d'hépatique épiphytes obligatoires (celles avec une préférence primaire pour les troncs d'arbre) montrent les plus fortes valeurs de couverture sous des expositions sud et ouest. Au contraire, les hépatiques épiphytes facultatives ne se retrouvent qu'à la base des arbres, et surtout sous des expositions nord et ouest. Les corrélations par paires entre les valeurs de couverture des espèces sont presque toujours positives et la couverture de l'espèce la plus abondante, l'*Isothecium myosuroides*, montre également une corrélation positive avec la richesse locale en espèces et autres taxons bryophytes. Ces deux patrons suggèrent que les interactions compétitives entre espèces de bryophytes ne sont pas fortes dans cette communauté. Il y a peu de preuve que la fertilisation ou l'éclaircie aient des effets sur la couverture totale des bryophytes ou la richesse en espèces. Cependant, les analyses de composition de la communauté et les réactions spécifiques à l'espèce indiquent qu'il y a des effets négatifs significatifs de l'éclaircie sur certaines espèces de bryophytes. La différenciation des patrons de l'habitat observée, les associations interspécifiques, et les réactions aux traitements suggèrent que l'hydrologie de la station et le microclimats sont de première importance dans la détermination de la distribution et de l'abondance des bryophytes corticoles dans les forêts aménagées.

Mots clés : bryophytes corticoles, hépatiques, mousses, fertilisation azotée, diversité végétale, éclaircie sylvicole.

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S.C. Thomas,[1,2] D.A. Liguori, and C.B. Halpern. Division of Ecosystem Sciences, College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195, U.S.A.

[1] Corresponding author (e-mail: sc.thomas@utoronto.ca).

[2] Present address: Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, ON M5S 3B3, Canada.

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Introduction

Corticolous bryophytes, that is, moss and liverwort species characteristically found on live tree trunks, contribute significantly to plant diversity in temperate forests. In the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) region of the Pacific Northwest, more than 60 native bryophyte species are primarily or exclusively trunk inhabiting (Lawton 1971; Schofield 1976; Jonsson 1996; D.H. Wagner, personal communication). In addition, numerous bryophytes mainly associated with humus or woody debris (humicolous and xylicolous species) also commonly occur on tree bases (e.g., Barkman 1958; Pike et al. 1975; Söderström 1993; Peck et al. 1995*b*). Although a large proportion of forest lands in the Pacific Northwest region are now managed on rotation lengths of ~40–100 years, essentially all research on corticolous bryophytes has been conducted in mature or old-growth stands. This emphasis is found in both descriptive floristic accounts (Coleman et al. 1956; Hoffman and Kazmierski 1969; Pike et al. 1975) and quantitative ecological surveys (Pechanec and Franklin 1968; Hoffman 1971; Peck et al. 1995*a*, 1995*b*; Lyons et al. 2000). A similar emphasis also prevails outside of the Pacific Northwest (Palmer 1986; Schmitt and Slack 1990; Söderström 1993; Kuusinen 1996; Hornberg et al. 1997; but see Frisvoll and Prestø 1997). Some data are available on bryophyte occurrence in older (>70 years) second-growth stands, particularly on forest floor and decaying wood substrates (Lesica et al. 1991; Rambo and Muir 1998*a*, 1998*b*). However, essentially no information is available on distribution patterns or responses to management of corticolous bryophytes in young, intensively managed forests.

Canopy epiphytes are a conspicuous element of forests in the Pacific Northwest region and have been the subject of numerous recent studies, including analyses of forest management impacts (e.g., Lesica et al. 1991; McCune 1993; Sillett et al. 2000). In contrast, corticolous bryophytes characteristically found near the base of tree trunks have received more limited attention, although many of these species are also of conservation concern (FEMAT 1993). The present study seeks to describe corticolous bryophyte communities in managed forests representative of much of the lowland western hemlock zone, in particular species-specific distributional patterns and responses to two widespread management practices: thinning and nitrogen fertilization. We also briefly compare our results with previous surveys in late-successional forests, noting the important limitation that directly comparable old-growth stands no longer exist in the region surveyed.

Because bryophytes are small and generally lack the waxy leaf cuticle found in vascular plants, desiccation is a critical aspect of bryophyte ecology (Proctor 1990). Young forest stands, particularly prior to stand closure, experience a higher peak temperature and lower ambient humidity than do old forests (Ahlgren 1981; Myakushko and Plyuta 1985; Chen et al. 1993, 1995; Arnott and Beese 1997). This may result in increased water stress among bryophytes in young stands. Corticolous species are also affected by removal of all or most of their substrate (i.e., tree trunks) during harvest operations, and must recolonize trees in young stands. Disturbance effects, substrate limitations, and increased exposure to drought might be expected to result in reduced abundance or local extinction of corticolous byrophytes in young stands. Desiccation tolerance may also be of central importance in determining patterns of distribution and abundance among those species that do persist.

Silvicultural thinning and addition of nitrogen fertilizers are two of the most common intermediate silvicultural treatments used in Douglas-fir plantations west of the Cascade Range (Bengtson 1979; O'Hara 1989; Chappell et al. 1992). Thinning generally results in increased light penetration into the understory and in an increased abundance and diversity of vascular understory plants (Bailey et al. 1998; Thomas et al. 1999). Thinning may also lead to higher subcanopy temperature maxima, increased subcanopy air movement, and reduced ambient humidity (Cheo 1946; Aussenac 1987; Bartos and Amman 1989; Green et al. 1995). Corticolous bryophytes that are sensitive to desiccation could, therefore, be adversely affected by thinning. Nitrogen fertilization at high dosages reduces the abundance and diversity of understory vegetation, a response due, in part, to direct toxic effects when urea is used as a nitrogen source (Kellner 1993; Thomas et al. 1999). Forest floor bryophytes may be particularly sensitive to nitrogen fertilization (Malysheva 1981; Kellner 1993; Makipaa 1995). However, corticolous bryophytes that are attached to a bark substrate above the forest floor are likely to be buffered from the direct effects of altered soil chemistry or volatilization of ammonia following fertilizer additions. If fertilization accelerates stand closure, fertilization might actually favor bryophyte species sensitive to desiccation. We are aware of no prior experimental studies examining the effects of either silvicultural thinning or fertilization on corticolous bryophytes.

The present study takes advantage of a series of long-term experimental plots involving a factorial design of thinning and urea fertilization in Douglas-fir plantations in western Washington state, U.S.A. We pose the following questions: (1) What bryophyte species are found on tree stems in young Douglas-fir plantations? (2) How are bryophyte species distributed with respect to height and aspect on tree trunks in young stands? (3) How do corticolous bryophytes respond to silvicultural thinning and nitrogen fertilization, and do these responses differ from those of understory vascular plants (as reported in a parallel study by Thomas et al. 1999)?

Materials and methods

Experimental design

The study was conducted in Douglas-fir plantations on Weyerhaeuser Company lands in western Washington state. Stands were within the "stem exclusion" stage (sensu Oliver 1981) at the time of sampling, and ranged in age from 25 to 28 years. Sample locations were a subset of those utilized in a companion study examining responses of vascular plants to thinning and nitrogen fertilization (see Table 1 in Thomas et al. (1999)), and included Griffin Creek (47°30′N, 122°00′W), Lucas Creek (46°30′N, 123°15′W), and Trestle Swamp (47°80′N, 121°15′W). Elevations ranged from 305 to 335 m, and slopes, from 5 to 15%. Vegetation was characteristic of the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Dominant herbaceous and shrub species included *Polystichum munitum* (Kaulf.) K. Presl, *Berberis nervosa* Pursh, *Gaultheria shallon* Pursh, and *Acer circinatum* Pursh (Thomas et al. 1999). All experimental stands were initially planted with 2-

year-old Douglas-fir stock at ~1680 trees/ha. Thinning and fertilizer addition treatments were implemented in a factorial design replicated at each location. "Precommercial" thinning treatments were conducted soon after stand closure, 8–11 years after planting, by which time the trees were ~6–10 cm DBH (diameter at breast height) with dominant individuals 5–7 m in height. Felled trees were systematically selected to yield relatively even tree spacing and were left in place. Thinning treatments examined in this study included a control (no thinning) and a relatively high level of thinning (final stem densities of 494 trees/ha). Fertilized plots were subjected to five repeated additions of granular urea at dosages of 49–64 kg $N \cdot ha^{-1} \cdot year^{-1}$, rates somewhat higher than those used operationally, but intended to evaluate maximal potential responses of the forest system. Treated plots measured 35.4 m on one side (1250 m^2) and were separated by untreated buffer regions of at least 53 m in width. Additional details regarding experimental treatments are given in Thomas et al. (1999).

Bryophyte sampling and ecological classification

In a prior study (Thomas et al. 1999), five sample points were established in each experimental unit. Points were arranged in a cross pattern, with one at the plot center and four others 5.6 m from the central point along perpendicular radii. The standing live tree nearest to each pre-established sampling point was sampled for bryophyte cover and species composition. In nearly every instance (58 of 60), sampled trees were planted Douglas-fir. One red alder (*Alnus rubra* Bong.) and one bigleaf maple (*Acer macrophyllum* Pursh.) were also sampled. Tree lean can be an important determinant of corticolous bryophyte distributions; however, trees sampled in this study showed negligible lean, so this factor was not considered. A 15 × 15 cm quadrat grid transposed on a transparent acetate sheet was placed at the cardinal directions (N, W, S, E) at two heights on each sampled tree: 0–15 cm (tree base quadrats) and 85–100 cm (stem quadrats). The quadrat image was pinned to the bark and percent cover of each bryophyte species was visually estimated. To visually guide cover estimates, the acetate quadrat image was marked with indicators of 1, 10, and 25% cover. Cover values estimated at <0.2% were scored as a "trace" and treated as 0.1% in statistical analyses. For estimated cover values >10%, the midpoints of each 10% interval (i.e., 15, 25,…, 95%) were used. Where field identifications were uncertain or not possible, specimens of each bryophyte were collected and labeled for verification in the laboratory.

Nomenclature for mosses and liverworts follows Anderson et al. (1990) and Stotler and Crandall-Stotler (1977), respectively. Voucher specimens were deposited in the University of Washington herbarium (WTU). Previously published descriptions were used to classify species as obligately or facultatively epiphytic. We use the first term to designate species showing a primary substrate affinity for live tree stems, even though such species do generally occur on a variety of substrates. We consider facultatively epiphytic species to be those showing a primary affinity for other substrates, primarily deadwood or humus. Sources for such descriptions included Lawton (1971), Schofield (1976), Smith (1990), and D.H. Wagner (personal communication).

Statistical analysis

The overall design of the study is a two-way factorial experiment with thinning and fertilization treatments applied in three geographically isolated locations, with subsampling of trees conducted within experimental plots. A mixed-model ANOVA (Underwood 1997) was used in analyzing variation in cover and species richness of mosses, liverworts, and total bryophytes. In addition to thinning and fertilization treatments, sampling height, aspect, and individual tree were considered as main effects. Details concerning nesting, designation of effects as "fixed" vs. "random", and corresponding estimated mean square terms are given in Table 1. Only a subset of possible interaction terms is included in the model; preliminary analyses indicated that most interaction terms of second order or higher were not close to significant and so were omitted. Variables did show moderate deviations from normality and homoscedasticity (e.g., 8.5% of sampled quadrats had no bryophyte cover), and these deviations were not readily removed by transformation. Analyses presented were conducted on nontransformed data, and probability levels should therefore be judged conservatively. Comparisons between cover and species richness in N vs. S and E vs. W quadrats were treated as a priori contrasts within each height class.

In addition to univariate analyses, we used nonparametric multiresponse permutation procedures (MRPP; Zimmerman et al. 1985) to test for differences in community composition among treatments and quadrat locations (height and aspect). Species cover values were not transformed prior to MRPP analysis, and all species were included in analyses reported. Permutations were conducted within experimental plots for MRPP tests of thinning and fertilization effects, and within trees for height and aspect effects. MRPP analyses were conducted using CANOCO v. 4.0 (ter Braak and Smilauer 1998). The test statistic used was the "trace" (sum of eigenvalues) of a redundancy analysis (RDA; ter Braak 1995), with 9999 permutations per test.

To compare responses to thinning and fertilization treatments among taxa differing greatly in average cover, we calculated response coefficients as in Thomas et al. (1999) and compared response coefficients among groups (e.g., bryophytes vs. liverworts) by ANOVA. The response coefficient values estimate the proportional response of a given species to a change of one "unit" of thinning or fertilization. The same general linear model specified in Table 1 was used in this analysis, but the thinning × fertilization term was omitted, and thinning and fertilization levels were treated as nominally continuous variables (scored as 0 and 1 for fertilization, and 0 and 3 for thinning). This latter designation was necessary to allow direct comparisons with prior results (Thomas et al. 1999), since only the most intense of three thinning levels in the original experiment was sampled in the present study. Slope coefficients for thinning and fertilization effects were divided by mean species' cover, averaged across all sample quadrats, to yield a scaled coefficient corresponding to the expected proportional change in cover per "unit" change in the treatment. Coefficients for vascular plant species were calculated using the same three replicates available for corticolous bryophytes so as to ensure comparability among groups. Thus, mean values and error estimates differ slightly from those reported in the larger sample by Thomas et al. (1999). A posteriori contrasts between groups used Scheffé's method (Sokal and Rohlf 1981).

Tests for directional effects on corticolous bryophyte distributions employed circular statistical techniques (Batschelet 1981). For each species, we calculated a weighted average angle as the vector sum of cover values in each cardinal direction (i.e., angle = $\arctan[(C_N - C_S)/(C_E - C_W)]$, where C_N, C_S, C_E, and C_W are the cover values in the N, S, E, and W directions, respectively, summed over the entire sample of 60 trees). We then used these species-specific angle values to test for deviations of groups of species from a uniform circular distribution using the Rayleigh test (Batschelet 1981). Probability levels for this test were estimated using the following (original) approximation function: $P = a/nr^2 + b\exp(-c\,nr^2)$, where P is the probability level, n is sample size, r is the mean vector magnitude, and a, b, and c are constants (a = –0.003 713 657 1; b = 1.035 204 45; c = 1.007 125 92). This expression explained more than 99.99% of the variation in tabulated probability levels over the range n = 5–200 and P = 0.001–0.9 (Table H in Batschalet 1981).

Spearman rank correlations were used to analyze pairwise associations among species cover values (e.g., O'Connor and Aarssen 1987). To test for deviations of association patterns from random expectation, we compared the observed frequencies of positive and

Table 1. Specification of effects and estimated mean square (EMS) values for the ANOVA model used in analyzing cover and species richness patterns of bryophytes.

Source of variance	Effect type	df	EMS	*F* denominator
Loc	Random	2	Tree + Loc	Tree
Thin	Fixed	1	Loc × Thin + Tree + Thin	Loc × Thin
Fert	Fixed	1	Loc × Fert + Tree + Fert	Loc × Fert
Tree	Random*	48	Tree	Error
Asp	Fixed	3	Asp	Error
Ht	Fixed	1	Ht	Error
Loc × Thin	Mixed	2	Loc × Thin + Tree	Tree
Loc × Fert	Mixed	2	Loc × Fert + Tree	Tree
Thin × Fert	Fixed	1	Thin × Fert + Tree	Tree
Ht × Asp	Fixed	3	Ht × Asp	Error
Error		415		
Total		479		

Note: Loc, location; Thin, thinning; Fert, fertilization; Asp, aspect; Ht, height.

*The tree term is nested within individual experimental plots (i.e., within location × thinning × fertilization combinations).

Table 2. List of corticolous plant species identified in systematic surveys of 60 trees (480 15 × 15 cm quadrats) in Douglas-fir plantations in western Washington.

	Species	Substrate	Frequency	Cover (%)
Mosses				
1	*Isothecium myosuroides* Bird.*	Cort, Gen	0.893	14.294
2	*Hypnum circinale* Hook.[†]	Cort, Gen	0.163	0.108
3	*Plagiothecium denticulatum* (Hedw.) Schimp.	Gen	0.084	0.199
4	*Eurhynchium praelongum* (Hedw.) Schimp.*	Hum	0.077	1.276
5	*Orthotrichum lyellii* Hook. & Tayl.	Cort	0.046	0.030
6	*Neckera douglasii* Hook.[‡]	Cort	0.044	0.059
7	*Rhizomnium glabrescens* (Kindb.) T. Kop.*[†,‡]	Xyl	0.031	0.004
8	*Plagiothecium undulatum* (Hedw.) Schimp.*[†]	Xyl	0.029	0.025
9	*Tetraphis pellucida* Hedw.[†]	Xyl	0.025	0.025
10	*Rhytidiadelphus loreus* (Hedw.) Warnst.	Hum	0.015	0.069
11	*Aulacomnium androgynum* (Hedw.) Schaegr.	Xyl	0.006	0.015
12	*Dicranum fuscescens* Turn.*[†]	Xyl	0.004	<0.001
Liverworts				
13	*Lophocolea heterophylla* (Schrad.) Dum.[†]	Cort, Gen	0.193	0.200
14	*Frullania nisquallensis* Sull.*[‡]	Cort	0.096	0.057
15	*Porella navicularis* (L. & L.) Lindb.	Cort	0.050	0.057
16	*Metzgeria conjugata* Lindb.[†]	Cort	0.019	0.006
17	*Radula bolanderi* Gottsche*[†]	Cort	0.017	<0.001
18	*Scapania bolanderi* Aust.	Xyl	0.011	<0.001
19	*Calypogeia muelleriana* (Schiffn.) K. Müll[†]	Hum	0.006	0.015
20	*Cephaloziella divaricata* (Sm.) Schiffn.*	Xyl	0.004	<0.001
21	*Calypogeia fissa* (L.) Raddi.[†]	Hum	0.002	0.008
22	*Lepidozia reptans* (L.) Dum.*[†]	Xyl	0.002	<0.001
23	*Lophocolea cuspidata* (Nees) Limpr.[†]	Cort, Gen	0.002	<0.001
24	*Radula complanata* (L.) Dum.	Cort, Sax	0.002	<0.001

Note: Species are arranged in descending order of frequency, with data pooled among all experimental treatments. Predominant substrate for each species (Cort, live tree stems; Hum, litter; Sax, rock; Xyl, dead wood; Gen, generalist) is based on prior literature.

*Old-growth indicator according to Rambo and Muir (1998*b*).

[†] Old-growth associated species according to FEMAT (1993).

[‡] Endemic to Pacific Northwest region.

negative pairwise correlations with null expectations generated by permuting observed species cover values among replicate sample quadrats. We used 100 permutations (57 576 total correlations) to generate the expected values. Other statistical methods (*G* tests, tests for nonzero correlation, and parametric *t* tests with unequal sample size) follow Sokal and Rohlf (1981).

Results

Community-level patterns

Twenty-four bryophyte species were recorded in systematic samples of 60 trees at the three study locations

(Table 2). The most common species encountered was *Isothecium myosuroides*, which was present in 89% of the quadrats. Other commonly encountered mosses included *Eurhynchium praelongum*, *Hypnum circinale*, *Plagiothecium denticulatum*, and *Orthotrichum lyellii*. Together, these five moss species accounted for >97% of total moss cover in all quadrats. Only three species of liverworts were found in >3% of the 480 sampled quadrats: *Lophocolea heterophylla*, *Frullania nisquallensis*, and *Porella navicularis*. These species accounted for ~90% of the total observed liverwort cover.

Total bryophyte cover averaged 22% on tree base quadrats (0–15 cm) vs. 11% on stem quadrats (85–100 cm). Data pooled across aspects showed a similar pattern for total moss and liverwort cover, with values averaging ~2 times higher for tree base than for stem samples. Differences between sampling heights were significant for moss cover (Fig. 1*a*), but not for liverwort cover (Fig. 1*b*). Pooled moss and liverwort cover values showed quite different directional patterns. Total moss cover was lower on northern aspects than on other aspects at both sampling heights (Fig. 1*a*), averaging 1.9-fold higher on the south than on the north side ($P < 0.001$; planned comparison *F* test). In contrast, total liverwort cover was much higher on the north side for tree base quadrats, with an average cover 3.6-fold greater than that of the south side ($P = 0.022$; planned comparison *F* test; Fig. 1*b*). Comparisons between east and west aspects did not reveal significant differences for total moss or liverwort cover at either sampling height.

Species richness for mosses followed a pattern similar to that found for total cover: higher at the tree base and slightly elevated at the south side in comparison to the north side of the tree ($P = 0.014$; planned comparison *F* test; Fig. 2*a*). Liverwort species richness was consistently higher on average at the tree base, but neither height nor directional effects were statistically significant (Fig. 2*b*). Differences in bryophyte communities between sampling heights and aspects were corroborated by MRPP tests, which were highly significant in both cases ($P = 0.0001$ for height; $P = 0.0013$ for aspect).

Species-specific distributions and neighbor relations

Most of the moss and liverwort species encountered showed pronounced patterns of habitat differentiation related to height (0–15 cm vs. 85–100 cm from the tree base) and aspect (Fig. 3). Species fell into four relatively distinct groups, which correspond to differences in taxonomic affiliation and primary substrate preference. Facultatively epiphytic mosses (species for which tree trunks are not a primary substrate) were predominantly found in tree base quadrats on south and west exposures. The two species of obligately epiphytic mosses (*Orthotrichum lyellii* and *Neckera douglasii*) and five species of obligately epiphytic liverworts were largely restricted to tree stem quadrats, with most species tending to occur on south and west exposures. The seven species of facultatively epiphytic liverworts, which occur primarily on dead woody debris (Table 2), were found only in tree base quadrats and with the greatest frequency on north exposures. The tendency for bryophytes of similar substrate affinity to display a similar directional distribution was examined using the Rayleigh test (Batschelet 1981). The observed patterns indicated significant deviations from a uniform circular distribution for facultatively epiphytic moss and liverwort species, and for bryophyte species as a whole (Table 3).

Pairwise rank correlations among species cover values re-

Fig. 1. Mean total cover of (*a*) moss and (*b*) liverwort species as a function of height and aspect on the stem. Tree base quadrats (open bars) were located at 0–15 cm height; tree stem quadrats (shaded bars) were located at 85–100 cm height. Significance levels are given for height, aspect, and height × aspect interaction terms in an ANOVA model that also included terms for thinning, fertilization, quadrat location, and individual tree variation (see Materials and methods). Mean values are plotted ±1 SE.

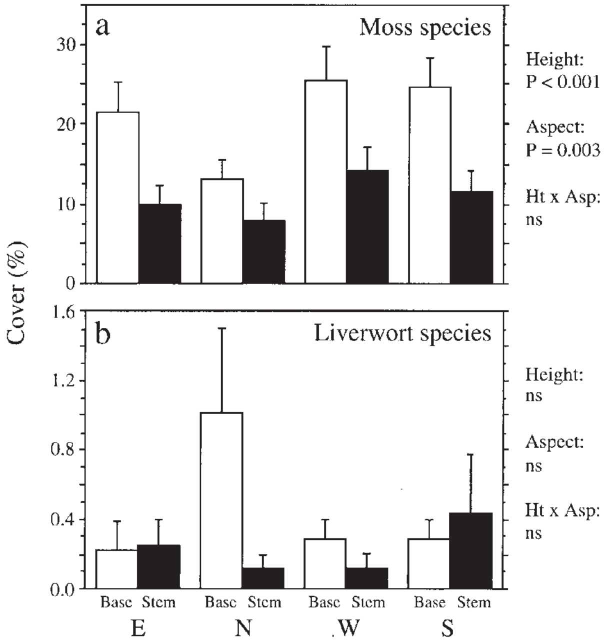


Fig. 2. Mean species richness per quadrat (15 × 15 cm) of (*a*) moss and (*b*) liverwort species as a function of height and aspect on the stem. See Fig. 1 for other details.

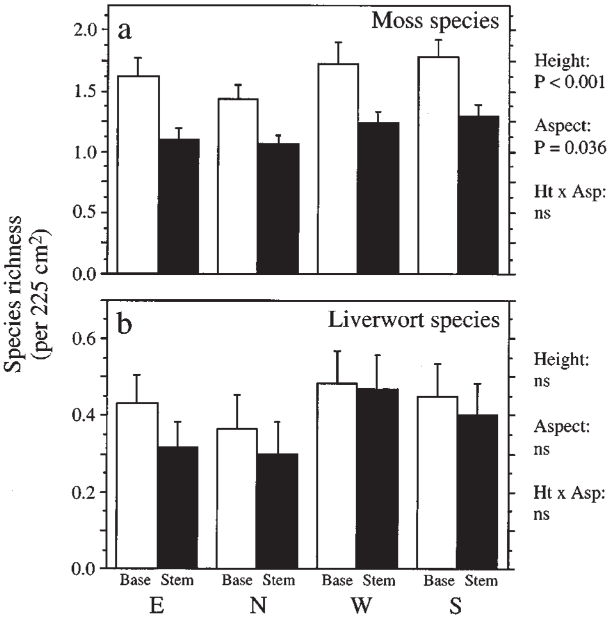
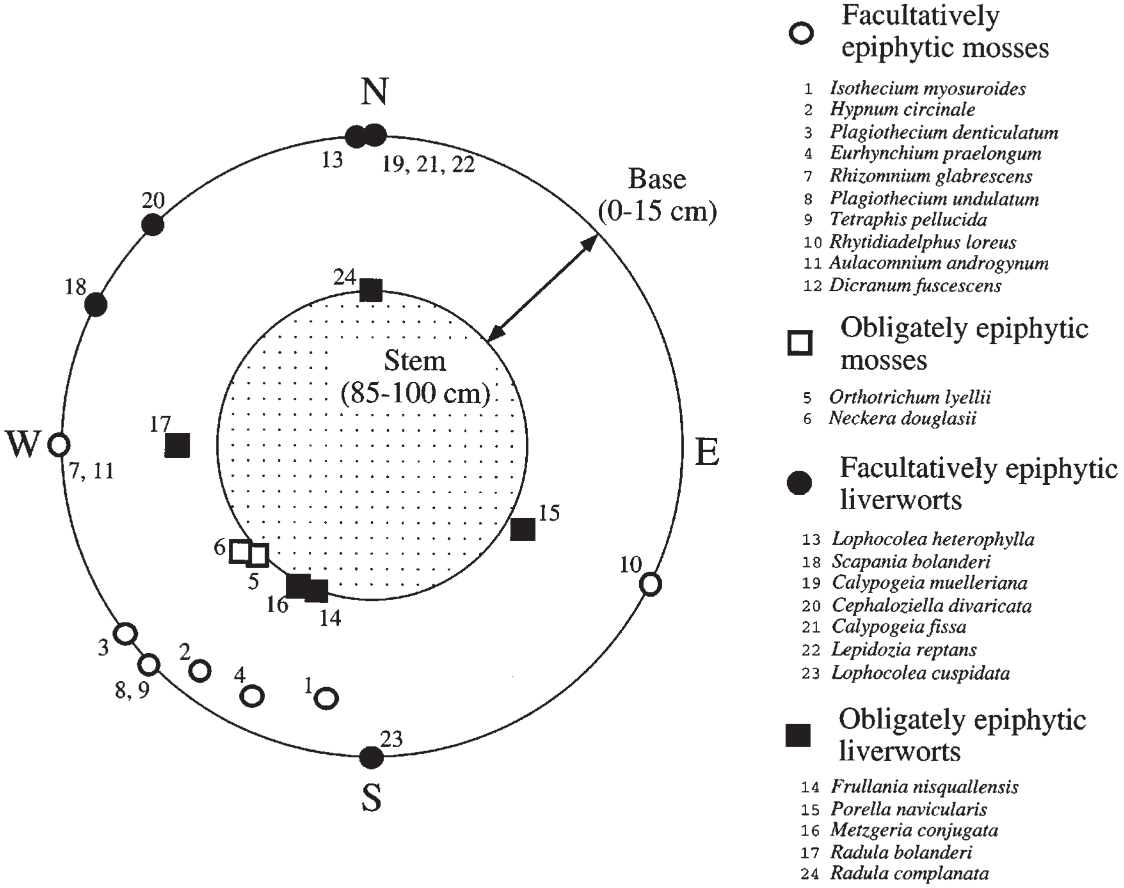


Fig. 3. Mean aspect and relative height of corticolous bryophyte species. The weighted average angle for each species was calculated as the vector sum of cover values in each cardinal direction. Relative height on the stem was calculated as the sum of cover values in stem quadrats divided by the total cover in both stem and tree base quadrats and is plotted as the distance from the outer to the inner circle on the diagram (as indicated by the double-headed arrow). Species are numbered to correspond with Table 2.



vealed a strong general trend toward positive patterns of covariation (Fig. 4). Considering the 480 total sample quadrats as variates, 22% of species pairs (60 of 276 possible combinations) showed positive correlations (with $P < 0.05$) and 0.7% (2 of 276) showed significant negative correlations. When we used mean cover values for individual trees ($N = 60$), 16% of species pairs showed positive correlations and none showed significant negative correlations. Deviations from the null expectation generated by randomly permuting species were highly significant in both cases ($P < 0.001$; G test). Positive correlations were especially prevalent for species pairs that include the more common moss species For example, *I. myosuroides* showed positive correlations with 10 of 23 species pairs in the quadrat-based analysis. A significant positive correlation was also observed between *I. myosuroides* cover and total bryophyte species richness ($r = 0.34$; $P < 0.001$; analysis based on quadrats with >1 species present). Such a relationship was also significant when *I. myosuroides* cover was included as a covariate in the general linear model describing species richness as a function of location, tree, height, aspect, and treatment effects ($P < 0.001$; F test).

Responses to thinning and fertilization

Total moss cover and species richness showed relatively little response to either thinning or fertilization treatments, although there was some indication of small negative effect of fertilizer additions in thinned stands (Fig. 5). Variance among locations and among trees within locations was quite high, and significant ($P < 0.05$) treatment × location terms were also present in the ANOVA model results. Treatment effects on total liverwort cover and species richness were also not significant (Fig. 6). However, in this case the quantitative differences between fertilized and unfertilized stands were large (~6-fold lower cover values in fertilized stands; Fig. 6*a*). Liverworts were patchily distributed, occurring in only 161 of 480 quadrats. Statistical power for detection of treatment effects was therefore low. MRPP tests indicated a significant effect of thinning ($P = 0.024$), but not fertilization ($P = 0.482$), on bryophyte community composition.

Observed responses for total cover obscure potential differences among taxa, particularly where a few species dominate the community. Responses of individual moss and liverwort species were quantified by calculating response coefficients, which estimate the average proportional change in cover to a change in thinning or fertilization level (following Thomas et al. 1999). This analysis reveals a somewhat different picture of corticolous bryophyte response to thinning and fertilization (Fig. 7). While understory vascular plant groups consistently showed positive responses to thinning,

Table 3. Tests for the deviations of bryophyte angular distribution patterns from a uniform circular distribution, based on the Rayleigh test (Batschelet 1981).

Group	No. of species	Mean angle	r*	P
Facultatively epiphytic mosses	9	221° (SW)	0.762	0.005
Obligately epiphytic mosses	2	227° (SW)	0.999	0.137
Facultatively epiphytic liverworts	4	332° (NW)	0.891	0.041
Obligately epiphytic liverworts	4	202° (S)	0.622	0.215
All bryophyte species	19	236° (SW)	0.541	0.003

Note: Individual variates are cover-weighted mean angles for individual species, as listed in Table 2, omitting species that occurred in fewer than 3 of 480 quadrats.

*Mean vector length for the sample.

Fig. 4. Significance and direction of Spearman's rank correlations between all pairs of species (species corresponding to numbers in row and column headings are listed in Table 2). +, positive correlation at $P < 0.05$; –, negative correlation at $P < 0.05$; blank squares, nonsignificant correlations. Symbols above the diagonal treat the 480 sampled quadrats as individual data points, those below the diagonal are based on average cover values for the 60 sampled trees in the survey.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	▨	+	+			+	+	+			+	+	+		+			+						
2	+	▨					+	+		+	+		+										+	
3			▨				+	+	+	+	+	+	+	-				+		+				
4				▨			+	+	+	+		+	+							+				
5					▨									+	+									
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responses of corticolous moss and liverwort species were, on average, negative (Fig. 7*a*), although liverwort species responses were not significantly different from zero. In the case of moss species, this tendency was significant (P = 0.007; t test for null hypothesis that the average response is zero). Corticolous liverwort species showed a negative response to fertilization similar to vascular plants (Fig. 7*b*). In contrast, corticolous moss species showed, on average, a positive response to fertilization. However, fertilization responses were highly variable among species, and in neither case were average response coefficients significantly different from zero (P > 0.05; t test).

Discussion

Species distributions and patterns of covariation

The distribution of corticolous bryophytes with respect to height and aspect on the tree is a classic problem in the ecology of epiphytic cryptogams (e.g., Potzger 1939; Barkman 1958). Corticolous bryophytes generally show pronounced differences in position on tree boles. Species whose primary substrate is coarse woody debris or humus are found typically only at the base; other more strictly epiphytic species occur farther up the tree trunk (Barkman 1958; Hoffman and

Fig. 5. Moss cover (*a*) and species richness (*b*) as a function of thinning and fertilization treatment combinations. Thinning treatments included a control (1680 trees/ha) and removal of 70% of tree stems (494 trees/ha) at a stand age of 8–11 years. Fertilization treatments included a control (open bars) and repeated additions of urea at an average dosage of 48–61 kg N· ha^{-1}·$year^{-1}$ (shaded bars). Significance levels are given for thinning, fertilization, thinning × fertilization interaction, location, and individual tree variation terms in an ANOVA model that also included terms for aspect and height (see Materials and methods). Mean values are plotted ±1 SE.

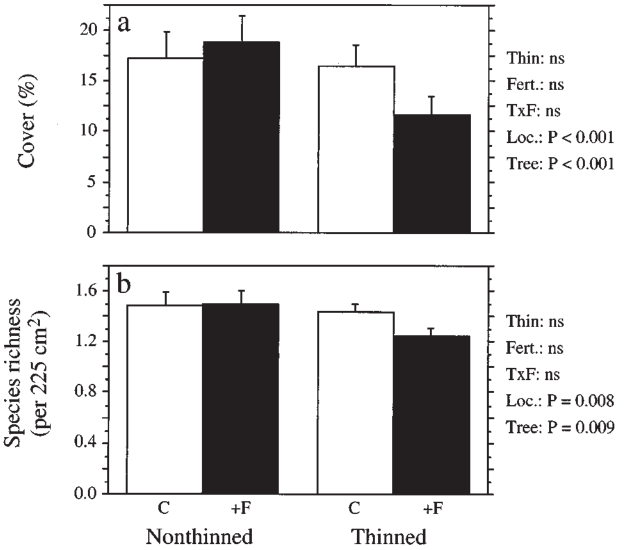


Fig. 6. Liverwort cover (*a*) and species richness (*b*) as a function of thinning and fertilization treatment combinations. See Fig. 5 for other details.

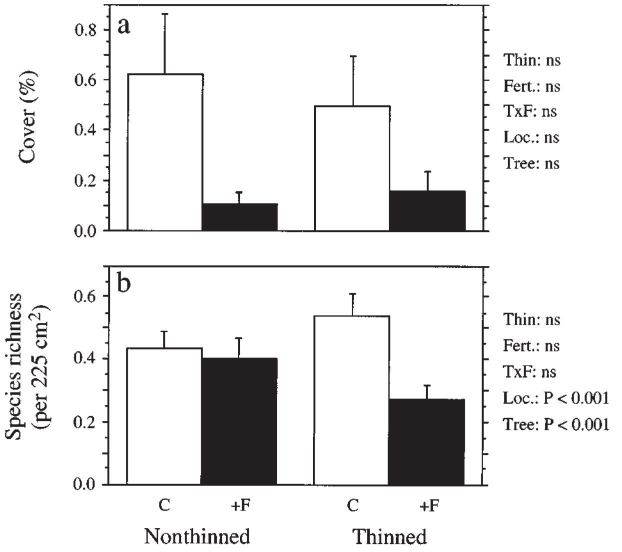
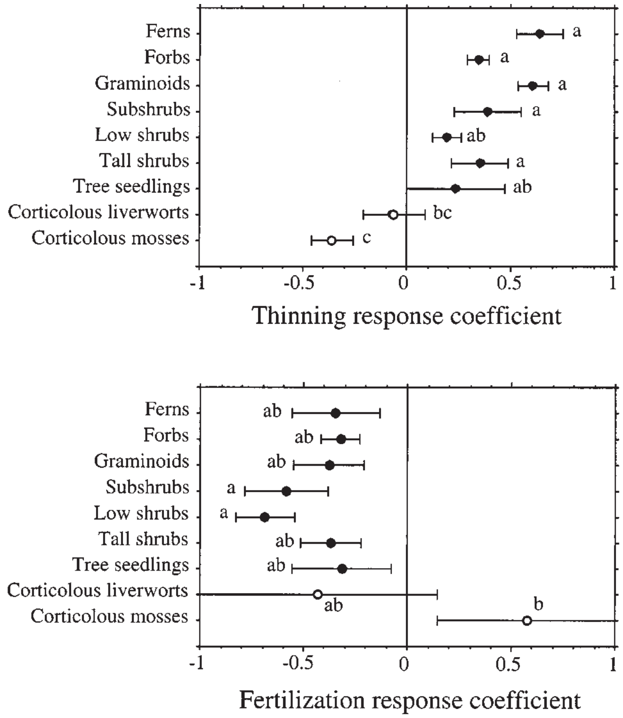


Fig. 7. Mean responses of corticolous bryophyte (open symbols) and understory vascular plant (closed symbols) species to thinning and fertilization treatments. To allow comparisons among taxa differing in absolute cover, response coefficients represent the expected proportional change in cover per increase in one "unit" of thinning or fertilization (see Materials and methods for details). Letters indicate significance of a posteriori contrasts between groups at $P < 0.05$. Means are plotted ±1 SE.



Kazmierski 1969; Hoffman 1971; Pike et al. 1975; Kenkel and Bradfield 1996). In addition, there are commonly differences in abundance between north- and south-facing sides of the tree (Barkman 1958; Stringer and Stringer 1974; Trynoski and Glime 1982).

It has been asserted previously that corticolous species on young trees show little or no variation according to height or aspect, since there is little variation in microclimate on small-diameter stems (Barkman 1958, p. 40). This may be so for saplings or for trees grown in isolation; however, our results indicate pronounced differences in distribution with height and aspect in young Douglas-fir plantations. For example, total moss cover was 1.9-fold higher on the south side than on the north side of trees, and liverworts were 3.6-fold more abundant on the north side than on the south side at the tree base. Previous studies in older forests in the region typically have found smaller directional effects. Hoffman (1971) reported that total cryptogam cover ranged from 76% higher to 15% lower on NE and SW exposures of tree bases at sites on the Olympic Peninsula. At a very wet site in the Queen Charlotte Islands, Peck et al. (1995*b*) found 20% higher cover of liverworts on north exposures, and no directional effect for mosses. We speculate that the drier microclimate found in young forest stands may generally result in exaggerated patterns of microhabitat differentiation compared with older stands.

Reduced bryophyte abundance on southern exposures (or northern exposures in the south hemisphere; e.g., Franks and Bergstrom 2000), as seen here in liverwort species occurring at the tree base, is generally ascribed to a desiccation mechanism. The more surprising pattern of higher than expected cover on southern exposures, as found here for mosses, has been less frequently reported (Trynoski and Glime 1982). We suggest two possible mechanisms for this pattern. First, the prevailing southwesterly winds in the region may result in increased rain and fog exposure in this direction. Second, increased light availability on southern exposures, while adversely affecting drought-sensitive liverworts, may benefit less drought-sensitive, but more light-demanding, bryophyte species. Subcanopy light levels may be particularly low during the stem exclusion phase of stand development (Mitscherlich 1940; Oliver 1981; Fried et al. 1988; Lowe 1993). Although bryophytes are generally considered highly shade tolerant, young closed-canopy stands may present light levels sufficiently low to limit performance in some bryophyte species. During summer months at midlatitudes, tree crowns are likely to obscure incoming light, except during early morning and late afternoon (Geiger 1965), suggesting that north–south directional differences may result from light limitation manifested during winter months. Temperature differences during winter may be important in favoring corticolous bryophytes on southern exposures in some forests (Trynoski and Glime 1982). However, temperature effects seem less likely to be of great importance in Douglas-fir systems west of the Cascade Range, where hard frosts below –4°C are relatively infrequent.

Epiphyte communities have been hypothesized to display a hierarchy of competitive dominance among species, with, for example, algae and crustose lichens being overgrown by foliose lichens or mosses, which are in turn overgrown by larger mosses or fruticose lichens (Barkman 1958; Lawrey 1991). Spatial patterns of covariation among species may give some insight into the relative importance of such competitive interactions (e.g., John and Dale 1995). Negative associations would generally be expected if competitive interactions were a strong influence on community composition. Here we found that species covariation at the spatial scales assessed was almost always positive. This result contrasts strongly with that observed in a *Quercus rubra* stand, where positive and negative associations were approximately equally represented (John and Dale 1995).

Although caution must be used in inferring dynamic processes from any analysis of static patterns, the prevalence of positive associations among species suggests that there are not strong competitive effects operating in corticolous bryophyte communities in young managed stands. The absence of such interactions is also suggested by the positive correlation between the abundance of the most common species, *I. myosuroides*, and the local diversity of other species. Several possible explanations may account for these trends. First, similar responses of species to microclimate or substrate quality could account, in whole or in part, for positive associations among species. Second, propagules for various species may derive from the same sources, such as large residual stumps and logs, resulting in an aggregated pattern of colonization. Similarly, variation in bark texture or exposure could result in an aggregated pattern of spore trapping. Finally, facilitative interactions among species may be important. This last mechanism, while speculative, is consistent with prior studies, indicating the importance of bark pH as a limit to bryophyte distributions (e.g., Gustafsson and Eriksson 1995), and the likelihood that established bryophytes will increase substrate pH by trapping organic matter. In this respect, bryophyte colonization of tree stems in conifer plantations may be similar to early plant succession in salt marshes (Bertness and Hacker 1994). Experimental tests of these alternative mechanisms (generalized habitat quality, aggregated colonization, and facilitation), would be relatively simple to conduct in corticolous bryophyte communities in young forest plantations.

Responses to silvicultural treatments

In a related study using the same long-term experimental plots, we found large negative effects of fertilization and postitive effects of thinning on vascular plant cover and species richness (Thomas et al. 1999). Similar patterns were also apparent for understory bryophytes sampled on humus and deadwood substrates (data not included). In the present study, we found little evidence for effects of silvicultural treatments on the total cover or species richness of corticolous bryophytes. However, species-specific responses and multivariate analyses indicate significant effects of thinning, with corticolous mosses generally being reduced in thinned stands. Although total liverwort cover was much lower in fertilized than nonfertilized stands (Fig. 6), this pattern was not statistically significant given high variance associated with the patchy distribution of liverworts in the study.

Why should corticolous bryophytes show a different pattern of response to thinning than either vascular plants or bryophytes occurring on the forest floor? Corticolous bryophytes are likely to be especially susceptible to drought effects, since they are largely dependent on water inputs via stemflow and condensation (Potzger 1939; Proctor 1990). Management effects on stand hydrological status and temperature are thus likely to influence corticolous species to a greater extent than forest floor species. Thinning will generally result in increased solar radiation and peak temperatures (Cheo 1946; Aussenac 1987) and increased wind exposure in the understory (Green et al. 1995). By decreasing projected crown area, thinning may also result in decreased stemflow (Ford and Deans 1978).

There is wide interest in comparisons of bryophyte communities in young vs. old-growth forests in the Pacific Northwest (e.g., Lesica et al. 1991; FEMAT 1993; Rambo and Muir 1998*a*). Unfortunately, no old-growth stands remain near the area sampled that would allow for a meaningful direct comparison. However, bryophytes found in the plantation stands sampled in this study are largely the same as those previously enumerated in old-growth sites in the region (Pechanec and Franklin 1968; Hoffman 1971). Two-thirds of these species have actually appeared on “indicator species” lists for old-growth forests (see Table 2), though many of these species were found at very low abundance in the managed stands considered here. More extensive surveys of managed and old-growth forests are necessary to elucidate differences in bryophyte communities related to stand age. At this point, we can only infer from our results that many species of corticolous bryophytes found in old-growth forests can also be found in young plantations.

Conclusions

Corticolous moss and liverwort species in young, managed Douglas-fir stands show pronounced directional differences in abundance on tree stems and a preponderance of positive spatial associations among species. Corticolous mosses also appear to be negatively affected by silvicultural thinning, the opposite of the response observed for understory vascular plants. We suggest that these patterns point to the importance of microclimate and drought limitation in determining the amount and diversity of corticolous bryophytes in managed stands, in contrast with light limitation of vascular understory plants. Our results imply that stand interventions appropriate for enhancing abundance and diversity of one guild of organisms (e.g., vascular understory plants) can potentially reduce abundance and diversity of other guilds (corticolous bryophytes). Such differences in response illustrate the importance of examining management impacts on little-studied organisms such as corticolous bryophytes, and also the challenge of effectively managing forests to maintain diversity of all organisms.

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