

Lichens on down wood in logged and unlogged forest stands

Fred L. Bunnell, Toby Spribille, Isabelle Houde, Trevor Goward, and Curtis Björk

Abstract: Lichen communities of forests often appear to be negatively affected by timber harvest presumably because of reduction of suitable substrate and increased desiccation. We examined species richness and composition of lichens on wood of logs of the same decay class in unlogged stands (>140 years old) and logged, 20- to 30-year-old stands. There was no significant difference in species richness or mean lichen cover between logged and unlogged stands, but species composition differed, including species that were unique to either logged or unlogged stands. Crustose lichens accounted for 71% of rare species and all of the species occurring more commonly in unlogged stands; macrolichens accounted for 82% of common species and 60% of the species occurring more commonly in logged stands. Diameter at breast height and decay characteristics of down wood were the best predictors of lichen richness. Among lichen-rich, decay class 3 logs, relatively small amounts of retained down wood sustained lichen richness equivalent to unlogged stands. It appears important to ensure that decay classes favourable to lichens are retained after harvest.

Résumé : Dans les forêts, les communautés de lichens semblent souvent être affectées négativement par la récolte de bois vraisemblablement parce qu'elle entraîne la perte de substrats appropriés et accentue la déshydratation. Nous avons examiné la composition et la richesse en espèces de lichens sur des billes de bois appartenant à la même classe de décomposition dans des peuplements non exploités âgés de plus de 140 ans et des peuplements exploités âgés de 20 à 30 ans. Il n'y avait pas de différence dans la richesse en espèces ou la couverture moyenne par les lichens entre les peuplements exploités et non exploités, mais la composition en espèces était différente, incluant la présence d'espèces propres soit aux peuplements exploités, soit aux peuplements non exploités. Les lichens crustacés représentaient 71 % des espèces rares et toutes les espèces présentes plus fréquemment dans les peuplements non exploités. Les macrolichens représentaient 82 % des espèces communes et 60 % des espèces les plus communes dans les peuplements exploités. Les caractéristiques du diamètre à hauteur de poitrine et de la décomposition du bois au sol étaient les meilleurs prédicteurs de la richesse en lichens. Parmi les billes riches en lichens dans la classe de décomposition 3, une quantité relativement faible de billes au sol qui avaient été conservées supportaient une richesse en lichens équivalente à celles des peuplements non exploités. Il semble important de s'assurer que des classes de décomposition favorables aux lichens soient conservées après la récolte.

[Traduit par la Rédaction]

Introduction

Lichens commonly inhabiting down wood (coarse woody debris) appear to be vulnerable to harvest of forest canopy for several reasons. First, most lichens have no efficient means of water storage and are sensitive to changes in microclimate encouraging prolonged desiccation and exposure to light (Lange et al. 1999; Gauslaa and Solhaug 2000). Removal of forest canopy increases radiation, maximum air temperatures, and wind speed, and decreases the humidity level. Impacts of these changes are variable among lichen species, but, for some species, growth and natural occurrence are a delicate balance between light availability and desiccation risk (Sillett and Antoine 2004; Gauslaa et al. 2006). Second, harvest removes a portion of the substrate to

which some lichen species are restricted. Many lichens occur on both standing and down wood (e.g., Forsslund and Koffman 1998), so removal of standing wood reduces sources of lichen propagules to colonize newly created down wood within the area harvested. Third, recolonization from outside the site may be slow. Dispersal capability of crustose lichens (well represented on down wood) is poorly known, that of macrolichens is highly variable (Sillett et al. 2000; Walser et al. 2001; Bunnell et al. 2007).

Combined, these features have led to the endangerment of lichens growing on wood in areas where forestry has been practiced for long periods: Sweden (Berg et al. 1994; Thor 1998), Spain (Martínez et al. 2003), the United Kingdom (Rose 1992), and eastern North America (Selva 1994, 2003). The general pattern is sufficiently pronounced that

Received 4 April 2006. Resubmitted 6 September 2007. Accepted 24 October 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 24 April 2008.

F.L. Bunnell¹ and I. Houde. Department of Forest Sciences, The University of British Columbia, 3041–2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

T. Spribille. Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany.

T. Goward. Enlichened Consulting Ltd., Edgewood Blue, P.O. Box 131, Clearwater, BC V0E 1N0, Canada.

C. Björk. Stillinger Herbarium, University of Idaho, Moscow, ID 83843, USA.

¹Corresponding author (e-mail: fbunnell@interchange.ubc.ca).

some workers (e.g., Nilsson et al. 1995) have promoted lichens as useful surrogates for the presence of other threatened but less readily sampled groups, such as some arthropods. In western North America, most studies have focused on arboreal macrolichens, likely because they are more easily identified than are crustose lichens, they are sometimes important winter forage for deer and caribou, and some forms fix nitrogen. Less conspicuous groups, such as crustose lichens, appear to be more closely associated with older forests than are most macrolichens (e.g., Kruys and Jonsson 1997; Selva 2003), but fewer comparisons among stand age classes have been published for crustose lichens.

Because increased endangerment of many lichen species is associated with canopy removal, it often has been assumed that these species are old-growth dependent (e.g., Rose 1992; Selva 1994). In fact, most studies suggesting old-growth dependence have not made a clear distinction between amount and character of substrate remaining after logging. Few studies, for example, have measured both the amount and decay class of postharvest down wood, both of which determine available substrate for lichens. Crites and Dale (1998), Forsslund and Koffman (1998), and Kruys et al. (1999) are exceptions.

We examined two questions. First, does lichen richness and abundance on down wood of the same decay class differ between logged and unlogged stands? Second, within a decay class does a regenerating stand support the same species as those that occur in unlogged stands, or are there differences associated with age of the stand? One objective of retention silviculture is to retain structural elements of stands important to sustaining biodiversity on a harvested site (e.g., Beese et al. 2003). Answering these questions helps reveal the role retention silviculture can play in sustaining lichen richness, thus biodiversity.

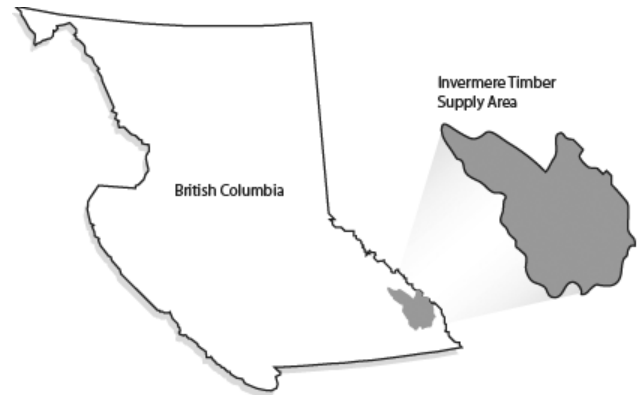
Methods

Study area

The study was conducted in the eastern half of the White River drainage of the Invermere timber supply area (TSA), southeast British Columbia (Fig. 1). The Invermere TSA is bounded by the Rocky Mountains to the east and the Purcell Mountains to the west. Between these two mountain ranges lies the Rocky Mountain Trench, a broad, flat valley of complex wetlands.

Forests of the TSA grow in four biogeoclimatic zones: the Englemann Spruce, Subalpine Fir, and Montane Spruce zones at elevations >1100 m, and the Interior Cedar Hemlock, Interior Douglas-fir, and Ponderosa Pine zones at lower elevations (Pojar et al. 1987). The landscape has a complex disturbance history dominated by stand-replacing fires (Van Wagner 1995). Fire suppression in the area is relatively recent (mid-1960s), and the latest large wildfires occurred in 1985 and 2002 (Stuart-Smith 2002). Commercial logging in the TSA has been extensive on moderate slopes and at lower elevations since 1958. Other elements of disturbance include cattle grazing, many roads and all-terrain-vehicle trails, pine beetle attack, and harvest of accessible large trees and snags near roads. The TSA is extensively used for recreation and tourism.

Fig. 1. Invermere timber supply area in British Columbia.



Sampling was restricted to the dry cool subzone of the Montane Spruce (MSdk; Pojar et al. 1987), which in Invermere TSA occurs at middle elevations (1100–1700 m). Climate in the subzone is characterized by cold winters and moderately short warm summers with forest cover dominated by hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Englem.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and western larch (*Larix occidentalis* Nutt.). In British Columbia, western larch occurs only in the eastern portion of the Montane Spruce zone; western redcedar (*Thuja plicata* Donn ex D. Don), present in wetter parts of the zone, represent a transition to the Interior Cedar Hemlock zone (Meidinger and Pojar 1991). Understory is well developed, with abundant shrubs and seedling trees. Fire and forest practices have encouraged extensive young and maturing stands of lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) throughout the landscape. Small amounts of paper birch (*Betula papyrifera* Marsh.) occurred in logged stands.

Treatments and replicates

Three broad criteria guided selection of sample sites: (i) availability and accessibility, (ii) similarity among replicates, and (iii) minimization of differences in features believed to affect the lichen flora. The candidate sites had similar slope (<25%), similar aspect (west northward through east), no sign of grazing by cattle and were located upland from immediate riparian areas. Replicates of two age classes (treatments) were sought: 20–30 years old and >140 years old. Stand age was determined from forest cover maps and harvest data. Definition of old growth in British Columbia, once considered >140 years, is in flux and incompletely indicated by forest cover maps (Delong et al. 2004). Stands designated >140 years old on forest cover maps were not previously logged and represented a natural baseline of uncertain but older age. The amount of older forests in the TSA is limited because of past and ongoing natural and human disturbances. Unlogged stands in the TSA tend to host smaller mature trees (dbh = 20–30 cm), but more, scattered large trees than in logged stands. There were too few unlogged stands to allow random selection within the site selection criteria; sites had to be actively sought.

Dominant trees in stands designated at least 140 years old were western larch and Douglas-fir; subdominants were primarily lodgepole pine, western redcedar, spruce, and birch.

Most stands 20–30 years postharvesting had been clear-cut, some contained small residual patches or scattered western larch seed trees. Stands had regenerated naturally without site treatment and hosted mixed tree species including western larch, Douglas-fir, lodgepole pine, and spruce. These young, logged stands were expected to have experienced sufficient time for potential effects of canopy removal to have impacted lichens, and yet be sufficiently “young” that if old-stand associates once present had disappeared, they may not have had time to recolonize. Six examples of the younger age class were randomly selected from a large pool that met criteria for site selection.

Replicate and substrate characteristics

Three plots were established at each of the 12 sites (6 in logged and 6 in unlogged stands), yielding 18 estimates of substrate variability for each age class. At each site, centres for three plot samples were randomly selected along a 165 m transect, with possible locations every 15 m after the first 60 m from the road (50 m is the empirical distance of most edge effects; Kremsater and Bunnell 1999). Circular plots (0.04 ha; 11.2 m radius) were sampled to evaluate substrate characteristics and availability, including live trees, snags, and downed wood. Snags were assessed because they are colonization sources for some lichen species occurring on downed wood. Within the plots, tree species and diameter at breast height (dbh) were recorded for all live and dead trees with dbh >7.5 cm. Basal areas were derived from all live or dead trees >7.5 cm dbh encountered within sample plots and scaled up to volumes per hectare. Decay classes of dead trees (snags) followed those of the Wildlife Tree Committee of British Columbia (2005): class 3, most branches present; class 4, most branches broken, may have a broken top; class 5, no branches, broken trunk; class 6, stump. Length, average diameter, and decay class were recorded for all down wood segments along three 11.2 m radial transects in each plot. Transects originated from the centre of the plot and extended outwards at 0°, 120°, and 240°. Downed wood per plot and for each stand age class was calculated using the standard formula described by the method of Van Wagner (1968). Recording of decay classes of down wood followed the BC Resources Information Standards Committee (Ministry of Forests of British Columbia 1998): class 1, recently fallen with branches and hard trunk; class 2, hard trunk but broken branches; class 3, hard trunk, no branches, little bark; class 4, soft trunk, no branches; class 5, soft and broken down trunk, partly integrated into soil.

Resources allocated to lichen identification allowed lichen sampling of only one log per plot (18 logs in each age class). The log of decay class 3 closest to each of the three plot centres at a site was selected. Because plot centres were randomly selected, logs were also randomly selected. Given limited resources, we restricted sampling to a single decay class to avoid confounding of decay class within age class. Decay class 3 logs are hard and round, with no twigs, only traces of bark, and with little or no litter and moss cover. This condition is highly favourable to lichen colonization (McCullough 1948; Muhle and LeBlanc 1975; Crites and Dale 1998; Jansová and Soldán 2006) providing a useful, repeatable index of lichen richness. To account for variation

within decay class 3, we recorded relative hardness of logs by a simple knife penetration test (Renvall 1995) using the broad categories “hard” (penetration at three points averaging <1 cm) and “soft” (penetration >1 cm).

Lichen surveys

A full inventory was made of all lichen species present on a 2 m length of each log, measured from the centre of the log and extending 1 m each way. Abundance of each lichen species was recorded as percent cover within the 2 m long area sampled. Total cover was assumed to be an index of general substrate suitability for lichens. Specimens were collected for any species that could not be identified in the field, especially crustose species that required microscopic examination for reliable identification. Over 400 specimens were collected. Crustose lichen species were identified using standard light microscope techniques. To ensure positive identification of sterile lichen samples, chemical constituents were determined for over half of the specimens using thin layer chromatography (Culberson 1972). Taxonomic concepts and nomenclature follow Goward et al. (1994), Goward (1999), and Spribille (2006). Lichen life forms were assigned as (i) macrolichens (species with three-dimensional aerial thalli, including all foliose, fruticose, and squamulose species; Goward et al. 1994; Goward 1999); (ii) calicioids (species bearing either stalked, unlichenized fruiting structures and (or) loose spore masses; Goward 1999); and (iii) crustose lichens (species with unstalked fruiting bodies and thalli so closely attached that their removal requires destruction of the substrate).

Statistical analysis

Amounts and characteristics of dead wood in both managed and unmanaged stands is highly variable (Harmon et al. 1986; Rouvinen and Kouki 2002; Aakala et al. 2007), hindering comparisons by means. Given the variable disturbance history in the study area, we evaluated whether characteristics of substrate within treatment truly were homogeneous. We evaluated homogeneity of woody substrates (trees and down wood) among sample sites within stand age class using χ^2 tests for heterogeneity ($\alpha = 0.05$). For each treatment (young, logged and old, unlogged stands), we evaluated the frequency of trees by tree species and by dbh class, and the frequency of all down wood pieces by dbh, decay, and length classes. Given the variability, significance of tests did not change whether measures were treated as plot means within a treatment or separately as representatives of the treatment; results of Table 1 are reported as derived from plot means. Many pieces of down wood were completely without bark, so we could not consistently identify species. We expect, but cannot confirm, that lichens become much less discriminating among tree species as the tree dies, loses bark, and becomes partially decayed (e.g., Barkman 1958; Kuusinen 1996). The metrics basal area and volume of down wood are derived from the diameters of live trees and logs, so show the same distributions as diameter (thus are not included in Table 1).

For analysis, diameter classes were 10 cm wide, from 5 to 105 cm. Length classes of down wood pieces were 5 m wide, from 1 to 30 m. Decay classes 1–5 for down wood followed those of the Ministry of Forests of British Colum-

Table 1. χ^2 tests of homogeneity on trees and down wood recorded in logged (20–30 years old) and unlogged (>140 years old) stands within the Invermere timber supply area, southeastern British Columbia.

	χ^2	χ^2 (0.05)	df	Mean	Median	SD	Range
Within unlogged stands (>140 years old)							
Trees							
Species frequency distribution	87.460 ^a	31.410	20	—	—	—	—
dbh classes (cm)	34.687	61.656	45	24.3	21.0	14.5	7.5–100.0
Tree basal area (m ² / ha)	—	—	—	42.9	43.4	9.2	27.8–55.2
Down wood							
dbh classes (cm)	13.861	31.410	20	13.9	14.5	9.1	3.0–45.0
Decay classes ^b	26.757	31.410	20	3.1	3	1.1	1–5
Length classes (m)	108.737 ^a	37.652	25	13.2	12.6	7.4	1.0–28.0
Volume (m ³ /ha)	—	—	—	140.5	92.8	108.5	37.9–292.2
Within logged stands (20–40 years old)							
Trees							
Species frequency distribution	74.847 ^a	31.410	20	—	—	—	—
dbh classes (cm)	25.544	31.410	20	13.9	13.0	6.1	7.5–47.0
Tree basal area (m ² / ha)	—	—	—	8.4	8.4	2.5	5.7–12.4
Down wood							
dbh classes (cm)	16.09	31.410	20	19.5	19.0	8.7	5.5–50.0
Decay classes ^b	32.234 ^a	31.410	20	3.4	4	0.8	1–5
Length classes (m)	30.12205	37.652	25	13.3	12.6	7.4	2.1–30.0
Volume (m ³ /ha)	—	—	—	92.8	114.5	56.4	18.0–143.4

Note: Homogeneity tests and range are reported within stand ages for all trees and logs; measures of central tendency and dispersion are provided for plot means.

^aReject, substrate is not homogenous.

^bDown wood decay classes are from the Ministry of Forests of British Columbia (1998): class 1, recently fallen with branches and hard trunk; class 2, hard trunk but broken branches; class 3, hard trunk, no branches, little bark; class 4, soft trunk, no branches; class 5, soft and broken down trunk, partly integrated into soil.

bia (1998). Observed frequencies among sample sites and within treatment were compared with expected frequencies as actual counts using χ^2 tests. Expected frequency for each sample site was calculated as the occurrence over all sample sites within treatment (age class). Differences in substrates (trees and down wood) between unlogged and logged stands used the same procedures as the tests within treatments. Where variables were homogeneously distributed within both logged and unlogged treatments, differences were evaluated by *t* test, using six site means for each treatment.

Where assumptions for parametric correlation were met, we tested two potential associations (log diameter and lichen species richness; percent lichen cover and lichen species richness) using simple linear correlation across plot means ($\alpha = 0.05$).

Lichen richness was normally distributed (cf. several substrate variables), so homogeneity of lichen species richness within stand age cases was tested using analysis of variance for the six sampling sites in unlogged and logged stands, respectively ($\alpha = 0.05$). Variances and means of lichen species richness were tested between unlogged and logged stands using two-tailed tests ($\alpha = 0.05$), as were potential differences between “soft” and “hard” logs. Analyses of variances were nested, plots within treatments.

A multiresponse permutation procedure (MRPP, Mielke and Berry 2001), the non-parametric equivalent to multivariate ANOVA, was used to test the a priori hypothesis of no difference in lichen community composition between logged and unlogged forest stands. MRPP was chosen because data on lichen occurrence did not meet distributional assumptions

of multivariate normality or homogeneity of variances (Levene's test, $P < 0.05$). Plot means were used within a nested design, with plots as a blocking variable. As a non-parametric test, MRPP measures whether one or more response variables are more alike within groups (e.g., unlogged stands) than would be predicted by chance on the basis of random data reshufflings. As chance-corrected within-group agreement (*A*) approaches 1, groups become more distinct from each other. Conversely, when *A* = 0, the results are random; and where values of *A* are closer to -1, the results indicate greater similarity among groups than within. While *A* gives the practical significance (effect size) of a test, the associated *P* value provides statistical significance of that effect (McCune and Grace 2002). PCORD, in conjunction with a Sørensen distance measure, was used to conduct the analysis (McCune and Mefford 1999).

Results and discussion

Stands and amount of substrate

The frequency distribution of tree species was not homogeneous in either logged or unlogged stands (Table 1). Generally, logged stands were dominated by western larch, spruce, and Douglas-fir. Paper birch represented about 10% of the trees recorded in logged stands, but was not found in unlogged stands. Unlogged stands were dominated by western larch, Douglas-fir, and western redcedar (which was not found in logged stands). Tree diameters were homogenous within stand age class, and were larger in unlogged stands (mean dbh = 24.3 cm), than in logged stands (mean dbh =

13.9 cm; Table 1; $t = 9.805$; $P < 0.001$). Means, however, are an incomplete descriptor, as some trees in unlogged stands exceeded 70 cm dbh. Mean basal area naturally follows a similar pattern: 42.9 m²/ha in unlogged stands and 8.4 m²/ha in logged stands (Table 1). Although highly variable, it also differs significantly ($P < 0.001$).

Diameter and its derivatives, basal area and volume, were the only measures distributed homogeneously in each age class. Factors potentially contributing to the similarity between age classes were retention of some larger postlogging debris in logged stands and provision of smaller diameter debris in unlogged stands through suppression mortality and wind breakage. The distribution of decay classes differed only among sampling sites in logged stands. Most down wood in logged stands was in decay classes 3 (37%) and 4 (45%). We expected to find more advanced decay among down wood in unlogged stands, but a large portion was in decay classes 2 (41%) and 3 (32%); the former were smaller logs, contributing little to volume. Both suppression mortality and windthrow contributed to the lower decay classes of unlogged stands. Some decay class 4 in logged stands were trees and snags fallen during harvest and left on site. Distribution of length classes of down wood in logged stands was homogenous with most pieces relatively short; more than half (65%) were <10 m. The larger mean diameter in logged stands reflects the fact that many were partially decayed butt ends of logs left on site. Conversely, lengths of down wood in unlogged stands were highly variable among sites (1–28.0 m), sometimes containing groups of recently wind-thrown trees showing little decay. Within this variability, the derived measure of mean volume per plot of down wood in logged stands was about two-thirds that in unlogged stands (Table 1) and did not differ significantly between the two stand types ($P > 0.9$). Unlogged stands, however, had about three times as much volume of downed wood in the decay class 3, most favourable to lichens: 96.6 m³/ha compared with 28.3 m³/ha in logged stands; $P = 0.249$).

Few snags were encountered in logged stands (1.8 per plot compared with 4.0 in unlogged stands; mean basal area of 1.0 m²/ha, compared with 6.7 m²/ha in unlogged stands). The majority of the snags in logged stands were decay classes 1 and 2 (median decay class = 2); mean dbh was half of that in unlogged stands (14.7 cm compared with 25.7 cm). Decay stage of snags in unlogged stands was more advanced (median decay class = 3). There was clearly more substrate for lichens using standing dead wood in unlogged than in logged stands.

Lichen abundance, richness, and down wood

Tests for homogeneity of variance for lichen cover, a broad index of suitability, and species richness within and between logged and unlogged stands were not rejected. On sample logs, lichen cover did not differ significantly between logged and unlogged stands: 33.5% and 26.7%, respectively ($t = 0.255$; $P > 0.05$). We directed analysis to species richness and community composition. A total of 109 lichen species were identified. An equal number of species, 86, were found in both logged and unlogged stands. We had expected higher species richness in unlogged stands, but found that mean species richness was similar: 22.1 and 18.1 species per log in logged and unlogged stands, respec-

tively ($t = 0.085$; $P > 0.05$). The ranges in species richness per log were nearly identical, 28 in unlogged stands, 29 in logged stands. Richness was significantly greater on the more decayed, “soft” logs than on the “hard” logs of decay class 3 (mean numbers of species per log were 23.4 and 12.7 on “soft” and “hard” logs, respectively; $t = 4.12$; $P = 0.001$). Among randomly selected sampled logs in both age classes, 25 of 36 were designated “soft” by the knife penetration test. Richness and cover on a log were positively correlated ($r = 0.695$, $P < 0.01$). Over the range of sample logs, 10–39 cm dbh, species richness was positively correlated with log diameter ($r = 0.707$, $P < 0.01$).

We found 26 species that have not been reported from bark, plant litter, or other non-wood substrates and appear to be dead wood obligates (Spribille 2006). There was no significant difference in species richness of these dead wood obligates between logged and unlogged stands (8.8 species per site in logged stands, 8.0 per site in unlogged stands). Twenty and 19 dead wood obligate species were found in logged and unlogged stands, respectively; 6 were unique to the logged stands, and 5 were unique to unlogged forests (not all species are listed in Table 2).

The near equality in species richness across age classes, including dead wood obligates, also has been reported from Sweden (Forsslund and Koffman 1998). Those authors speculated that logged stands behaved as sinks to nearby old forest source populations. We found some species more common in unlogged than in logged stands (e.g., Table 2), but several species occurred more frequently in logged stands or were common to both. After 20–30 years, potential source–sink differences may have diminished.

If a source–sink relationship were acting, it likely would be through available substrate because near-ground microclimate differences should not be marked between these age classes (shrub understories were similar). While species richness did not differ between forest age classes, there were differences associated with stage of decomposition (greater on soft logs). This finding corroborates a known pattern of succession of lichens on down wood: lichen richness generally increases from the time wood is first exposed until it becomes soft. As down wood continues to decompose, it loses form and becomes increasingly colonized by bryophytes and ultimately vascular plants. The pattern has been widely reported (e.g., McCullough 1948; Muhle and LeBlanc 1975; Jansová and Soldán 2006) and apparently holds true for our study area. The time of peak lichen richness, for generalists and dead wood obligates alike, appears to be centred around a time between bark loss and advancement to the bryophyte colonization stage. In our study, there was little difference between unlogged and logged sites in median decay class (Table 1), though unlogged sites had greater volumes of more favourable substrate.

The provision of dead wood suitable for lichen colonization is not as continual in logged stands as in long-standing forests, but more often is provided as a large pulse at harvest or at thinning. In this study, some large diameter pieces of down wood had been left on site after logging and served as a suitable substrate. As that wood becomes more decayed, it also will become less suitable for lichens and more suitable for bryophytes. Usually, as in this study, few snags remain in the logged stands after harvest, so recruitment of

Table 2. Species occurring on at least one sixth of logs grouped by age class affinity plus apparent dead wood obligates.

Species	Life form	Number of logs on which found		
		20- to 30-year- old stands	>140-year-old stands	Total
Non-differential species				
<i>Bryoria</i> sp. initials	Macro	12	10	22
<i>Hypogymnia physodes</i>	Macro	9	10	19
<i>Parmelia sulcata</i>	Macro	10	11	21
<i>Parmeliopsis ambigua</i>	Macro	18	17	35
<i>Parmeliopsis hyperopta</i>	Macro	17	15	32
<i>Placynthiella icmalea</i>	Crustose	12	13	25
<i>Tuckermanopsis chlorophylla</i>	Macro	9	8	17
<i>Vulpicida pinastri</i>	Macro	14	14	28
<i>Xylographa vitiligo</i> ^a	Crustose	9	9	18
Species more frequent in logged stands				
<i>Buellia chloroleuca</i> ^a	Crustose	8	1	9
<i>Cetraria ericetorum</i>	Macro	9	1	10
<i>Cladonia botrytes</i> ^a	Macro	7	1	8
<i>Cladonia cenotea</i>	Macro	8	1	9
<i>Cladonia ochrochlora</i>	Macro	14	7	21
<i>Cladonia sulphurina</i>	Macro	5	1	6
<i>Lecanora ramulicola</i> s.lat.	Crustose	6	1	7
<i>Letharia vulpina</i> s.lat.	Macro	11	1	12
<i>Ochrolechia gowardii</i>	Crustose	9	4	13
<i>Trapeliopsis flexuosa</i>	Crustose	7	3	10
Species more frequent in unlogged stands				
<i>Biatora rufidula</i>	Crustose	1	5	6
<i>Lecanora</i> sp. 1 ^a	Crustose	0	7	7
<i>Xylographa</i> sp. 1 ^a	Crustose	5	12	17
<i>Xylographa trunciseda</i> ^a	Crustose	2	9	11

Note: Data from the Montane Spruce zone of southeastern British Columbia.

^aDenotes dead wood obligates (Spribille 2006).

dead wood is reduced. Without some retention of snags or live trees left to die a natural death, there are likely to be gaps in the availability of substrate for lichen species preferring down wood. We found no evidence of such a gap in 20- to 30-year-old stands. However, where applied, close utilization standards eventually will reduce legacy logs and down wood. Then down wood, if retained at all, will consist mainly of fresh tops and felled hard snags. After the majority of down wood has reached advanced decay stages unsuitable for lichens and prior to input of new down wood through tree mortality, substrate availability will become limiting. Various forms of retention can help sustain provision of suitable substrate (e.g., Bunnell et al. 2002) and provide colonization sources.

Species composition

We found twice as many crustose lichens (73 species) as macrolichens (36 species). The species pool consisted primarily of “uncommon” species (recorded from 5 or fewer logs) and a small number of “common” species found on half or more of the sampled logs. Of the 109 species, 68 were considered “uncommon.” Only 10% of the species were common, and all but two of these had comparable frequency in logged and unlogged stands (Table 2): *Xylographa* sp. 1 occurred mainly in unlogged stands, and *Cladonia ochrochlora* was more frequent in 20- to 30-year-old

stands. Crustose lichens accounted for 71% of uncommon species and all of the species occurring more frequently in unlogged stands. Macrolichens accounted for 82% of common species and 60% of the species occurring more frequently in logged stands.

When tested with MRPP, a significant difference in lichen community composition was evident between logged and unlogged stands ($A = 0.02$, $t = -4.1$, $P < 0.002$). Lichen communities on logs sampled within groups were more similar to each other than they were to lichen communities sampled from logs across groups. To create a broad description of the lichen flora on down wood, we compared all species found on at least 6 of the 36 sample logs and excluded all others. Only one of these more frequently occurring species was restricted to logged or to unlogged stands, though some species occurred more frequently in logged or unlogged stands. Nonetheless, broad differences were apparent between the two age classes (Table 2). Four species (*Lecanora* sp. 1, *Biatora rufidula*, *Xylographa* sp. 1, *Xylographa trunciseda*) were recorded at least twice as often in unlogged stands as in logged stands; all are crustose lichens. Among the 10 species more frequent in logged stands, 6 were macrolichens occurring on at least twice as many logs in logged stands as in unlogged stands (Table 2). The number of species showing apparent preferences for either logged or unlogged stands likely would increase with increased sample size.

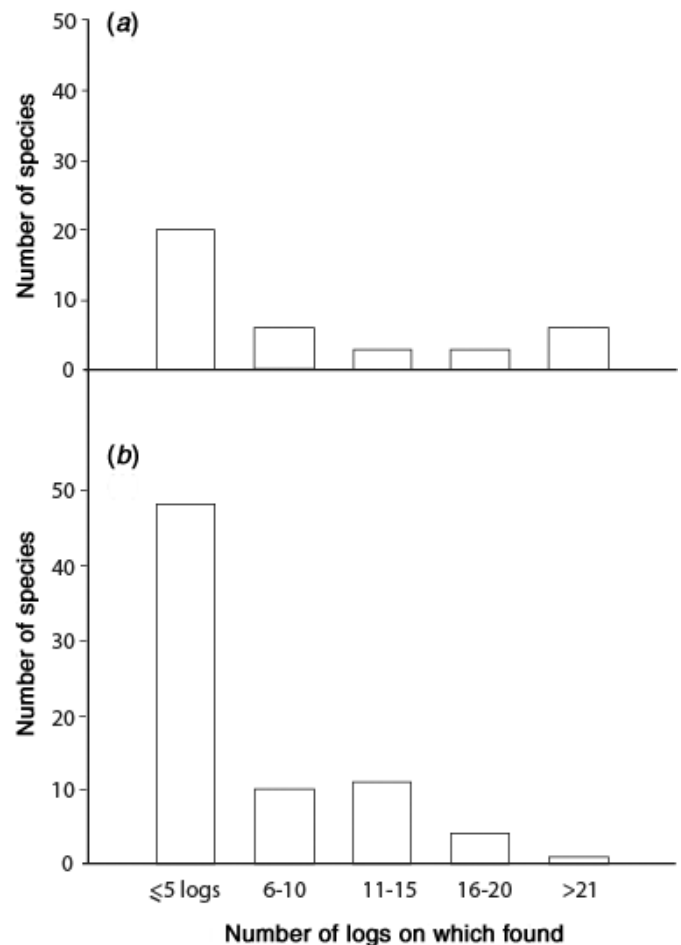
Reasons for specific age-class affinities are unclear. We believe near-ground differences in microclimate between the age classes are unlikely given the similar amounts of understory vegetation present in both age classes. We do not know whether 20–30 years is sufficient to permit a complete sharing of lichen flora across stand ages through colonization, establishment, and growth. Greater volume of decay class 3 logs in unlogged stands may have provided greater opportunities for microhabitats we did not sample and greater opportunities for colonization by naturally rare species.

Use of alternative substrates, other than snags, should have decreased the likelihood of a significant difference in lichen communities on logged and unlogged sites. For some lichens, occurrence on logs is not restrictive. For instance, all of the species common to both logged and unlogged stands (Table 2), with the exception of *Placynthiella icmalea*, are common on other substrates such as live tree trunks, branches, or plant litter available in both age classes. Six of the 10 species occurring more frequently on down wood in logged stands (Table 2) were also found on other substrates in those stands. Exceptions were *Buellia chloroleuca*, *Cladonia botrytes*, *Cladonia sulphurina*, and *Trapeliopsis flexuosa*, which are found primarily on wood (Goward 1999). Conversely, of the four species occurring more frequently in unlogged stands, three (*Lecanora* sp. 1, *Xylographa* sp. 1, and *Xylographa trunciseda*) appear to be dead wood obligates (Spribille 2006). Only *Biatora rufidula* has been documented to use other substrates, mainly tree bark and branches. Even so, this species appears to be more frequent in unlogged than in logged stands.

Some obligate wood-dwelling lichens may use snags, not logs, as their primary substrate. Forsslund and Koffman (1998) found that obligate wood-dwelling lichens were more frequent on snags than on logs or stumps. It is possible the species we found occurring more frequently in unlogged stands are primarily snag users that occur secondarily on nearby logs. Snags, and thus the colonization source, were scarce in logged stands. This suggestion is supported by our observations of numerous snag-dwelling species being almost completely restricted to old-growth forests in the same study area because of a lack of substrate in logged stands (Bunnell et al. 2004).

In general, we found more crustose lichens than macrolichens (Fig. 2). A greater proportion of macrolichens tended to be common species and species of logged sites, while crustose lichens tended to be rare species. Species occurring more frequently in unlogged stands were crustose (Table 2). While some of the characteristically common species on down logs are macrolichens, such as *Parmeliopsis ambigua*, the majority of the down wood species pool consists of infrequent species of crustose lichens (Fig. 2). This finding is similar to observations of Forsslund and Koffman (1998) and Rikkinen (2003) from large lichen species pools showing high site-to-site turnover of lichen composition on dead wood. The pattern can be interpreted in at least two ways. First, dispersal limitations may result in species not reaching potential niches. A second possibility, not exclusive of the first, is that many of the rare species are adapted to particular dead wood microniches, which were not discriminated at our sampling scale. Species of log conceivably contributes

Fig. 2. Number of lichen species by frequency class on logs in the Montane Spruce zone of southeastern British Columbia, both age classes combined: (a) macrolichens, (b) crustose lichens.



to the difference. Live tree species composition differed between unlogged and logged stands, which undoubtedly created differences in the species of logs presence in the two age classes. However, most sampled logs were in the soft stage of decay class 3, by which time bark, which has a strong influence on lichen affinities for particular trees species (Barkman 1958; Kuusinen 1996), is absent.

Conclusions

Down wood retained in harvested stands hosted a large number of lichen species within 20–30 years after harvest, but the species composition on logs differed from that in unlogged stands. More crustose than macrolichens were encountered, but crustose lichens were more sparsely distributed and represented all species occurring more frequently in unlogged stands. Substrate characteristics, such as diameter and decay state, had the greatest influence on lichen species richness. Although diameter of all down wood differed little between stand age class, volume of downed wood of the most favourable decay class was about three times greater in unlogged stands. Lichen species richness did not differ, presumably because legacies of prior disturbance (felled snags and preharvest logs) produced a median decay state somewhat more advanced in logged

stands, with many logs at stages of decay encouraging high richness in lichens. Without retention silviculture to provide a sustained source of dying and dead wood, we anticipate a decrease in lichen richness within harvested stands, particularly among crustose lichens.

Acknowledgments

We gratefully acknowledge support from the British Columbia Forest Sciences Program, Tembec Forest Industries Inc., and the British Columbia Ministry of Environment. A. Farr, E.B. Peterson, and anonymous reviewers improved the manuscript. We are particularly grateful to an Associate Editor.

References

- Aakala, T., Kuuluvainen, T., De Grandpre, L., and Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. *Can. J. For. Res.* **37**: 50–61. doi:10.1139/X06-201.
- Barkman, J.J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum Publishers, Assen, Netherlands.
- Beese, W.J., Dunsworth, B.G., Zielke, K., and Bancroft, B. 2003. Maintaining attributes of old-growth forests in coastal British Columbia through variable retention. *For. Chron.* **79**: 570–578.
- Berg, Å., Ehnstrom, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* **8**: 718–731. doi:10.1046/j.1523-1739.1994.08030718.x.
- Bunnell, F.L., Houde, I., Johnston, B., and Wind, E. 2002. How dead trees sustain live organisms in western forests. In *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4 November 1999, Reno, Nevada. Technical co-ordinators: W.F. Laudenslayer, Jr., P.J. Shea, B.E. Valentine, C.P. Weatherspoon, and T.E. Lisle.* USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181. pp. 291–318.
- Bunnell, F.L., Goward, T., Houde, I., and Spribille, T. 2004. A species accounting system to integrate indicators of biological diversity – lichen subproject. Report to British Columbia Forest Science Program. Available from www.for.gov.bc.ca/hfd/library/fia/2005/fsp_Y051045a.pdf [accessed 8 March 2008].
- Bunnell, F.L., Goward, T., Houde, I., and Bjork, C. 2007. Larch seed trees sustain arboreal lichens and encourage re-colonization of regenerating stands. *West. J. Appl. For.* **22**: 94–98.
- Crites, S., and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Can. J. Bot.* **76**: 641–651. doi:10.1139/cjb-76-4-641.
- Culberson, C.F. 1972. Improved conditions and new data for the identification of lichen products by a standardized thin-layer chromatographic method. *J. Chromatogr.* **72**: 113–125. doi:10.1016/0021-9673(72)80013-X. PMID:5072880.
- Delong, S.C., Burton, P.J., and Harrison, M. 2004. Assessing the relative quality of old-growth forest: an example from the Robson Valley, British Columbia. B.C. J. Ecosyst. Manage. **4**(2). Available from www.forrex.org/jem/ISS24/vol4_no2_art8.pdf [accessed 8 March 2008].
- Forsslund, A., and Koffman, A. 1998. Species diversity of lichens on decaying wood: a comparison between old-growth and managed forest. *Växt-ekologi, Botaniska Institutionen, Stockholms Universitet*. pp. 1–40.
- Gauslaa, Y., and Solhaug, K.A. 2000. High-light-intensity damage to the foliose lichen *Lobaria pulmonaria* within a natural forest: the applicability of chlorophyll fluorescence methods. *Lichenologist*, **32**: 271–289. doi:10.1006/lich.1999.0265.
- Gauslaa, Y., Lie, M., Solhaug, K.A., and Ohlson, M. 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia (Berl.)*, **147**: 406–416. doi:10.1007/s00442-005-0283-1.
- Goward, T. 1999. The lichens of British Columbia. Part 2. Fruticose species. British Columbia Ministry of Forests Research Program, Victoria, B.C.
- Goward, T., McCune, B., and Meidinger, D. 1994. The lichens of British Columbia. Illustrated keys. Part 1 – Foliose and squamulose species. Special Report Series 8, Research Program, British Columbia Ministry of Forests, Victoria, B.C.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- Jansová, I., and Soldán, Z. 2006. The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs. *Preslia (Prague)*, **78**: 67–86.
- Kremsater, L.L., and Bunnell, F.L. 1999. Edges: theory, evidence, and implications to management of western forests. In *Forest fragmentation: wildlife and management implications. Edited by J.A. Rochelle, L.A. Lehmann, and J. Wisniewski.* Brill, Leiden, the Netherlands. pp. 117–153.
- Kruys, N., and Jonsson, B.G. 1997. Insular patterns of Calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography*, **20**: 605–613. doi:10.1111/j.1600-0587.1997.tb00429.x.
- Kruys, N., Fries, C., Jonsson, B.G., Lamas, T., and Stal, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. *Can. J. For. Res.* **29**: 178–186. doi:10.1139/cjfr-29-2-178.
- Kuusinen, M. 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist*, **28**: 443–463. doi:10.1006/lich.1996.0043.
- Lange, O.L., Leisner, J.M.R., and Bilger, W. 1999. Chlorophyll fluorescence characteristics of the cyanobacterial lichen *Peltigera rufescens* under field conditions. II. Diel and annual distribution of metabolic activity and possible mechanisms to avoid photoinhibition. *Flora*, **194**: 413–430.
- Martínez, I., Aragón, G., Sarrión, F.J., Escudero, A., Burgaz, A.R., and Coppins, B. 2003. Threatened lichens in central Spain. *Cryptogam. Mycol.* **24**: 73–97.
- McCullough, H.E. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology*, **29**: 508–513. doi:10.2307/1932645.
- McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.
- McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach, Ore.
- Meidinger, D., and Pojar, J. (Editors). 1991. Ecosystems of British Columbia. Special Report Series 6. British Columbia Ministry of Forests, Victoria, B.C.
- Mielke, P.W., Jr., and Berry, K.J. 2001. Permutation methods: a distance function approach. Springer Series in Statistics, New York.
- Ministry of Forests of British Columbia. 1998. Field manual for describing terrestrial ecosystems. Land Management Handbook 25, Victoria, B.C. Available from www.for.gov.bc.ca/hfd/pubs/docs/Lmh25.htm [accessed 8 March 2008].
- Muhle, H., and LeBlanc, F. 1975. Bryophyte and lichen succession on decaying logs. 1. Analysis along an evaporational gradient in eastern Canada. *J. Hattori Bot. Lab.* **39**: 1–33.

- Nilsson, S.G., Arup, U., Baranowski, R., and Ekman, S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conserv. Biol.* **9**: 1208–1215. doi:10.1046/j.1523-1739.1995.9051208.x.
- Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* **22**: 119–154. doi:10.1016/0378-1127(87)90100-9.
- Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, **35**: 1–51.
- Rikkinen, J. 2003. Calicoid lichens and fungi in the forests and woodlands of western Oregon. *Acta Bot. Fenn.* **175**: 1–41.
- Rose, F. 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats. *In* *Bryophytes and lichens in a changing environment*. Edited by J.W. Bates and A.M. Farmer. Clarendon Press, Oxford, UK. pp. 211–233.
- Rouvinen, S., and Kouki, J. 2002. Spatiotemporal availability of dead wood in protected old-growth forests: a case study from eastern Finland. *Scand. J. For. Res.* **17**: 317–329. doi:10.1080/02827580260138071.
- Selva, S.B. 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *Bryologist*, **97**: 424–429. doi:10.2307/3243911.
- Selva, S.B. 2003. Using calicoid lichens and fungi to assess ecological continuity in the Acadian Forest Ecoregion of the Canadian Maritimes. *For. Chron.* **79**: 550–558.
- Sillett, S.C., and Antoine, M.E. 2004. Lichens and bryophytes in forest canopies. *In* *Forest canopies*. 2nd ed. Edited by M.D. Lowman and H.B. Rinker. Elsevier Academic Press, Oxford, UK. pp. 151–174.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., and Ruchty, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* **10**: 789–799. doi:10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2.
- Spribille, T. 2006. Connecting the dots: materials for an epiphytic crustose lichen flora for northwestern North America. Diplom. thesis. University of Göttingen, Germany.
- Stuart-Smith, K. 2002. Songbird communities in burned and logged stands with variable retention in the Canadian Rocky Mountains. Ph.D. dissertation. Oregon State University, Corvallis, Ore.
- Thor, G. 1998. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. *Biodivers. Conserv.* **7**: 59–72. doi:10.1023/A:1008807729048.
- Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. *For. Sci.* **14**: 20–26.
- Van Wagner, C.E. 1995. Analysis of fire history for Banff, Jasper, and Kootenay National Parks. Report to Parks Canada, Banff, Alta.
- Walser, J.-C., Zoller, S., Büchler, U., and Scheidegger, C. 2001. Species-specific detection of *Lobaria pulmonaria* (lichenized ascomycete) diaspores in litter samples trapped in snow cover. *Mol. Ecol.* **10**: 2129–2138. doi:10.1046/j.1365-294X.2001.01353.x.
- Wildlife Tree Committee of British Columbia. 2005. Wildlife/danger tree assessor's course workbook. Forest harvesting and silviculture module. Victoria, B.C. Available from www.for.gov.bc.ca/hfp/training/00016/2005WDTAC.harvsilv-Ch%201,%202.pdf [accessed 8 March 2008].