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Forage Litterfall in Douglas-fir Forests in the Central Interior of British Columbia

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EXECUTIVE SUMMARY

Douglas-fir and arboreal lichen litterfall are important components of mule deer winter diet in the Cariboo Forest Region, central British Columbia. Trees that produce the most litterfall per hectare are highly valuable and require special consideration in management plans for winter ranges.

Over a 3-year period at Tree Farm Licence (TFL) 5, we found that a 198-year-old stand produced more lichen litter than either a 60- or an 87-year-old stand. Also, a high volume 174-year-old stand growing on a mesic bench site produced more lichen litterfall than the 198-year-old stand on a subxeric steep slope. On Fox Mountain (near Williams Lake), trees in age classes over 100 years produced significantly ($p = .05$) more lichen litterfall than did younger classes. On TFL 5, more Douglas-fir litterfall fell in the 87- and 198-year-old stands than in the 60-year-old stand in 2 of 3 years. Rates did not vary between the two over-mature stands of similar age but different volume. On Fox Mountain, the mean Douglas-fir litterfall rates increased with class age but, because of high variability, were not significantly different. Both arboreal lichen and Douglas-fir litterfall rates vary greatly among and within years.

These results and additional observations led us to the following conclusions of interest to forest managers:

1. Trees beyond 100 years old supply the greatest potential amount of litterfall forage.
2. The natural clumpy arrangement of trees within dry-belt Douglas-fir stands should promote maximum litterfall as a result of breakage from crown contact. The clumpy structure of these stands can be maintained by the small group selection system described by Armleder *et al.* (1986).
3. Uneven-aged stand management will provide a continuous source of litterfall and a source of lichen fragments to inoculate the young trees.
4. Low volume partial cutting will not disrupt the microclimate necessary for lichen production. Low volume removal may be especially important on warm, dry aspects.

ACKNOWLEDGEMENTS

This project was funded by the Ministry of Forests research program and Weldwood of Canada (Quesnel Operations). The company received Section 88 funds to collect data from the Tree Farm Licence 5 study area. Also, we wish to thank S.D. Walker, who collected much of the data and contributed to the design of the TFL 5 project.

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INTRODUCTION

Conifer foliage and arboreal lichens are important components of the winter diet of Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) in the Cariboo Forest Region in central British Columbia.[1] Douglas-fir (*Pseudotsuga menziesii*) is the most common conifer, composing 15–90% of the diet. However, on drier winter ranges it usually constitutes 50–90%. On all winter ranges, it increasingly dominates the diet as other foods are covered by snow. Most Douglas-fir is obtained from litterfall because natural regeneration and small trees are rarely browsed in uneven-aged stands (Dawson *et al.* 1990).

Fruticose arboreal lichens, which include *Bryoria* spp., *Alectoria* spp. and *Usnea* spp., compose up to 12% of the diet based on faecal fragment analyses and as much as 26% according to rumen analyses.[1] Lichens are highly digestible (72–85% digestible dry matter) compared to other forage species (Rochelle 1980) and are generally underestimated in faecal fragment analyses. *Alectoria sarmentosa* appears to have a synergistic effect on digestion (Rochelle 1980) and may provide an important source of energy for wintering deer (Robbins 1987). Litterfall is the major available source of lichen, though small amounts are browsed from lower branches and fallen trees.

The litterfall rates from trees and stands of different ages within a winter range are important attributes of deer habitat quality. Stand types that produce more litterfall should be more valuable to deer in the winter. Large differences in litterfall rates between trees and stands of various ages and sizes on mule deer winter range could affect management decisions about the proportion and distribution of high litter-producing stand types.

Since Douglas-fir and arboreal lichens are important components of mule deer diet, we designed two studies to measure litterfall rates. In one we compared litterfall rates among three even-aged stands of different ages growing on similar sites; in the other we examined litterfall rates from 72 trees of various ages and sizes within an uneven-aged forest, several times over one winter. We present the results below, followed by a general discussion that focuses on the management implications of these findings.

LITTERFALL FROM EVEN-AGED STANDS OF DOUGLAS-FIR

Study Objectives

The main objective of this study was to compare Douglas-fir and arboreal lichen litterfall rates in three different-aged stands growing on similar sites. The second objective was to compare litterfall rates in two over-mature stands growing on dissimilar sites. The final objective was to document annual variation in litterfall rates in the various stand types. Low litterfall winters combined with deep snow conditions would make relatively high litter-producing stands valuable.

Study Area and Methods

The study was conducted on a mule deer winter range in Tree Farm Licence 5 (TFL 5), 35 km north of Quesnel, B.C., during the winters of 1986/87, 1987/88 and 1988/89. Sampling design varied slightly among the three winters.

In December 1986, three different-aged Douglas-fir stands, growing on similar sites, were selected as litterfall trapping areas. The three stands, described as immature ($\bar{x}$ = 60 years), young-mature ($\bar{x}$ = 87 years) and over-mature ($\bar{x}$ = 198 years), were not replicated because of a lack of suitable stands. All three sites were located on west-southwest aspects, on steep slopes, in submesic-subxeric moisture regimes and at similar elevations. In 1987 and 1988, the study was expanded to include a high volume over-mature stand on a productive, mesic, bench site comparable in age ($\bar{x}$ = 174 years) to the oldest stand on the steep slope.

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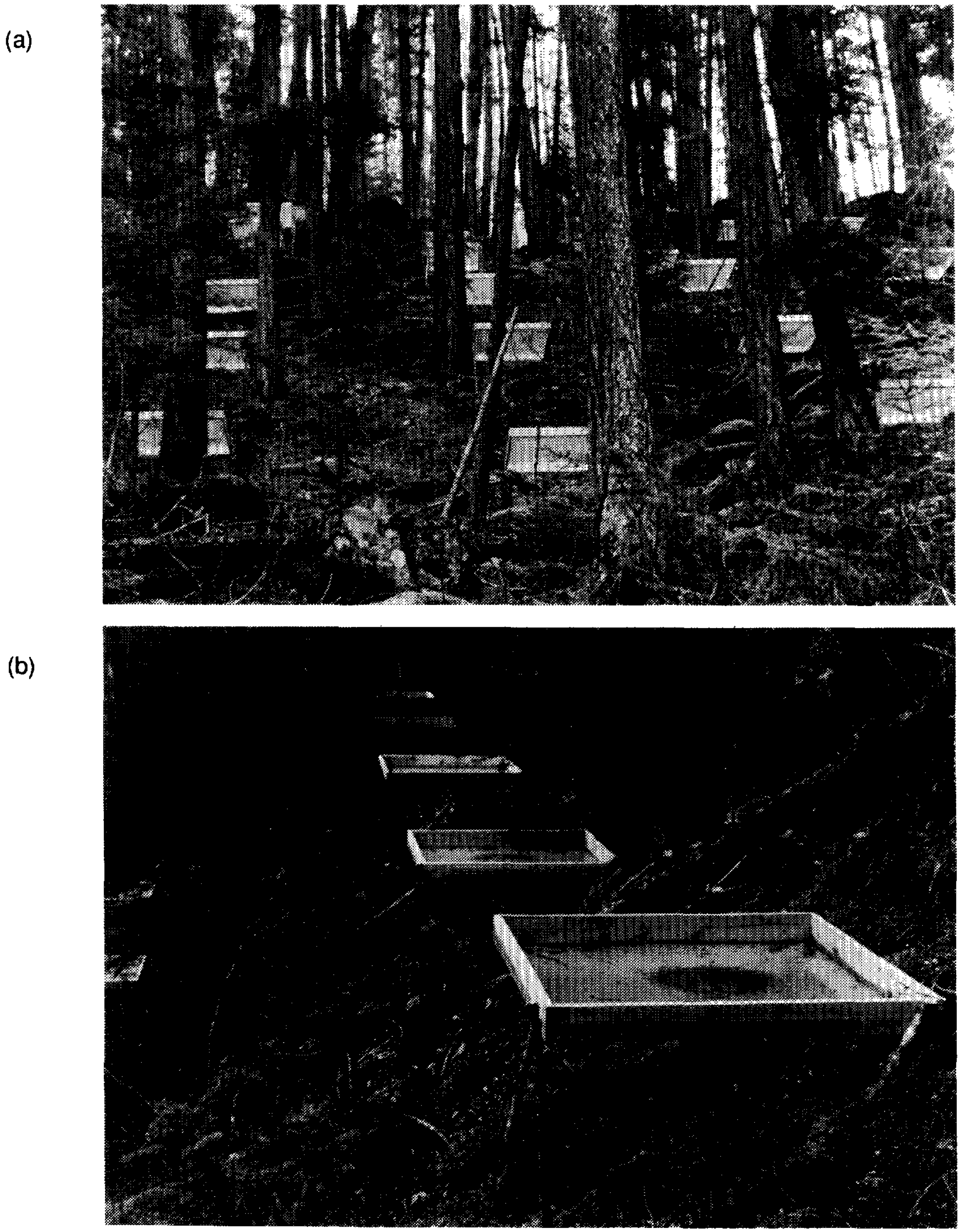
[1] M.J. Waterhouse, H.M. Armleder, and R.J. Dawson. 1990. Winter food habits of mule deer in the Central Interior of British Columbia. B.C. Min. For., Williams Lake, B.C. In prep.

In 1986, thirty litterfall traps in each stand were set in a rectangular grid with trap centres 4 m apart (Figure 1). Wooden frame traps, 1 m^2 long, were constructed from 1 x 4 inch lumber. The bottoms were covered with 10-mil plastic that was punctured with 4-mm drain holes. All traps were placed horizontally and then staked into position (Figure 1). The rectangular sampling area covered 480 m^2, including the traps and area surrounding each trap. In 1987, the total number of traps per stand was decreased to 24 and the sampling area in each stand was reduced to 384 m^2.



Stephen D. Walker

FIGURE 1. (a) Layout of litterfall traps in a stand on the TFL 5 study area. (b) View of a litterfall trap on a steep slope.

Douglas-fir is the dominant tree species in each stand. Subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) and hybrid white spruce (*Picea glauca* x *engelmannii* Perry x Engelm.) occur in small amounts in the understory of the oldest stands. In the young-mature and immature stands these species represent 20–30% of the total stems. Diameter at breast height (dbh) was measured and recorded for all trees over 4 cm dbh in the sampling areas. In the young-mature and over-mature sites, 25% of the trees were randomly selected and measured for age and height, while only 14% of the stems in the immature site were measured. Standard computer programs incorporating the Demaerschalt and Kozak equation (Demaerschalt and Kozak 1977) were used to calculate gross volume per hectare (trees over 4 cm dbh), gross merchantable volume per hectare (trees over 17.5 cm dbh), and the number of stems per hectare. Volume and stems per hectare were high, since the experimental plots were located in areas of higher than average stem density and no pathogenic factors were used. Crown closure was measured from each corner of every trap using a "moosehorn" (Bonner 1967).

At the end of January and March in 1986/87, the litterfall was collected and separated into conifer foliage and lichens. Woody material was trimmed from conifer samples. Only twigs with green foliage attached were kept for weighing. The January samples were separated from snow with a 6 x 6 mm metal mesh sieve. In 1987/88, the litterfall was collected and separated at the end of March. In 1988/89, the traps were cleared of debris mid-November and the litterfall was collected when free of snow in mid-April. The samples were frozen until they were oven-dried for 24 hours at 60°C. Loose needles, seeds and twigs were removed from the lichen samples before weighing.

The arboreal lichens from one trap in each site were sent to Trevor Goward (Lichenologist) in Clearwater, B.C., for identification. In addition to identifying the most common species, he visually estimated their abundance.

Records of daily wind speed, temperature and snowfall were obtained from the Quesnel Airport, which is 35 km south of the study area at slightly lower elevation (545 m). Wind speed was recorded with an anemometer at least hourly over a 2-minute period. Both the average speed and strongest gust speed were recorded. A day was considered windy if one peak hourly speed (average or gust) exceeded 16 knots (Environment Canada standard for a windy day). A detailed profile of each windy day was used to compare wind conditions of each winter. Hourly recordings per windy day were placed into 5-knot classes.

Sample weights from the high volume over-mature stand in 1987/88 should be considered minimums, since deer tracks were found near 22 of 24 of the traps. Tracks were not observed near traps in other stands or years.

Results

Since sites 1–3 have similar characteristics (Table 1), the differences in litterfall rates are primarily attributed to age and stand characteristics associated with age. Replications would have increased confidence by quantifying experimental error such as unknown site effects. Similarly, in a comparison of stands of similar age but different site quality, differences in litterfall rates could be due to factors other than site productivity. As in any unreplicated experiment, care must be taken in interpreting these results.

Among sites 1–3, the highest lichen litterfall rate occurred in the low-volume, over-mature stand in three different winters (Figure 2). The mean litterfall rates in the over-mature stand were 4.23 kg/ha per month in 1986/87, 14.55 kg/ha per month in 1987/88, and 6.17 kg/ha per month in 1988/89. These rates were almost double that of the younger stands each year. Though the pattern among stands was similar each winter, the rates were variable between winters. The within-stand variance of lichen litterfall is low (Figure 2; Appendix 1). On all four sites, *Bryoria fremontii* and *Bryoria capillaris* were the dominant litterfall lichens (Appendix 2).

The conifer litterfall collected was composed entirely of Douglas-fir, despite the small component of subalpine fir and white spruce in the two younger stands. The mean Douglas-fir litterfall rate did not vary greatly among the three stands in 1986/87. However, it was lower in 1987/88 and 1988/89 in the immature stand than in the young-mature or over-mature stands (Figure 3; Appendix 3). The wide overlapping confidence intervals about the sub-sample means in the young-mature and over-mature stands describe high within-stand variability of deposition. More Douglas-fir litter fell, especially in the two older sites, in 1988/89 than in the previous 2 years.

TABLE 1. Stand and site characteristics (mean and sample size) of four even-aged stands on the TFL 5 study area north of Quesnel, B.C.

Characteristic	**Stand type**			
	Immature	**Young-mature**	**Low volume over-mature**	**High volume over-mature**
Age (years)	60 (33)[a]	87 (25)	198 (10)	174 (9)
Gross volume (m^3/ha)[b]	171 (235)	265 (109)	472 (42)	1059 (28)
Gross merchantable volume (m^3/ha)[c]	12 (5)	144 (22)	456 (36)	1042 (21)
Dbh (cm)	8 (235)	12 (109)	27 (42)	34 (28)
Height (m)	9 (33)	14 (25)	17 (10)	33 (9)
Crown depth (m)	2 (33)	3 (25)	5 (11)	10 (9)
Mean crown completeness (%)	83 (120)	75 (120)	73 (120)	90 (96)
Stem density (no./ha)	6896	2834	896	737
Site index rating[d]	medium	poor	medium	good
Slope (%)	55	50	67	10
Aspect (°)	248	248	248	200
Moisture regime[e]	submesic-subxeric	submesic-subxeric	submesic-subxeric	mesic
Elevation (m)	675	600	610	660

[a] Mean (sample size).

[b] Gross volume: includes all trees with a minimum 4 cm dbh and a 30 cm stump height.

[c] Gross merchantable volume: includes all trees with 17.5 cm dbh and 4 cm diameter tops. Stump height = 30 cm. No decay, waste and breakage.

[d] Taken from forest polygons on 1:10 000 forest cover map compiled by Timberline for Weldwood Ltd., Quesnel, B.C.

[e] Based on SBSl subzone biogeoclimatic classification (SBSmh in updated classification).

The high volume over-mature stand growing on a silty, gently sloped mesic site produced greater quantities of lichen litter than the low volume over-mature stand located on the steep, moisture-deficient slope in 1987/88 and 1988/89 (Figure 4). The mean Douglas-fir litterfall rates in the two over-mature stands were similar in both years (Figure 5).

During the litterfall collection period, the airport recorded 20 windy days in 1986/87, 17 windy days in 1987/88, and 30 windy days in 1988/89. The average wind speed for each winter was 6.8 knots in 1986/87 and 1987/88, but 9.1 knots in 1988/89. Also, the number of hourly recordings per wind speed class were similar for the first two winters, but more readings occurred in the stronger classes in 1988/89 (Table 2).

Wind or snow may cause significant litterfalls. On windy days in 1986/87, minimum temperature ranged between 2 to -9°C, except on January 15 when it dropped to -14°C. This coincided with the heaviest snowfall (7 cm). In 1987/88, temperatures ranged between 0 and -8°C, except on January 29 when the minimum temperature was -25°C. Again, the heaviest snowfall (10.4 cm) fell on the same day. February 14, 1988, was the only other day where a snowfall exceeded 4 cm, and it was a windy day. In 1988/89, minimum temperatures ranged between 6 and -32°C. On January 30, a cold front (-19 to -32°C) accompanied by strong winds (>16 knots) persisted until February 3. December 28 and February 27 were the only other windy days accompanied by significant snowfall in 1988/89. In total, there were 1, 2 and 3 cold, snowy, windy days in 1986/87, 1987/88 and 1988/89, respectively.

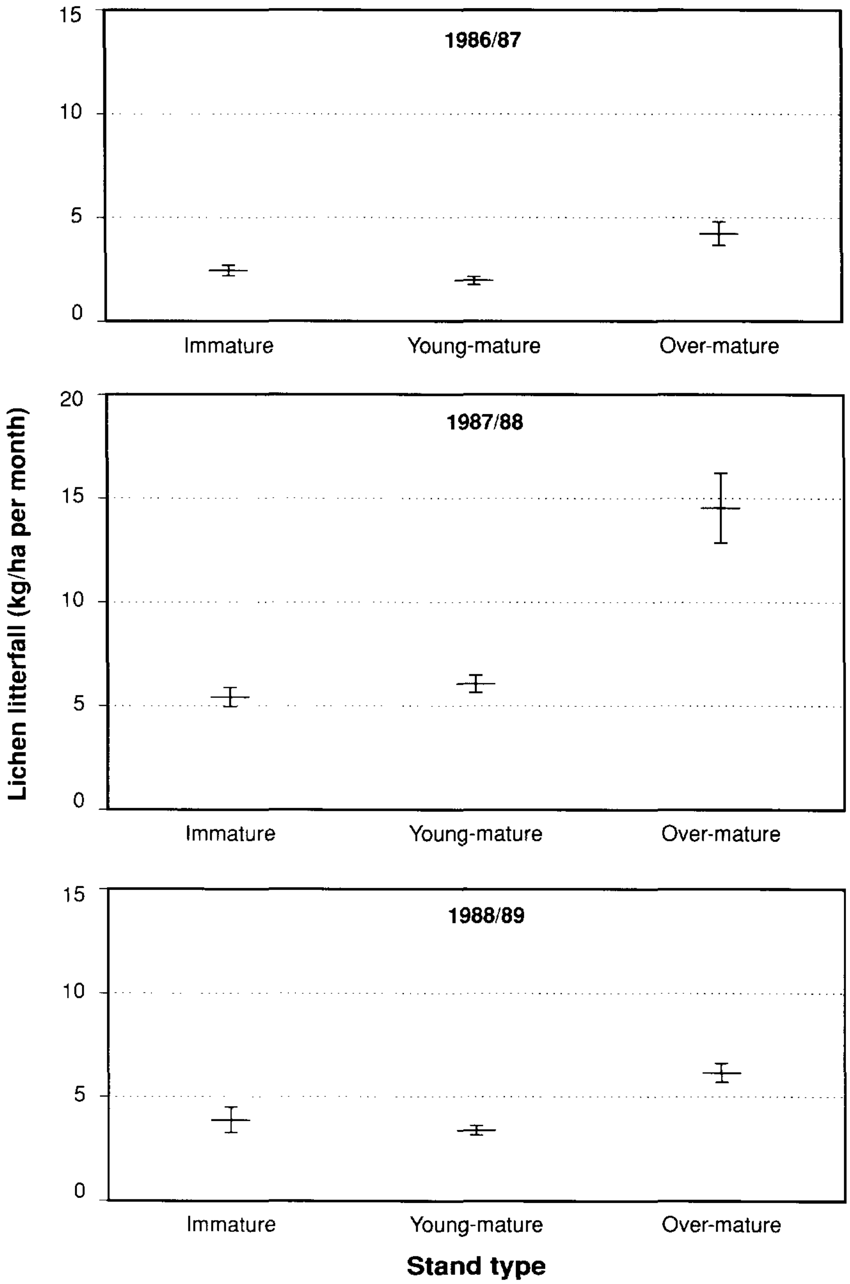


FIGURE 2. Lichen litterfall rates within each stand: immature (60 yr), young-mature (87 yr) and low volume over-mature (198 yr) (confidence limits = .95, n = 30 sub-samples in 1986/87 and n = 24 sub-samples in 1987/88 and 1988/89), on TFL 5, Quesnel, B.C.

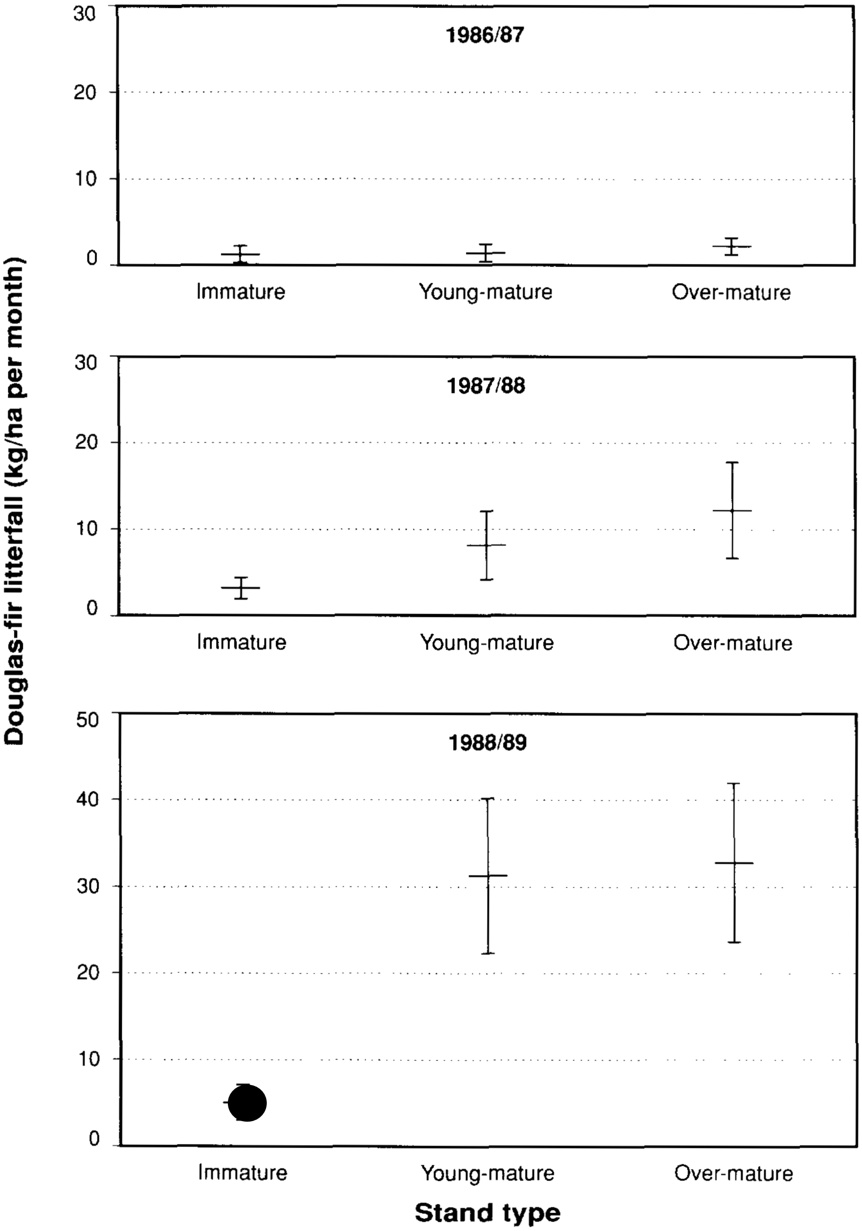


FIGURE 3. Douglas-fir litterfall rates within each stand: immature (60 yr), young-mature (87 yr) and low volume over-mature (198 yr) (confidence limits = .95, n = 30 sub-samples in 1986/87, and n = 24 sub-samples in 1987/88 and 1988/89), on TFL 5, Quesnel, B.C.

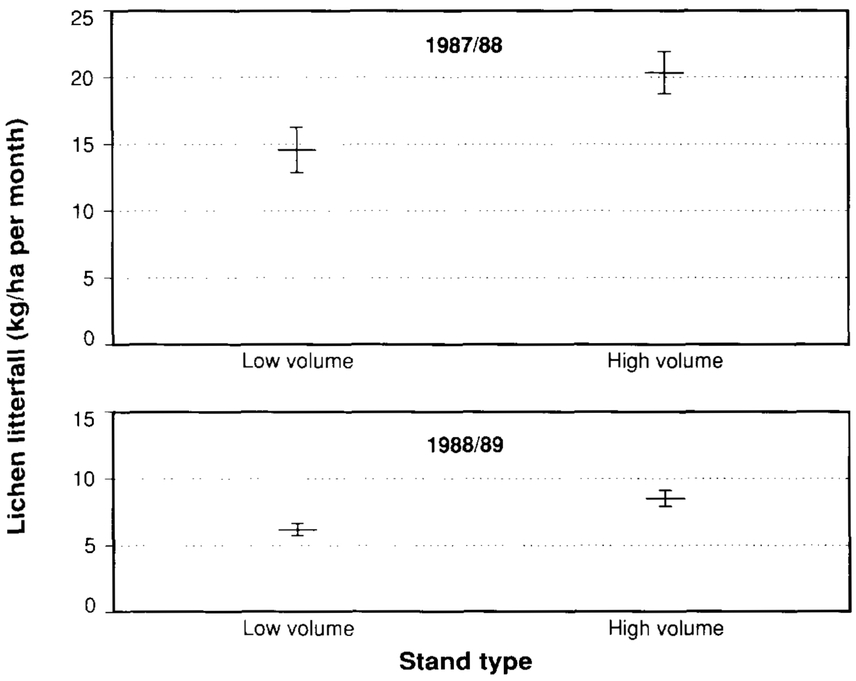


FIGURE 4. Lichen litterfall rates within a low volume over-mature stand and a high volume over-mature stand (confidence limits = .95, n = 24 sub-samples), on TFL 5, Quesnel, B.C.

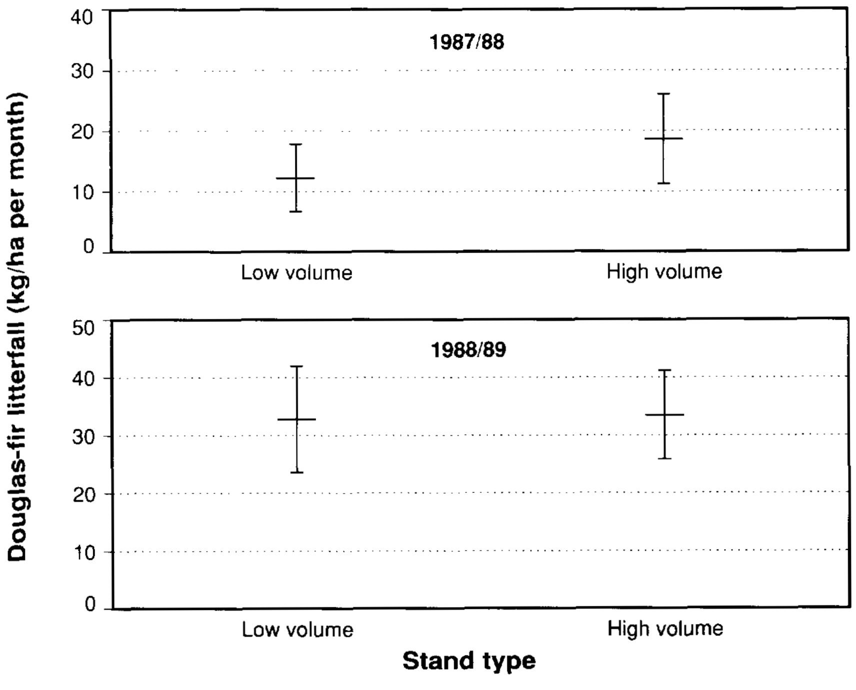


FIGURE 5. Douglas-fir litterfall rates within a low volume over-mature stand and a high volume over-mature stand (confidence limits = .95, n = 24 sub-samples), on TFL 5, Quesnel, B.C.

TABLE 2. Wind data collected at the airport in Quesnel, B.C.

Year	Average wind speed (knots)	Class (knots)[a]					Total number of samples
		0–5	6–10	11–15	16–20	21–25	
1986/87	6.8	237	149	113	22	2	523
1987/88	6.8	212	133	100	17	3	465
1988/89	9.1	222	206	271	85	10	794

[a] Samples taken every hour on every day where wind speed exceeded 16 knots at least once during the day.

Discussion

The arboreal lichen litterfall rates we found (2–20 kg/ha per month) are comparable to those in other studies in mixed Douglas-fir stands in B.C. Rochelle (1980) reported between 22 and 27 kg/ha per month for *Bryoria/Alectoria* spp. of lichen litterfall in mixed Douglas-fir stands during the winter on Vancouver Island, while Stevenson and Rochelle (1984) recorded .33–25.2 kg/ha per month in similar stands. Edwards *et al.* (1960) calculated 36 kg/ha per winter of *Alectoria* spp. available on fallen trees, and found 20.4 kg/ha per winter of unattached lichens on the ground in Wells Gray Park, B.C. The average lichen litterfall rate would be about 11 kg/ha per month based on a 5-month winter. Stevenson (1986) quoted 9 kg/ha per month (106 kg/ha per year) from a Vancouver Island study (W. Kale, unpublished data).

Douglas-fir litterfall rates in different-aged stands ranged between 1.28 and 33.47 kg/ha per month. Rochelle (1980) found that the conifer litterfall rate varied between 0.6 and 4.2 kg/ha per month in coastal Douglas-fir. Grier and Logan (1977) found litterfall rates of green foliage between 0.4 and 4.2 kg/ha per month in Douglas-fir old-growth stands in Western Oregon.

The amount of litterfall we recorded varied greatly among years. Daily weather data recorded at Quesnel airport, then summarized for each study period, could not predict the total amount of winter lichen litterfall. On-site, daily weather and lichen collections need to be made. Douglas-fir litterfall is the major food of mule deer in deep snow conditions on TFL 5. It is more variable among years than lichen litterfall, particularly in the young-mature and over-mature stands. Douglas-fir litterfall rates in these stands may be affected by winter wind conditions. The winter of 1988/89, which produced the most Douglas-fir litterfall, was much windier than the previous two winters and had more cold, snowy, windy days. Very cold temperatures in conjunction with wind may have caused major litterfalls. Frozen twigs and branches become brittle and snap easily when rubbed against each other.

Lichen litterfall rates increased with stand age. In three different winters, the over-mature stand deposited more lichen than either the immature or young-mature stands. Stevenson (1985) cautiously concluded that arboreal lichen abundance is usually great only in Douglas-fir stands older than 100–150 years, though there are instances of high abundance in younger stands. Lang *et al.* (1980) found that total lichen biomass increased with stand age of balsam fir. Older stands may provide microniches more favourable for lichen growth because of their structure and biomass, which affect microclimate and number of attachment sites (Stevenson 1985).

Stand age is also related to annual lichen turnover rates. Older stands lose proportionally more of their standing biomass of lichen every year than younger stands do. Examining several studies in the literature, Stevenson (1986) reported 5–10% turnover in all stands except old growth (> 300 years), where the turnover rate was 15%.

Stevenson (1986), in summarizing the literature, also found that although the ranges overlapped, more total woody litter fell in old-growth Douglas-fir stands (>300 years) than in young-growth stands (20–100 years). Grier (1988) suggests that older stands are more prone to damage from wind or snowstorms than younger stands. We did not find significant differences in litterfall rates between age classes in 1986/87. However, in 1987/88 and 1988/89, the young-mature and over-mature stands clearly produced more Douglas-fir litter than the immature stand. Differences in litterfall may be related to factors associated with stand age such as foliage biomass, susceptibility to breakage and stand structure.

Site quality appears to affect lichen litterfall rates. In both study years, the high volume over-mature stand on the mesic bench site produced more lichen litterfall than did the low volume stand on the subxeric-submesic steep slope. Because of better growing conditions on the bench, the stand has double the volume, height and crown depth. Presumably, this stand provides more climatically favourable microniches for *Bryoria capillaris* and *B. fremontii* growth.

Bray and Gorham (1964) reported increased total conifer litterfall with increased site quality. However, we did not find Douglas-fir litterfall rates to be higher in the high volume stand. Less vigorous trees, growing under stressful environmental conditions, may be more susceptible to breakage.

Litterfall rates that we present should be interpreted as potential amounts of deer forage available rather than as actual amounts. All stands were subject to sporadic litter-producing storms and frequent snowfalls which bury litter. Lichen samples collected from the trays may have included pieces too small for deer consumption. Furthermore, deer may have consumed litter from the traps in the high volume over-mature stand over the winter period. We also did not measure the contribution of blowdown trees. Decadent over-mature trees are particularly susceptible to blowdown and provide huge quantities of conifer and lichen.

LITTERFALL FROM TREES WITHIN UNEVEN-AGED DOUGLAS-FIR STANDS

Study Objectives

The main objective of this study was to examine whether age or dbh of a tree within an uneven-aged stand could be used to predict the quantity of litter it would produce. The outcome affects management decisions as to the number and distribution of high-litter producing trees to be left on a winter range if partial cutting takes place.

There were three secondary objectives:

1. to determine whether over-mature trees (141 years and older) produced more lichen and Douglas-fir litter than trees in three younger age classes (1–60 years, 61–100 years and 101–140 years) in an unlogged and a partially cut forest;
2. to quantify the arboreal lichen which fell to the ground attached to twigs, branches and bark, because clumps of lichen attached to wood may be more visible to deer; and
3. to document how the winter weather conditions affected litterfall rates.

Study Area and Methods

The study area was located on Fox Mountain, 1.5 km northeast of Williams Lake, B.C. (52° 08′ N, 122° 07′ W). Elevation is 900 m. Although the area is no longer used by wintering deer because of its proximity to people and dogs, it has many features typical of mule deer winter range: a mature, uneven-aged Douglas-fir forest (DFb$_2$),[2] gentle to moderately steep, south- to west-facing slopes, and topographic variability including small ridges and gullies.

Two sites were selected for detailed study. Site 1 was a mixed-age, unlogged stand located on a west to northwest 11% slope; site 2 was a partially cut stand on a southwest 15% slope, where in the mid-1950's most of the large trees were removed. Appendices 4 and 5 show the differences in stand structure. The logged site contains 106 m^3/ha gross merchantable timber and the unlogged site contains 205 m^3/ha based on 7.5 cm dbh, 5 cm top diameter, and 30 cm stump height.

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[2] Forest Sciences Section, Cariboo Forest Region. 1982. A field guide for the identification and interpretation of ecosystems of the Cariboo Forest Region (revised 1989). B.C. Min. For., Williams Lake, B.C. Unpubl. draft.

Trees were selected and aged in each of the two sites according to the following criteria. First, sample trees had to be within the stand, not on an edge. Second, the three to five selected trees from each 5 cm dbh class had to have no crown overlap with other trees and had to be isolated, especially from trees of a different size class. Small trees were removed from below the crowns of larger sample trees. In total, 51 trees were selected in the unlogged site and 20 trees in the logged site.

The ground surface under the crown of each sample tree was the litterfall plot for that tree. The radius of the circular plot was the average width of crown measured from the trunk to the crown perimeter in the four cardinal directions. If the tree leaned or was lopsided, the centre of the crown was determined by visual inspection, then vertically projected to the ground. This point was marked by a stake and used as the plot centre.

The litterfall plots were raked and handpicked to remove all branches, slash and litter on November 10, 1988. This date marks the beginning of the first period of green Douglas-fir and lichen litter accumulation. Litter was collected four times throughout the winter on the following dates: December 1, January 24, February 6, and April 10. Elapsed time for each period of litter accumulation was measured from the end of the most recent snowfall up to the collection day. The fourth period of litter accumulation was calculated by subtracting the days in which litter accumulated in the other collection periods, from the total number of days in the study. The snow was gone so all litter was collected. At each collection, the perimeter of each plot was outlined in the snow using the previously determined radius.

During collection, lichen was separated into two types: attached and unattached. Attached lichen fell attached to bark, twigs or branches; unattached lichen fell independent from any woody material. Green Douglas-fir litter was divided into two size classes. Branches were defined as greater than 1 cm in diameter on the main stem; twigs were defined as less than 1 cm in diameter. In both groups, the Douglas-fir litterfall was trimmed to include only stems with green foliage attached. The samples were frozen, then later oven-dried for 24 hours at 60°C. Needles, seeds and other debris were removed from all lichen samples before weighing. Six samples of lichen litterfall were sent to Trevor Goward (Lichenologist) who identified them and estimated the abundance of each common species within each sample.

Records of daily wind speed, daily maximum and minimum temperatures, and daily snowfall were obtained from Williams Lake airport located 6.0 km northeast of the study area at a slightly higher elevation (940 m). Wind speed was recorded at least hourly with an anemometer. Both the average and strongest gust were recorded. A day was considered windy if one hourly speed (average or gust) exceeded 16 knots (Environment Canada standard). Detailed profiles of windy days were used to compare overall wind conditions of each collection period. The hourly recordings per windy day were placed into 5-knot classes.

Simple linear regression was used to examine relationships between litterfall quantity, tree age, and dbh. Each collection period and the whole winter were tested separately for both sites. Plots of residual sums of squares showed data to be fairly normally distributed, although variance tended to increase with tree age. Trees within each site were also grouped into B.C. Forest Service forest cover map categories: immature (1–60 yr) (Class 1–3), young-mature (61–100 yr) (Class 4–5), silviculturally mature (101–140 yr) (Class 6–7) and over-mature (141+ yr) (Class 8–9). Confidence intervals and analysis of co-variance were used to test for differences in quantities of litter produced between sites and age classes.

Results

Only a small percentage of the variance in attached lichen, unattached lichen, total lichen and total Douglas-fir litterfall was accounted for by age or dbh in both logged and unlogged sites (Appendices 6 and 7). However, the low probability level ($p = .003$) for total lichen and age on the unlogged site indicates a strong linear trend. Litterfall rates were also compared in broad age categories. We found that significantly ($p = .05$) more lichen litterfall accumulated under trees in the unlogged site than in the logged site in three different age classes (1–60 yr, 61–100 yr, and 101–140 yr) (Figure 6). Figure 6 also illustrates greater lichen litterfall in the two older age classes (101–140 yr and 141+ yr) than in the two younger classes (1–60 yr and 61–100 yr) within the unlogged site. However, trees in the silviculturally mature and over-mature classes did not produce significantly different ($p = .05$) amounts of lichen litterfall. These observations were confirmed with analysis of co-variance. Significantly more lichen litterfall was produced from trees in the unlogged site than in the logged site ($F = 33.03$; $p = .0001$). And, the increase in litterfall with age (co-variate) was also significant ($F = 12.81$; $p = .0006$).

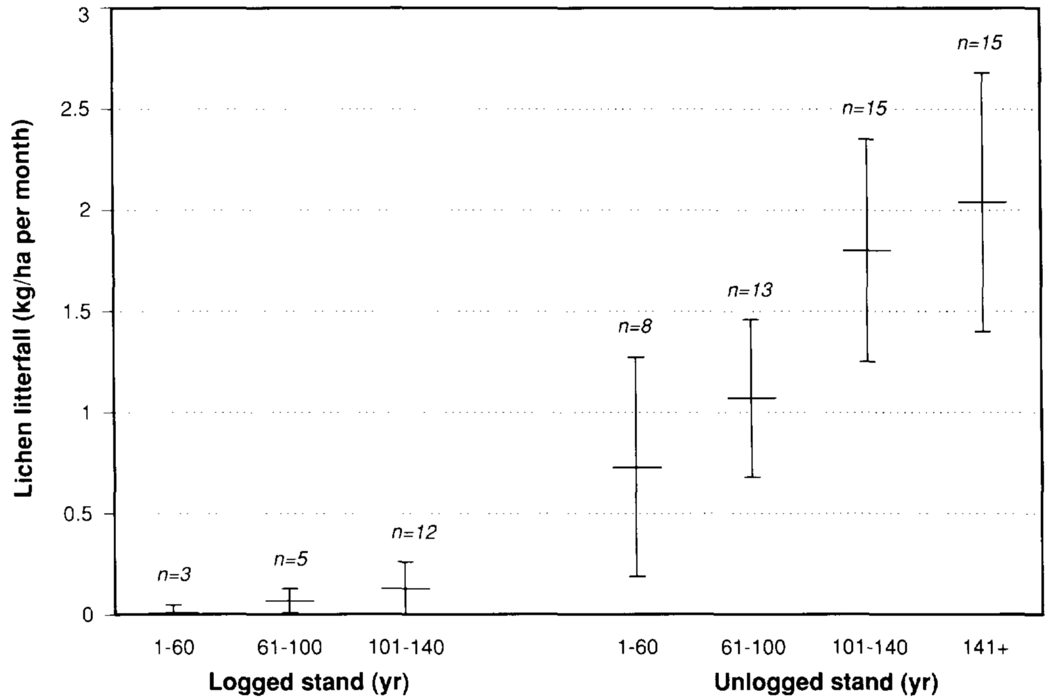


FIGURE 6. Mean and 95% confidence limits of lichen litterfall rates from individual trees within each age class in the logged and unlogged stands on Fox Mountain, Williams Lake, B.C.

Quantity of Douglas-fir litter from trees within the four age classes did not differ significantly (p = 0.5) between age classes. Although mean Douglas-fir litterfall was greater in the unlogged stand for all three comparable age classes, the difference was only statistically significant between the 61–100 year classes (Figure 7).

Figure 8 compares the proportion of elapsed time for each collection period with the proportion of the total litterfall that was collected during each period. The amount of Douglas-fir deposited in the first two periods was similar to the proportion of elapsed time. However, the quantity that fell in collection period 3 was approximately 10 times greater than the proportion of elapsed time in that collection period (44–48% of the total Douglas-fir litterfall fell during this 7-day period). One storm caused most of this litterfall. As a cold front moved in, the temperature fell from 7.8 to -31°C within 24 hours. A total of 7.2 cm of snow, which changed from heavy and wet to light and dry, fell. Maximum wind speeds were between 15–24 knots during the snowstorm and the 2 following days. On the litterfall collection date, fresh twigs were scattered over the snow surface. Douglas-fir tterfall was concentrated (covering 30–40% of snow surface) underneath clumps of even-aged poles (15–25 cm dbh) with overlapping crowns. Twigs made brittle by sudden freezing were likely broken when the strong wind caused them to rub against each other.

The low temperatures and storm associated with the large Douglas-fir litterfall in collection period 3 did not have a similar effect on lichen deposition. In collection periods 1–3, the proportion of attached lichen and unattached lichen generally exceeded the proportion of time. The opposite was true for the fourth collection period (Figure 8). It was not as windy as collection periods 1–3 as indicated by fewer wind samples in the strong wind classes (Table 3). However, since collection 4 was made at the end of the study just after snow melt, there may have been some deterioration of the lichen samples over the study period and especially during spring thaw. It is also more difficult to see small pieces of lichen on the bare ground than on the snow surface, and therefore some lichen may have been missed.

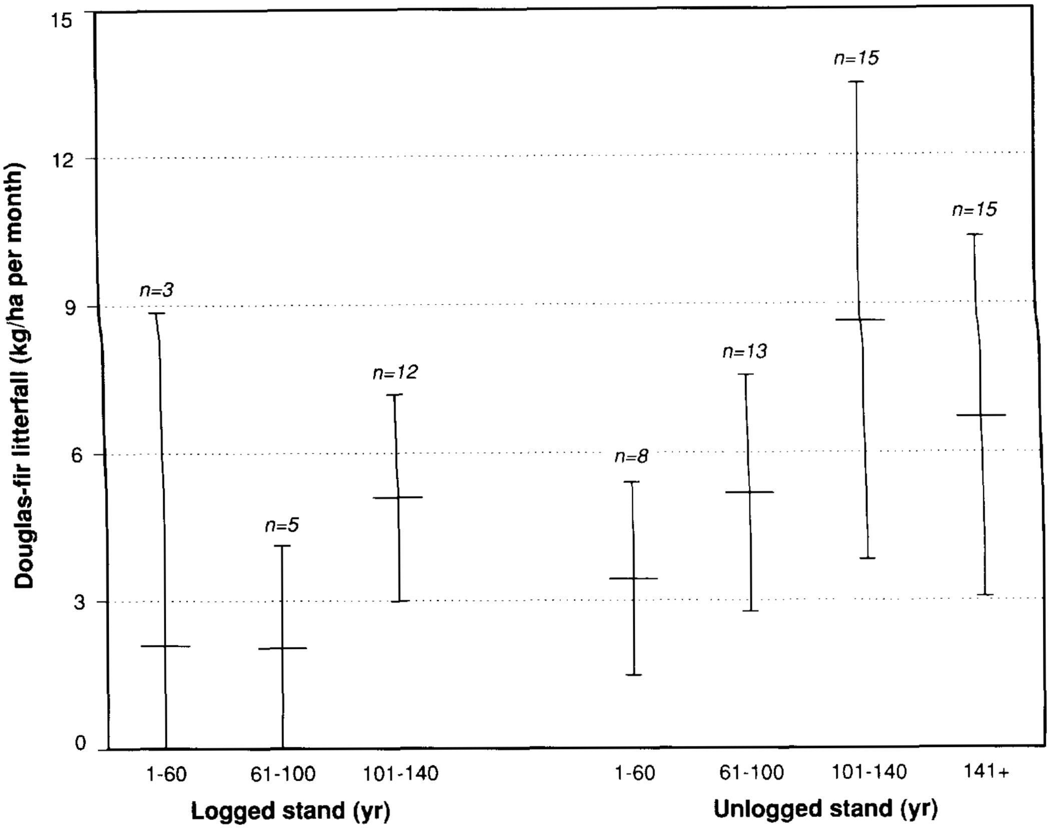


FIGURE 7. Mean and 95% confidence limits of Douglas-fir litterfall rates from individual trees within each age class in the logged and unlogged stands on Fox Mountain, Williams Lake, B.C.

TABLE 3. Weather data collected at the airport in Williams Lake, B.C.

Collection period	Period of accumulation (days)	Mean min. temperature (°C)	Mean[a] windspeed (knots)	Class (knots)[a]						Total number of samples
				0–5	6–10	11–15	16–20	21–25	26+	
1	21	-4.5	11.6	52	49	83	51	11	0	246
2	8	-10.5	15.2	6	22	27	26	1	11	93
3	7	-31.5	12.1	10	9	19	12	2	0	52
4	114	-10.5	11.1	251	256	305	129	20	1	962

[a] Samples taken every hour on every day where windspeed exceeded 16 knots at least once during the day.

The proportion of attached to unattached lichen in each collection period was 2.1 (n = 4; s = 1.4) times in the logged stand and 2.7 (n = 4; s = 1.0) in the unlogged stand. These proportions remained fairly constant as tree age and diameter increased.

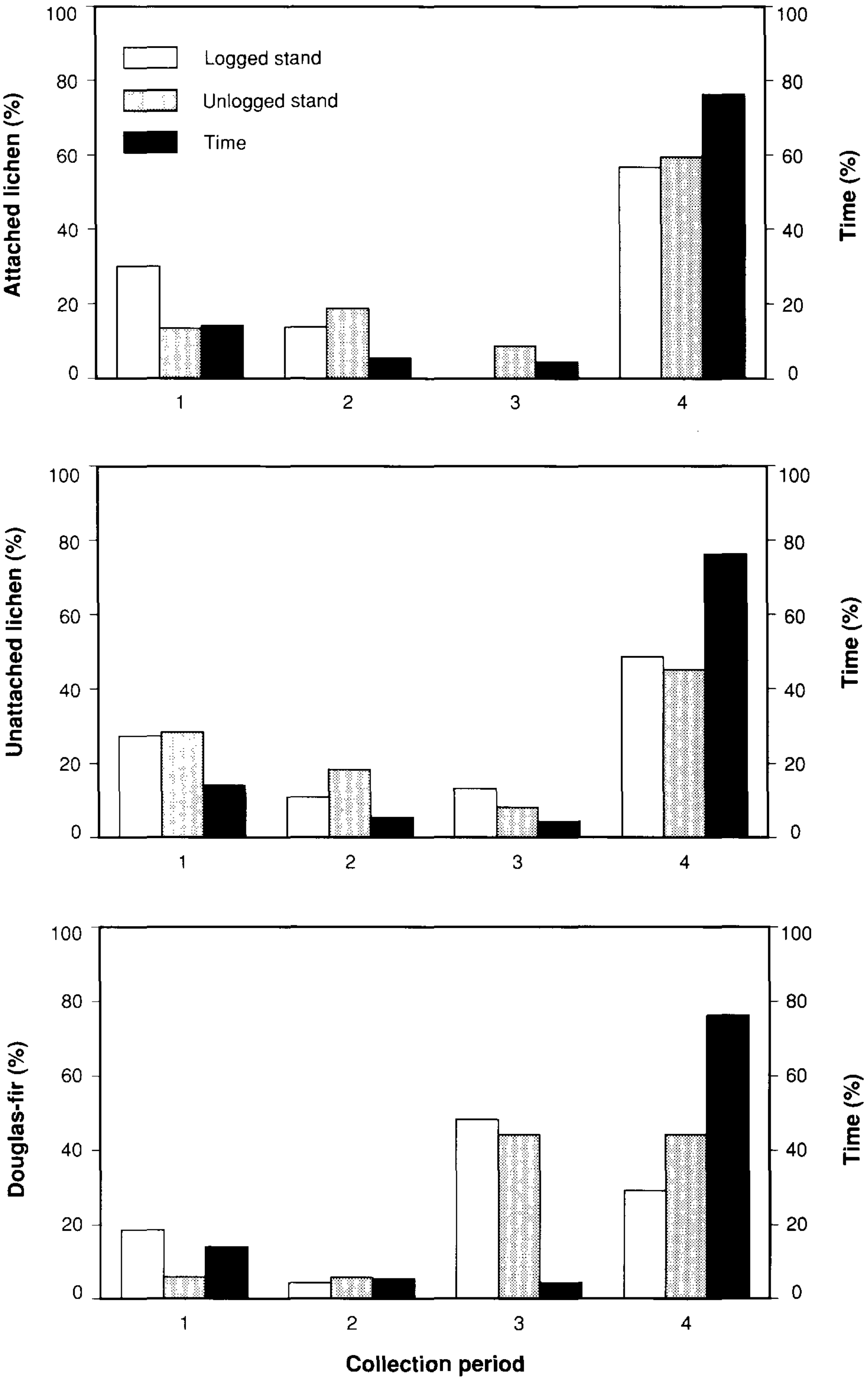


FIGURE 8. Proportion of elapsed time for each collection period compared to proportion of total lichen and Douglas-fir litterfall collected during each period on Fox Mountain, Williams Lake, B.C.

Discussion

We found no predictive linear relationships between tree age or diameter and quantity of lichen or Douglas-fir litterfall. High variability in the data probably resulted from the study design. The wind could have dispersed the litterfall beyond the plot. Taller trees may be affected more because they intercept more wind, and litter has a greater distance to fall to the ground. Also, plots may have become contaminated with litter from neighbouring trees. Additionally, while we were collecting samples, we noticed that a large amount of Douglas-fir fell just outside the plots under the larger trees. Possibly the tips of the exterior branches of the crowns of large trees are more susceptible to wind pruning than the interior branches are. We did not notice a similar pattern of accumulation under younger trees. Finally, younger trees over a period of years may have intercepted lichen litterfall from older trees, in turn dropping it as litterfall.

Data were split in broad age classes to see if there were any significant differences in litter production. Similar to our results from TFL 5, trees over 100 years produced significantly more lichen litterfall than younger age classes. Antifeau (1987) reported, in the 0–6 m forest canopy stratum, more lichen in stands over 100 years old than in younger ones in the Engelmann spruce-subalpine fir zone in British Columbia. Stevenson (1985) also concluded that lichens are generally more abundant in stands 100–150 years old because the older stands have more favourable microniches and better microclimates for lichen growth than do younger stands.

There was significantly less lichen litterfall from trees in the logged stand than from those in the unlogged stand. In Interior Douglas-fir forests, especially on warm aspects, removal of large trees may cause the microclimate to become too dry for lichen growth. Schroeder (1974) states that the occurrence of *Alectoria* spp. and *Bryoria* spp. may be limited by humidity in southeastern British Columbia. Perhaps, *Usnea* spp., the common species on Fox Mountain, are also moisture limited. As well, the larger trees may be necessary to "seed" the younger trees with lichen thallus fragments. Stevenson (1988) found lichen abundance in second growth to be directly related to distance from mature timber, and to suitability of the stand for colonization. Colonization drops off within 300–400 m of the lichen source. In our study, trees within the logged stand are within 50–500 m of the unlogged stand.

The proportions of lichen litterfall attached and not attached to wood may be affected by forest type, site conditions and species composition. We found that more than twice as much *Usnea* spp. fell attached to bark and twigs than dropped independently. Pike (1971) found that 55% of lichens fell attached to woody material in a Garry oak forest. However, on the moister TFL 5 study area, we noticed that *Bryoria* spp., the most common genus, generally dropped independent of woody material. Arboreal lichens that fall attached to larger pieces of woody material may be more visible to foraging deer. Dead branches, common in the lower canopy, provide good lichen attachment sites. Forest practices such as thinning, which promote tree growth and maintenance of existing live branches, may cause a reduction in attached arboreal lichen litterfall.

Douglas-fir litterfall appears episodic rather than consistent over the winter, which affects its availability to deer. During collection period 3, one storm characterized by very rapid temperature decline and high winds caused a major Douglas-fir litterfall. The other collection periods were also windy but not extremely cold. Similarly, on the coast, Rochelle (1980) found that the amount and timing of litterfall was associated with the occurrence of winter storms, especially those with strong winds and heavy snowfall. Grier (1988) also commented on the episodic nature of canopy damage resulting from wind pruning and breakage during high intensity storms.

GENERAL DISCUSSION OF MANAGEMENT CONSIDERATIONS

Bray and Gorham (1964) concluded, after analyzing worldwide litterfall data, that many factors such as seasonal and annual variation, site quality, moisture regime, stand density, climate, latitude, elevation, aspect and stand age affect litterfall rates. We found that both arboreal lichen and Douglas-fir litterfall rates are affected by annual variation in winter weather, episodic storms, stand and tree age, and site characteristics. These results should influence decisions about age composition and extent of harvesting on mule deer winter ranges where deer depend on litterfall.

Douglas-fir litterfall rates can be related to the daily winter food requirements of mule deer. Based on a forage consumption rate of 20 g oven-dried natural forage per kilogram of body weight per day (Nichol 1938; Alldredge 1974; Carpenter and Baker 1975), a 95 kg adult female mule deer would require 1.9 kg of oven-dried Douglas-fir per day to maintain condition. Based on the 1987/88 Douglas-fir litterfall rates at TFL 5, the immature, young-mature and low volume over-mature stands would potentially provide forage for .06, .14, and .21 deer per hectare per month. The high volume over-mature stand would provide forage for .33 deer per hectare per month. Deer would spend less time and energy foraging in older stands than in younger ones. Extensive logging of older stands and trees over an entire winter range would reduce food supply and could lessen the carrying capacity of the winter range.

Although young-mature and over-mature trees on the TFL 5 produce similar amounts of Douglas-fir litterfall (in some years), and logging over-mature trees may have economic and silvicultural benefits, this practice may not be justified for several reasons. First, the quality of the Douglas-fir litterfall must be considered. Dawson *et al.* (1990) found that mule deer strongly prefer foliage from older, large diameter (> 40 cm) trees than from those in smaller size classes. Marginal differences in palatability may determine survival when deer depend on a poor forage such as Douglas-fir. Second, food availability is only one aspect of winter range quality. Large, older trees effectively intercept snow, making travelling, foraging and avoiding danger less energetically demanding. Finally, trees in decline or with large spreading crowns may be more susceptible to branch and bole breakage than would healthy or smaller crowned trees. Sporadic windfalls provide much forage which could potentially last for a longer period of time independent of snow depth or additional storms.

Douglas-fir deposition is highly variable among and within years, especially in older age classes, so it is important to keep high litter producing trees within the stand to provide an adequate amount of forage at all times. In contrast to Douglas-fir litterfall, the quantity of lichen litterfall appears to be more consistent among years and within winters, providing a more reliable food source, especially in low Douglas-fir deposition years.

Arboreal lichen is not as common in the winter diet of mule deer as Douglas-fir. Faecal fragment analyses of pellets collected from the TFL 5 in shallow snow winters found lichen in only 0–8% of the diet, compared to 10–53% Douglas-fir. However, faecal fragment analysis probably underestimates lichen abundance. Despite the smaller quantity, lichens improve the quality of the winter diet. We have observed deer consuming the lichen before nipping off the twig ends on freshly fallen trees. Arboreal lichen is highly digestible compared to conifers and shrubs (Rochelle 1980) and can provide an important source of energy (Robbins 1987). It may also provide a carbohydrate source which facilitates the use of recycled urea (Jenks 1986). Rochelle (1980) and Robbins (1987) found that overall digestion was improved when *Alectoria sarmentosa* was present. Perhaps other arboreal lichens have a similar effect. White (1983) states that even small improvements in diet quality can greatly influence animal condition and productivity over time.

Over-mature stands on TFL 5 and trees in the two older age classes on Fox Mountain produced significantly more lichen litterfall than the younger ones. Also, on Fox Mountain, there was little lichen litterfall from the trees in the logged stand compared with those in the unlogged stand. The higher concentrations of lichen under large, older trees increases foraging efficiency. These older stands and trees are potentially capable of supporting more wintering deer.

Age is indicative of the lichen litterfall capabilities of trees and stands. However, it is characteristics associated with age — such as standing biomass, stand structure and annual lichen turnover rate — that affect the litterfall rate. Stevenson (1985) concluded that the microclimate and microniches favourable for arboreal lichen growth are more abundant within older coastal Douglas-fir stands. Lang *et al.* (1980) found that lichen biomass in balsam-fir forests is related to the number of dead boles, the number of dead branches, and tree height as well as stand age.

Since lichen is important in mule deer diet, rehabilitation of logged areas of winter ranges may include methods to promote lichen growth. Stevenson (pers. comm., Oct. 1990) recommended that young Douglas-fir stands be thinned by girdling. This would leave dead trees for lichen attachment. She also suggested seeding these stands with lichen thallus parts because dispersal distance from large trees may be a limiting factor in lichen establishment. Similar treatments could be tried in interior Douglas-fir stands which have been clearcut or partially cut. However, lichens may not be able to re-establish immediately if the microclimate has been significantly altered by removal of the overstory.

As part of an overall mule deer-forestry management strategy, Armleder *et al.* (1986) describe a low volume partial cutting system for winter range. This harvesting system incorporates the following conclusions, based on our litterfall data and the literature:

1. Trees and stands over 100 years old generally supply more litterfall forage than younger ones.
2. A clumpy arrangement of trees should promote maximum Douglas-fir litterfall as a result of crown contact.
3. Removal of a high proportion of the merchantable trees may disrupt the microclimate necessary for arboreal lichen growth.
4. Uneven-aged stand management leaves residual trees to provide deer with a continuous source of litterfall and to inoculate the regeneration with lichen fragments.

RESEARCH RECOMMENDATIONS

1. Repeat the litterfall study using even-aged stands. Each age class and site should be replicated to improve the scope and statistical validity of the results.
2. Establish a study in an uneven-aged forest where plots are systematically placed on a grid. Each plot should be characterized by the surrounding trees, which may contribute litter. Multiple regressions could determine whether number of stems, biomass, age of trees, basal area, etc., are influencing litterfall rates.
3. Survey the lichen abundance and species composition in mature, untouched stands on various winter ranges. This would provide some baseline data for lichen rehabilitation work on logged areas.
4. Measure the actual standing conifer foliage and lichen biomass that are potentially available from various size trees, to determine how it increases with age or size.
5. Survey a large area of a winter range for quantity of large branch and tree blowdown. This may contribute substantially to litterfall forage.
6. Experimentally "seed" with lichen fragments in areas where the mature timber was logged to see whether dispersal or microclimate is limiting lichen production.
7. Measure on-site weather conditions and frequently collect litterfall to describe the effect of weather on litter production accurately.

APPENDIX 1. Lichen litterfall rates in four stands over three winters on the TFL 5 mule deer winter range near Quesnel, B.C.

Stand type	Mean lichen litterfall rates (kg/ha per month)								
	1986/1987			1987/1988			1988/1989		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Immature	30	2.47	.64	24	5.42	1.07	19	3.88	1.26
Young-mature	30	1.98	.54	24	6.07	.98	24	3.39	.55
Over-mature (low volume)	30	4.23	1.55	24	14.55	3.96	24	6.70	1.10
Over-mature (high volume)	–	–	–	24	20.35	3.74	24	8.50	1.43

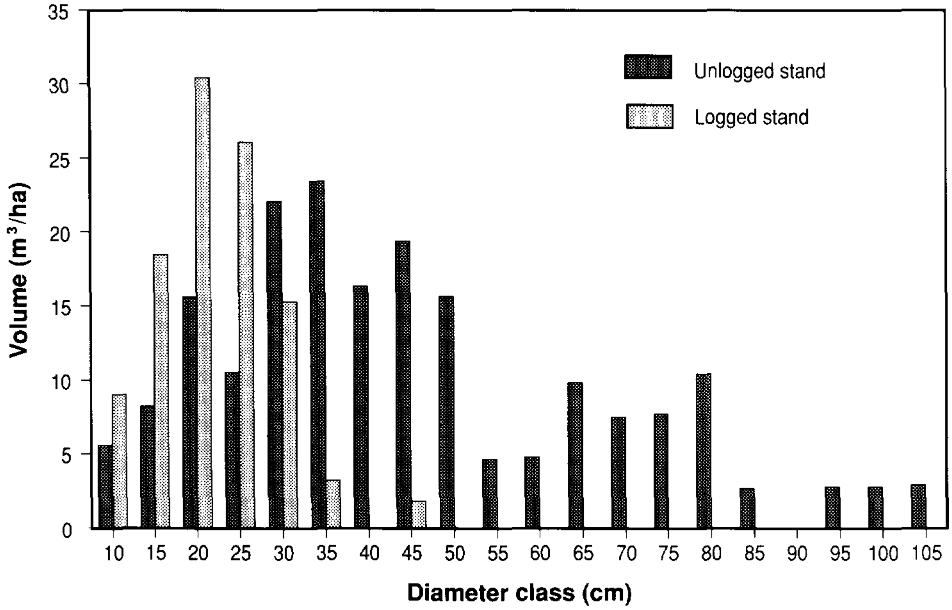
APPENDIX 2. Species composition and abundance of arboreal lichen in litterfall samples from four stands on the TFL 5 study area near Quesnel, B.C.

Stand type	Species	Percent of sample
Immature	*Bryoria capillaris*	50
	Bryoria fremontii	50
Young-mature	*Bryoria capillaris*	90
	Bryoria fremontii	10
Low volume over-mature	*Bryoria capillaris*	40
	Bryoria fremontii	60
High volume over-mature	*Bryoria capillaris*	80
	Bryoria fremontii	20

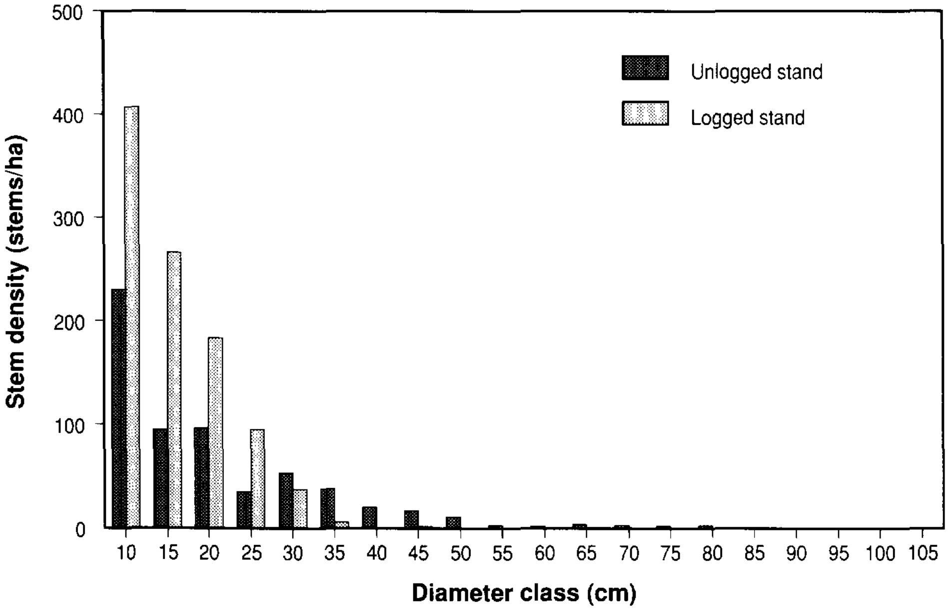
APPENDIX 3. Douglas-fir litterfall rates in four stands over three winters on the TFL 5 mule deer winter range near Quesnel, B.C.

Stand type	Mean Douglas-fir litterfall rates (kg/ha per month)								
	1986/1987			1987/1988			1988/1989		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Immature	30	1.28	2.57	24	3.18	2.97	19	5.04	4.13
Young-mature	30	1.44	2.76	24	8.14	9.31	24	31.25	21.14
Over-mature (low volume)	30	2.24	2.58	24	12.22	13.20	24	32.79	21.71
Over-mature (high volume)	–	–	–	24	18.61	17.52	24	33.47	18.23

APPENDIX 4. Volume, by diameter class, of the logged and unlogged stands on Fox Mountain, Williams Lake, B.C.



APPENDIX 5. Stem density, by diameter class, of the logged and unlogged stands on Fox Mountain, Williams Lake, B.C.



APPENDIX 6. Simple linear regression of litterfall and tree diameter in a logged and an unlogged stand on Fox Mountain, near Williams Lake, B.C.

Stand type	Litterfall type	n	r^2	Sy.x	P
Logged	Douglas-fir	20	.16	2.98	.08
	Lichen (total)[a]	20	.12	.16	.13
	Attached lichen	20	.10	.13	.17
	Unattached lichen	20	.18	.03	.06
Unlogged	Douglas-fir	51	.01	6.50	.54
	Lichen (total)[a]	51	.14	.97	.008
	Attached lichen	51	.08	.94	.05
	Unattached lichen	51	.28	.19	.0001

[a] Attached and unattached lichen.

APPENDIX 7. Simple linear regression of litterfall and tree age in a logged and an unlogged stand on Fox Mountain, near Williams Lake, B.C.

Stand type	Litterfall type	n	r^2	Sy.x	P
Logged	Douglas-fir	20	.31	2.69	.01
	Lichen (total)[a]	20	.09	.16	.19
	Attached lichen	20	.08	.13	.23
	Unattached lichen	20	.12	.04	.14
Unlogged	Douglas-fir	51	.02	6.44	.27
	Lichen (total)[a]	51	.17	.96	.003
	Attached lichen	51	.11	.93	.02
	Unattached lichen	51	.24	.20	.0003

[a] Attached and unattached lichen.

APPENDIX 8. Species composition and abundance of arboreal lichen in litterfall samples collected from plots beneath trees of various ages on the Fox Mountain study area near Williams Lake, B.C.

Tree number	Age	Dbh (cm)	Type of sample	Species	Percent of sample
16	185	77	Unattached	*Usnea cavernosa*	70
				Usnea fulvoreagens	20
				Usnea hirta	5
				Usnea spp.	5
35	218	76	Unattached	*Usnea cavernosa*	60
				Usnea fulvoreagans	25
				Usnea hirta	10
				Usnea spp.	5
41	202	68	Unattached	*Usnea cavernosa*	100
28	67	31	Attached	*Usnea cavernosa*	70
				Usnea spp.	20
				Bryoria fuscescens	10
5	233	89	Attached	*Usnea cavernosa*	15
				Usnea fulvoreagens	20
				Usnea hirta	15
				Usnea subfloridana	15
				Usnea spp.	10
				Bryoria fuscescens	15
				Bryoria lanestris	10
49	60	17	Attached	*Usnea cavernosa*	95
				Bryoria fuscescens	5

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