

University of Montana

## ScholarWorks at University of Montana

---

Graduate Student Theses, Dissertations, &  
Professional Papers

Graduate School

---

1999

### Occurrence of two genera of arboreal lichen and their utilization by deer and elk on selected winter ranges in west-central Montana

Richard L. Ward  
*The University of Montana*

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

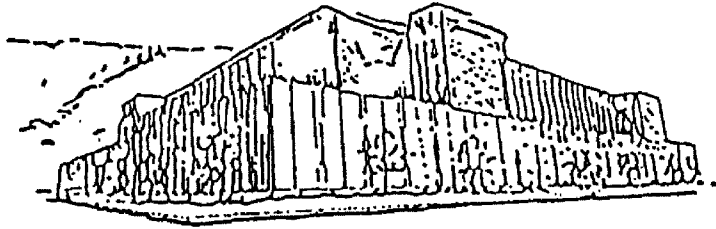
**Let us know how access to this document benefits you.**

---

#### Recommended Citation

Ward, Richard L., "Occurrence of two genera of arboreal lichen and their utilization by deer and elk on selected winter ranges in west-central Montana" (1999). *Graduate Student Theses, Dissertations, & Professional Papers*. 6467.  
<https://scholarworks.umt.edu/etd/6467>

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).



Maureen and Mike  
**MANSFIELD LIBRARY**

The University of **MONTANA**

---

Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

*\*\* Please check "Yes" or "No" and provide signature \*\**

Yes, I grant permission

No, I do not grant permission

Author's Signature Richard J. Vard

Date 5-28-99

Any copying for commercial purposes or financial gain may be undertaken only with the author's explicit consent.



**THE OCCURRENCE OF TWO GENERA OF ARBOREAL LICHEN AND  
THEIR UTILIZATION BY DEER AND ELK ON SELECTED WINTER  
RANGES IN WEST-CENTRAL MONTANA**

By

Richard L. Ward

B.S. Eastern Washington University, 1996

B.A. University of Washington, 1993

Presented in partial fulfillment of the requirements for the

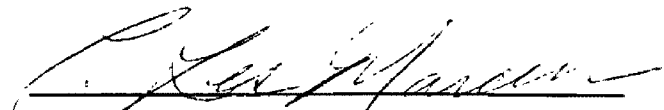
degree of

Master of Science

University of Montana

1999

Approved by:



Chairman, Board of Examiners



Dean, Graduate School

5-28-99

Date

UMI Number: EP37268

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI EP37268

Published by ProQuest LLC (2013). Copyright in the Dissertation held by the Author.

Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against unauthorized copying under Title 17, United States Code




ProQuest LLC.  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106 - 1346

## ABSTRACT

Ward, Richard L., M.S. May 1999

Wildlife Biology

The Occurrence of Two Genera of Arboreal Lichen and Their Utilization by Deer and Elk on Selected Winter Ranges in West-Central Montana.

Director: C. Les Marcum 

Few studies have been conducted to determine the use of lichens as a winter food source for deer and elk in the northern Rocky Mountains. I studied the availability and use of arboreal lichen litterfall by wintering deer and elk in western Montana. In May and June of 1997 and 1998, lichen litterfall was collected inside and outside ungulate exclosures to assess deer and elk use of lichens during winter. *Bryoria* spp. composed > 99% of the lichen litterfall. For the severe winter of 1996-97, lichen litterfall use by deer and elk averaged 8.24 kg/ha and 6.55 kg/ha for the relatively mild winter of 1997-98. The greater use of lichens in winter 1996-97 was probably due to an increased number of elk and mule deer utilizing forested habitats over mild to normal winters. A strong linear relationship between lichen availability and lichens consumed suggests that lichen use was driven by availability rather than tree stand characteristics.

Biomass of arboreal fruticose lichens was studied in second-growth forested stands in west-central Montana. Total standing crop of arboreal lichens was estimated from lichen litterfall. *Bryoria* spp. composed about 99% of arboreal pendulant lichen litterfall. Estimates of *Bryoria* standing crop were 7.0 – 1558.0 kg/ha. Basal area of larch showed a strong positive relationship with lichen biomass. It is unclear if larch provides a suitable substrate and microclimate for lichen growth, or if it is due to other environmental variables favorable to both, but not measured in this study. Additional significant variables were canopy cover, number of snags/ha, mean tree DBH, and SD of tree DBH. More variation in lichen biomass was explained when stands were grouped by structure type than when all stands were combined.

Provision of deer and elk winter range with potential for high rates of lichen litterfall would benefit these species in all winters. Preliminary results from this study suggest that retention of larch and large snags and increased overstory canopy cover in sites with 1 or 2 canopy layers and diversely sized trees in 3 and multi-layer sites would benefit wintering ungulates by providing lichen forage through litterfall.

## ACKNOWLEDGEMENTS

There are numerous people I would like to thank for making this project come to completion. First, I would like to thank my committee. Dr. Les Marcum provided immense support in every aspect of this study and always looked out for my best interests throughout my time at the University of Montana. I am deeply indebted. Dr. Paul Alaback generously provided assistance with study design and data analysis that became very frustrating at times. Paul taught me much and always managed to make me feel confident about my study. I would also like to thank Dr. I. Joe Ball for helpful critiques that made this report much better than I ever could have done alone.

I would like to thank the institutions that provided the funding and logistics: The McIntire – Stennis Federal Forestry Program; U.S. Forest Service Rocky Mountain Research Station; U.S. Forest Service, Lolo National Forest; Lubrecht Experimental Forest; Montana Department of Natural Resources and Conservation; and Montana Department of Fish, Wildlife and Parks.

I thank Dr. Clint E. Carlson and Leon Theroux at the U.S. Forest Service Rocky Mountain Research Station for helpful input on study design, financial support and providing generous lab space. Mike Hillis at the Lolo National Forest acquired funding and provided much needed vehicles, as well as generous input on study design. Hank Goetz and Frank Maus at Lubrecht Experimental Forest allowed me access to the forest and let me rummage through data records in search of that perfect study site. At Montana Department of Natural Resources and Conservation I would like to thank Ross Baty, who provided excellent help in determining study sites and who's past research provided invaluable throughout my study, and Steve Wallace, who allowed me to assemble ungulate exclosures on state forest lands. Mike Thompson at Montana Department of Fish, Wildlife and Parks provided immense input and support throughout this study and who's knowledge and suggestions always proved useful.

Assembling ungulate exclosures would not have been possible without the help of field assistants. I would like to thank Kurt Aluzas, George Ritchotte and Ron Uchytel for braving those bitter cold winter days and sometimes frustrating experiences to help me with my study. Thanks also to Joe Boyer for making the best post-pounder known to man. I would also like to thank Jamey Jonkel for helping to educate me in the ways of fence building, providing input on study site locations and helping with logistics. Jamie was always more than willing to lend a hand.

A special thanks to my wife Kim, who put her own career on hold so I could pursue mine. Sometimes a field assistant, sometimes a practice audience, but always a loving and caring wife who's patience and understanding provided immense emotional support. Thank you, Kim for your time and companionship throughout the trials and tribulations of graduate school.

## TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGMENTS .....	iii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES .....	vii
LIST OF APPENDICES.....	viii
CHAPTER I: Use of Lichen Litterfall by Wintering Deer and Elk.....	1
INTRODUCTION .....	1
STUDY AREA .....	3
METHODS .....	7
Field Methods .....	7
Analytical Methods.....	10
RESULTS .....	12
Utilization of Lichen Litterfall by Deer and Elk.....	12
Relation Between Lichen Availability and Utilization.....	14
Relation Between Utilization and Stand Characteristics .....	18
DISCUSSION .....	23
Use of Lichen Litterfall by Deer and Elk.....	23
Nutrition and Foraging Ecology .....	29
Relation Between Utilization and Stand Characteristics .....	33
CHAPTER II: Influence of Forest Structure on the Occurrence and Biomass of Arboreal Lichens.....	37
INTRODUCTION .....	37
STUDY AREA .....	38
METHODS .....	41
Site Selection .....	41
Field Methods .....	43
Analytical Methods.....	46



RESULTS .....	49
Relation Between Canopy Layers and Lichen Biomass .....	49
Relation Between Stand Characteristics and Lichen Biomass .....	52
DISCUSSION .....	61
Ecology of Alectorioid Lichens .....	61
Comparison with Other Studies .....	65
Lichen Biomass Values .....	66
Stand Structure and Microclimate .....	67
Lichen Correlation with Western Larch .....	69
Between Year Variations .....	70
Availability to Deer and Elk .....	71
SYNTHESIS .....	72
Further Studies .....	73
Management Recommendations .....	75
LITERATURE CITED .....	76
APPENDICES .....	81

## LIST OF TABLES

### Chapter I.

Table 1. <i>Bryoria</i> quantities available, consumed, and percent of available <i>Bryoria</i> consumed for winters 1996-97 and 1997-98.....	16
Table 2. Regression equations and associated statistics for biomass of <i>Bryoria</i> consumed for winters 1996-97 and 1997-98.....	20
Table 3. Comparison of arboreal lichen litterfall rates and consumption values among deer studies.....	24
Table 4. Comparative digestibility, protein content, and energy content of arboreal fruticose lichens among deer and caribou studies.....	30

### Chapter II.

Table 5. Distribution of study sites based on USFS Fire Groups, tree stand layers, and percent canopy cover.....	44
Table 6. <i>Bryoria</i> biomass and relevant stand characteristics for 45 sample sites.....	50
Table 7. Regression equations and associated statistics for biomass of <i>Bryoria</i> and <i>Usnea</i> standing crop in forest stands differentiated by number of canopy layers.....	54

## LIST OF FIGURES

### Chapter I.

Figure 1. Study area location in western Montana.....	4
Figure 2. Average daily temperatures and snow depths at Seeley Lake, Montana for 5 winter months during 1996-1998.....	6
Figure 3. <i>Bryoria</i> litterfall quantities inside and outside exclosures, and <i>Bryoria</i> litterfall quantities consumed and percent of available <i>Bryoria</i> consumed for winter 1996-97 .....	13
Figure 4. <i>Bryoria</i> litterfall quantities inside and outside exclosures, and <i>Bryoria</i> litterfall quantities consumed and percent of available <i>Bryoria</i> consumed for winter 1997-98 .....	15
Figure 5. <i>Bryoria</i> litterfall quantities consumed and percent of available <i>Bryoria</i> consumed for two-year plots for winters 1996-97 and 1997-98.....	17
Figure 6. Relationship between <i>Bryoria</i> quantity available, <i>Bryoria</i> quantity consumed, and percent of available <i>Bryoria</i> consumed for winters 1996-97 and 1997-98.....	19
Figure 7. <i>Bryoria</i> quantity consumed and <i>Bryoria</i> quantity available versus independent variables for winter 1996-97 and 1997-98.....	22

### Chapter II.

Figure 8. Study area location in western Montana.....	40
Figure 9. Standing crop of <i>Bryoria</i> biomass and <i>Usnea</i> biomass estimated from litterfall in forested stands differentiated by overstory tree layers.....	53
Figure 10. Biomass of <i>Bryoria</i> standing crop versus 3 independent variables for study sites with 1 and 2 tree canopy layers .....	57
Figure 11. Biomass of <i>Bryoria</i> standing crop versus 3 independent variables for study sites with 3 and multiple tree canopy layers .....	58
Figure 12. Biomass of <i>Bryoria</i> standing crop versus 3 independent variables for all study sites combined .....	59
Figure 13. Biomass of <i>Usnea</i> standing crop versus 2 independent variables for study sites with 3 and multiple tree canopy layers .....	60

## LIST OF APPENDICES

Appendix A. Diagram representing paired utilization transects and control transects.....	81
Appendix B. Lichen litterfall collection methods.....	82
Appendix C. Lichen biomass values and P-values for <i>Bryoria</i> and <i>Usnea</i> collected inside and outside ungulate exclosures.....	83
Appendix D. Diagram representing a productivity stand with 20 random productivity plots.....	86
Appendix E. Independent variables measured, recorded, or calculated for each productivity site.....	87
Appendix F. Coefficient correlations for multiple linear regression equations for productivity sites grouped by stand structure class.....	88

# CHAPTER I: USE OF LICHEN LITTERFALL BY WINTERING DEER AND ELK

## INTRODUCTION

Winter foods utilized by Rocky Mountain elk (*Cervus elaphus nelsoni*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*) have generally been thought to be composed primarily of woody browse, understory vegetation and available grasses and sedges (Hoskins and Dalke 1955, Morris and Schwartz 1957, Kufeld 1973). However, numerous studies have mentioned lichen use by deer and elk in the northern Rocky Mountains (DeNio 1938, Hildebrand 1967, Hash 1973, Marcum 1975, Janke 1977, Baty 1995), but none have attempted to quantify the extent to which deer and elk forage on lichens. Hildebrand (1967) noted that lichens appeared in high frequency in rumen samples taken from white-tailed deer during winter months in the Swan Valley in northwest Montana. Hash (1973) determined that arboreal lichens were more important than forbs throughout the winter and spring for elk in Idaho. Baty (1995) observed lichen use by both deer and elk on winter range in west-central Montana, but used fecal pellet techniques to determine food habits; quantifying lichen use through fecal analysis is not currently possible because arboreal lichens are up to 85% digestible (B. Davitt, pers. comm.). To date, no studies have been conducted to quantify the use of arboreal lichens by deer and elk in the northern Rocky Mountains.

The limited research that has been done on quantifying arboreal lichen use by deer and elk has been conducted primarily on black-tailed deer (*O. hemionus columbianus*) of northern Vancouver Island (Stevenson 1978, Rochelle 1980). Rochelle (1980) determined that arboreal lichens constituted 86% of winter litterfall used as forage

by black-tailed deer and lichens may be a more important source of deer forage than understory vegetation during periods of deep snow. Lichen frequencies as high as 100 percent were observed in rumen samples of deer collected in mature conifer stands during such periods (Rochelle 1980). Ditchkoff and Servello (1998) concluded that arboreal lichens were not a significant source of forage when suspended in the trees, but became available as litterfall. Esseen (1984) found that lichen litterfall was greatest during the period from late autumn to the beginning of summer.

Studies focusing on the nutritional aspects of lichens indicate that epiphytic lichens enhance energy balance during winter, when poorly digestible browse species make up the bulk of winter diets (Rochelle 1980, Jenks and Leslie 1988, Jenks and Leslie 1989, Gray and Servello 1995). When lichens were not available and deer and elk consumed browse of low digestibility, digestible energy was a limiting factor for populations. In areas where lichens were available, digestibility increased through an additive effect of increased dietary lichen (Rochelle 1980). In addition, a diet high in lichens is thought to increase the total amount of body water, which may act as a thermal buffer against changes in temperature (Hodgman and Bowyer 1985).

I studied the use of lichens by wintering deer and elk because winter is generally considered the most stressful period for deer and elk in northern latitudes. Prolonged consumption of poor-quality diets is often the primary factor that increases winter mortality and reduces fawn and calf production (DeNio 1938, Osborn and Jenks 1998). Consequently, lichen production and availability may be a limiting factor for ungulate populations during winter, particularly on otherwise marginal forested ranges. The objectives of my study were to determine the use of lichens by wintering deer and elk in

West-central Montana, and determine the influence of tree stand characteristics on lichen use by these ungulates.

## STUDY AREA

The study was located in west-central Montana, primarily on and near the Blackfoot-Clearwater Wildlife Management Area (BCWMA) approximately 70 km northeast of Missoula, MT (Fig. 1). The core winter range covered about 9,000 ha. Elevations ranged from 1,200 to 1,700 m and topography was predominantly gentle. Sixty-three percent of the area was forested. The forest overstory was dominated by second growth Douglas-fir (*Pseudotsuga menziesii*) stands >12 m tall with sparse canopies and well developed understories of shrubs and patchy Douglas-fir saplings. These stands remained after extensive logging over the past 60 years. Mature ponderosa pine (*Pinus ponderosa*) stands were common along the western boundary of the study area and along forest–bunchgrass ecotones. Mixed stands of western larch (*Larix occidentalis*), sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea englemannii*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*) were typical of cool or moist sites (Baty 1995).

Characteristic weather patterns originate from the Pacific Ocean, and air masses move from west to east. Mean monthly temperatures normally range from  $-7.0^{\circ}$  C in January to  $16.8^{\circ}$  C in July. Annual precipitation ranges from 30–75 cm with a mean of about 45 cm. Summers are hot and dry, with over 66% of the annual precipitation falling

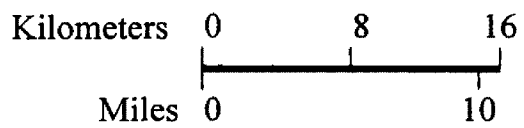
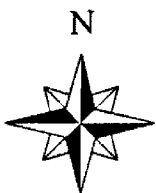
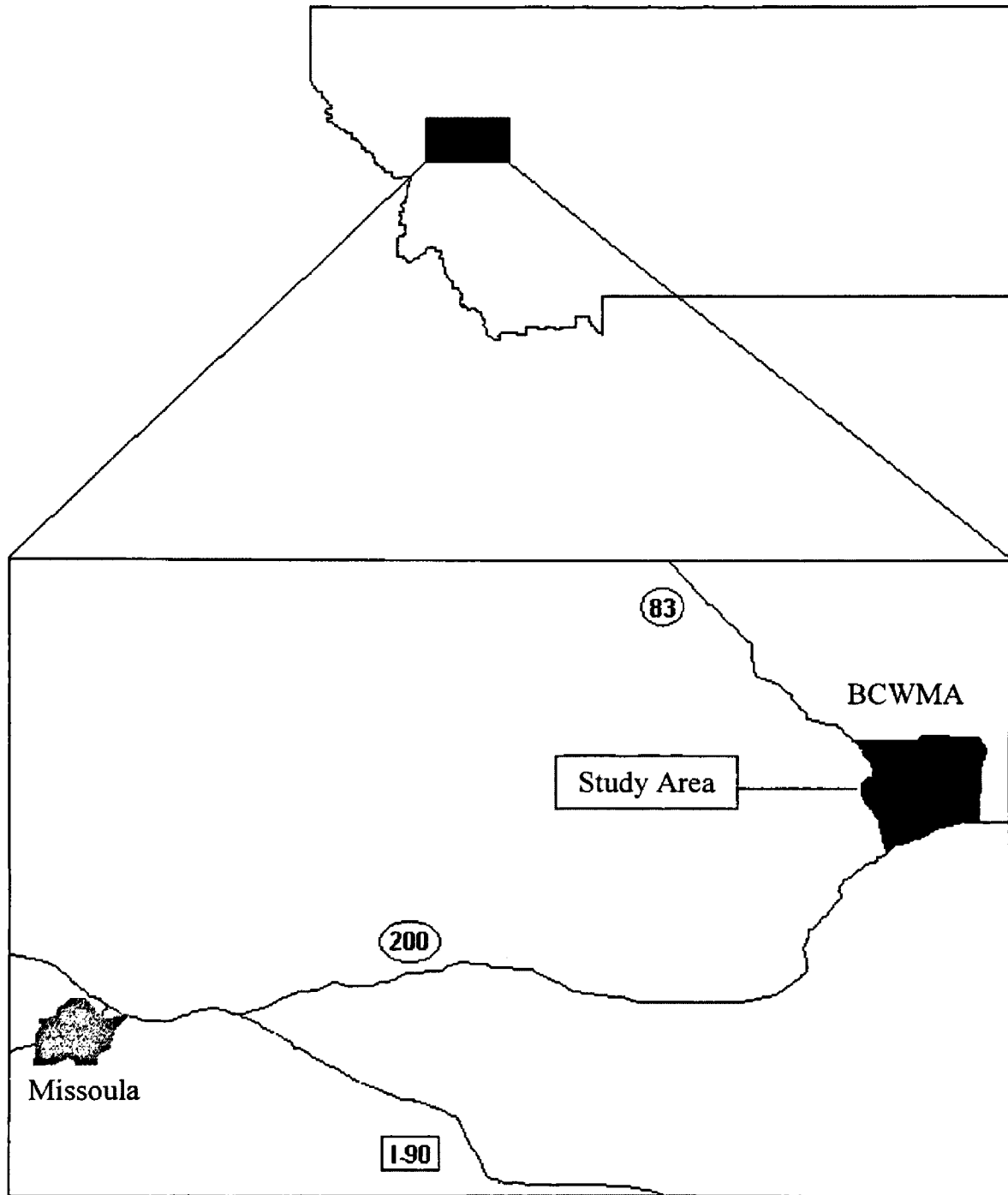


Fig.1. Study area location in western Montana (BCWMA: Blackfoot – Clearwater Wildlife Management Area).



from December through June. Snow depth is generally greatest in February with a mean of 58.4 cm.

The winter of 1996-97 was characterized by above-average snow accumulation and below-average temperatures. Mean January temperature was  $-8.7^{\circ}$  C. and mean February snow depth was 109.0 cm. Conversely, the winter of 1997-98 was characterized by below-average snow accumulations and above-average temperatures. Mean January temperature was  $-4.5^{\circ}$  C. and mean February snow depth was 46.0 cm. (Fig. 2).

Estimates of the number of wintering elk during the study ranged from 758 - 862, all within an area of about 90 km<sup>2</sup>. This is the primary winter range for a herd whose summer range encompasses about 1,300 km<sup>2</sup>. Herd estimates for white-tailed deer were 155 - 455 and mule deer estimates were 326 - 524 (Montana Dept. of Fish, Wildlife & Parks, unpublished data).

Additional study sites with similar elevation and topography were located on the Lolo National Forest adjacent to the BCWMA. Vegetation types on these sites were characterized by an overstory composed of widely spaced, very large (>65 cm dbh) larch. These stands developed following a severe forest fire in the 1930's. Fire suppression and a complete lack of logging since that time has resulted in a well developed canopy cover with a mature Douglas-fir second story and immature third story. Present wintering ungulate numbers in these areas are unknown, but winter track observations and direct animal observations indicate that these areas were heavily used by white-tailed deer and used little or not at all by mule deer and elk.

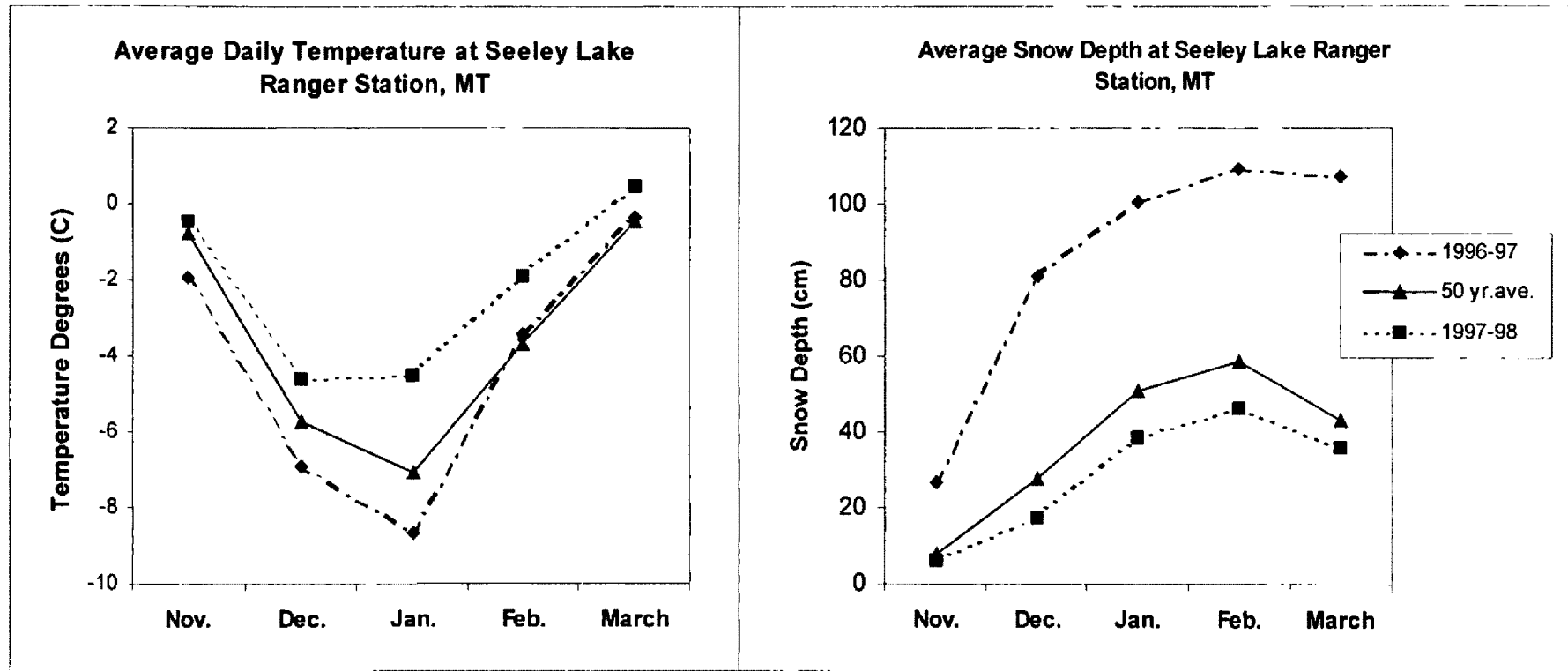


Fig. 2. Average daily temperatures and snow depths at Seeley Lake, Montana for 5 winter months during 1996 - 1998. (Local climatological data, National Weather Service, Missoula, Montana)

## **METHODS**

### **Field Methods**

A series of ungulate exclosures was established as control sites within areas known to be used by deer and elk during the winter (Baty 1995). They ranged in size from approximately 200 m<sup>2</sup> to 400 m<sup>2</sup>, and were built with 1.2 m high field fence. Existing trees and 3 m steel fence posts were used and upper and lower layers of fence were nailed or wired to the trees and posts for a total fence height of approximately 2.4 m.

Control transects within exclosures were used to approximate the quantity of lichens potentially available to deer and elk. Five 2 m x 8 m control transects were laid out systematically within each exclosure. This was done by first establishing a 2.4 m wide buffer strip along the inside of the fence that served to minimize interference from the fence on lichen litterfall. An 8 m baseline was established running parallel to the longest side of the exclosure, but within the buffer strip. From this baseline, 2 m increments were marked off with survey stakes. Transects were delineated using twine and wood survey stakes. A total of 80 m<sup>2</sup> was sampled in each control site (2 m x 8 m x 5 transects). In exclosures containing more than 5 potential transects, I selected 5 transects at random.

Utilization transects were used to approximate the quantity of lichens consumed by deer and elk. Utilization transects were established adjacent to control transects and in a similar manner, with the exception of the buffer strip. Because of the clumped distribution of trees on the study area, some modification of the utilization transect

selection was required. If utilization sites were not available immediately adjacent to control sites or were too small in size, the nearest stand of the same composition to that of the control site was used. Composition was based on tree species, tree density, tree diameter at 1.4 m height (DBH), slope and aspect.

Use of arboreal lichens by deer and elk was determined by comparing lichen quantities in control transects with utilization transects. Lichen quantities were divided into group A and group B, where group A was lichen litterfall, either on the ground or hanging in the understory up to 2 m high, but not attached to or growing on any substrate (McCune 1994). This also included lichens attached to fallen branches up to 10 cm diameter at the base. Group B included all other lichens up to 2 m high, either attached to large fallen branches or growing on trees or snags. Lichens found up to 2 m high were considered to be within reach of ungulates during the winter. Total arboreal lichens considered available to ungulates was the sum of lichens A and B.

The most abundant arboreal lichen species found in the study area were *Bryoria* spp. (primarily *B. fremontii*) and *Nodobryoria* spp. (primarily *N. abbreviata*). These two genera are ecologically and morphologically similar (McCune and Goward 1995). Personal observation and informal feeding trials suggest that deer and elk do not differentiate between the two genera. For these reasons and in an effort to conserve time, these two genera were not separated for analysis and are referred to collectively as *Bryoria*. Other fruticose lichens common to the study area include *Usnea* spp., a lichen considered to be palatable for ungulates (Stevenson 1978, Ditchkoff and Servello 1998), and *Letharia* spp. (primarily *L. vulpina*), a lichen which contains vulpinic acid (Vitt et al. 1988). *Letharia* was not considered to be a forage item because of its toxicity and a lack

of evidence to indicate any use as forage. Only arboreal fruticose lichens were considered for examination because they constitute the vast majority of arboreal lichen biomass in forests of western Montana. In addition, there is no evidence to indicate that deer or elk forage on any other lichens in the northern Rocky Mountains (R. Baty, C.L. Marcum, M. Thompson, pers. comm.).

Nine ungulate exclosures were built on the BCWMA in January 1997. Ten additional exclosures were built in November and December 1997, 6 on the BCWMA and 4 on adjacent U.S. Forest Service Land. In total, 9 exclosures were available to determine ungulate use of lichens for winter 1996-97 and 19 exclosures were available for winter 1997-98. Two-year plots refer to plots sampled for both winter 1996-97 and 1997-98 (sites established in Jan. 1997).

In May and June 1997 and 1998 available lichens were collected from both control and utilization transects, bagged, labeled and air dried for storage. Later, the lichens were cleaned of all foreign matter and sorted by genera. Samples were oven dried at 60°C for 24 hours and weighed to the nearest 0.01 gram.

Detailed stand variables recorded for each control and utilization stand were habitat type, stand age, height of lichen browse line, tree diameter, and selected tree heights. These measurements were taken on a 400 m<sup>2</sup> fixed area circular plot centered in the middle of the transects. Each stand was assigned a habitat type based on the presence of tree and undergrowth species (Pfister et al. 1977). Stand age was determined by increment boring the two largest trees from each distinct canopy layer (Pfister 1995). The distance from the ground to the lichen browse line was measured on a tree deemed representative of the plot. All trees > 1.4 m in height were measured for diameter at 1.4

m height (DBH) and a visual estimate of pendulant lichen biomass was assigned to each tree. In addition, tree species were recorded so that species composition and densities could be determined. Tree heights were measured for two trees per canopy layer by taking the percent slope for the top and bottom of the tree from a known distance and calculated using trigonometric hypsometry (Hays et al. 1981). All trees  $\leq 1.4$  m were tallied by species. DBH and species for snags  $\geq 13.0$  cm DBH were recorded as well. Topographic measurements taken for each productivity site were elevation, slope, and aspect.

Overstory canopy cover was measured at the center of each transect at 1 m, 3 m, 5 m, and 7 m from the start of the transect using a moosehorn coverscope (Garrison 1949). This method has been found to be more accurate than spherical densimeters (Bunnell and Vales 1990). In addition, lichen presence or absence was recorded for each of the 25 points on the coverscope.

### **Analytical Methods**

Mass values of available lichens were normalized using a natural log transformation to allow the use of parametric statistical tests. Differences in lichen quantities inside and outside exclosures were assessed using a T-test for 2 independent samples and lichen quantities between stands were compared using a one-way analysis of variance. Lichen consumption and availability values between years were compared using the Mann-Whitney U test for differences between independent samples for individual sites and the Kruskal-Wallis non-parametric test for differences between means for all sites combined. Consumption and availability data that resulted in negative

values for quantity consumed and percent consumed were converted to 0.00 (i.e. paired transects that had more lichens in the utilization transect than in the control transect).

I used multiple linear regression analysis to determine which stand level variables were most useful in distinguishing lichen availability and use between stands. In this study regression was used to measure association between lichen use, stand structure, and environmental variables, not to forecast lichen use values for a given set of independent variables. Assumptions of multiple linear regression include selection of the appropriate model, independence, homoscedasticity, normality of dependent variables and no outliers (Ryan 1997). Each dependent variable model was assessed for violations of these assumptions according to Norusis (1995). Percent canopy cover was transformed to arcsin of percent canopy cover to obtain a more normal distribution of residuals. Assumptions for other variables and models were met. All data were analyzed using SPSS 8.0 (1998). Nomenclature of lichens follows McCune and Goward (1995).

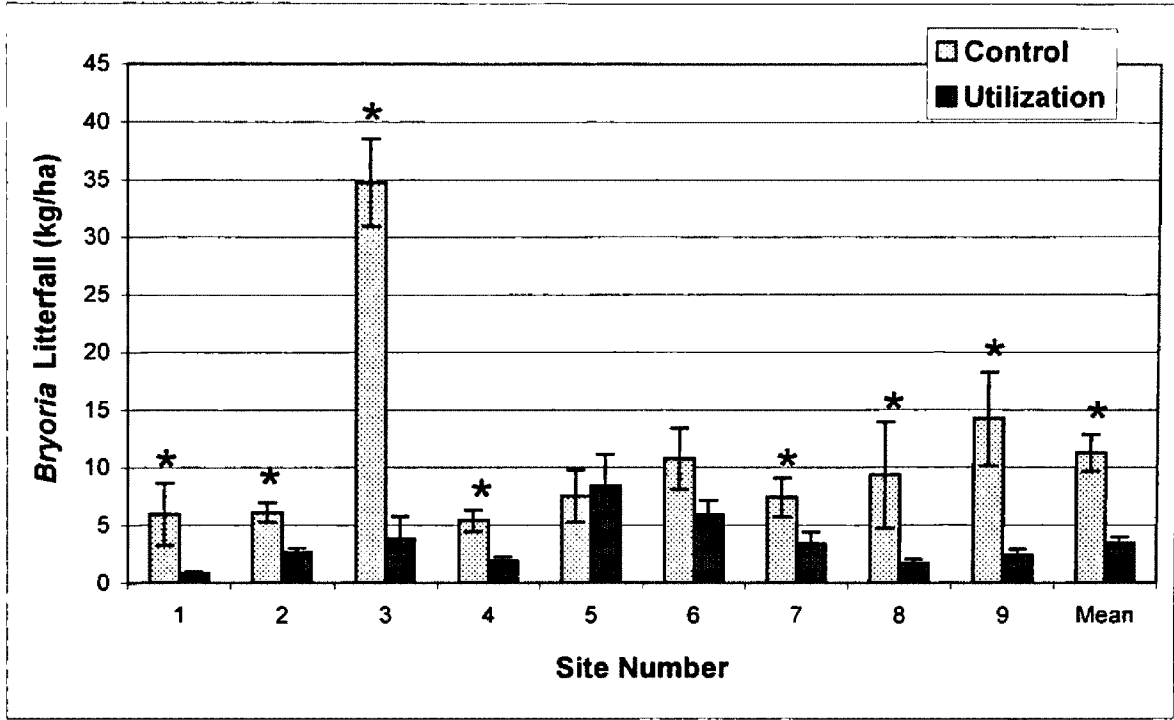
## RESULTS

### Utilization of Lichen Litterfall by Deer and Elk

For both winter 1996-97 and winter 1997-98, differences in available lichen biomass between control and utilization sites were due primarily to differences in *Bryoria* litterfall (type A). *Bryoria* type B (attached to a substrate) and *Usnea* type A and B had little impact on total lichens available to ungulates. Both availability and consumption of *Usnea* was apparently minimal. Due to the slow growth rates of epiphytic lichens (Rochelle 1980), availability of type B lichens in two-year plots (sites 1-10) for the winter 1997-98 was 0.0 kg/ha for all sites. This was a result of their removal for measurement during the previous season. A natural log transformation of *Bryoria* type A resulted in a normal distribution, allowing the use of parametric statistical tests. For these reasons, all results pertaining to lichen availability and consumption are reported as *Bryoria* type A only. Tests run on combined values for both *Bryoria* types A and B and all lichens combined did not result in the addition or removal of any sites from those with significant differences in lichen utilization and, in most cases, did not change the p-value.

For winter 1996-97, lichen quantities were significantly greater inside than outside enclosures for all sites combined, as well as 7 of the 9 individual sites ( $P \leq 0.05$ ). The difference between quantities of available lichens inside and outside each enclosure provides an approximation of the utilization of lichens at each site. Utilization values ranged from 2.6 kg/ha to 30.9 kg/ha of lichens consumed. Utilization ranged from 19 to 88% of available lichens consumed (Fig. 3).





\* Significant at P < 0.05

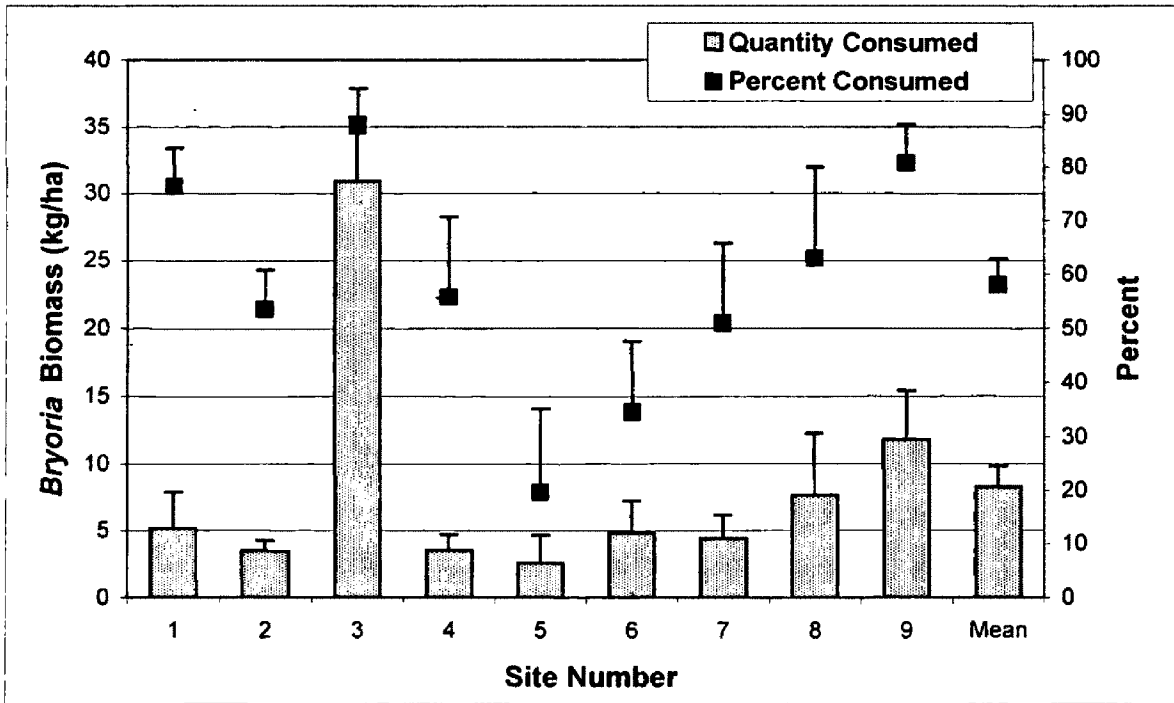


Fig. 3. Mean ( $\pm$  1 SE) *Bryoria* litterfall quantities inside and outside exclosures (top) and mean ( $\pm$  1 SE) *Bryoria* litterfall quantities consumed and percent of available *Bryoria* consumed (bottom) for winter 1996-97.

In 1997-98, lichen quantities were again significantly greater inside than outside exclosures for all sites combined ( $P \leq 0.05$ ). Nine of the 19 sites had significantly more lichens inside the exclosure than outside ( $P \leq 0.05$ ). Utilization values ranged from 0.4 kg/ha to 25.2 kg/ha of lichens consumed. Utilization ranged from 10 to 88% of available lichens consumed (Fig. 4).

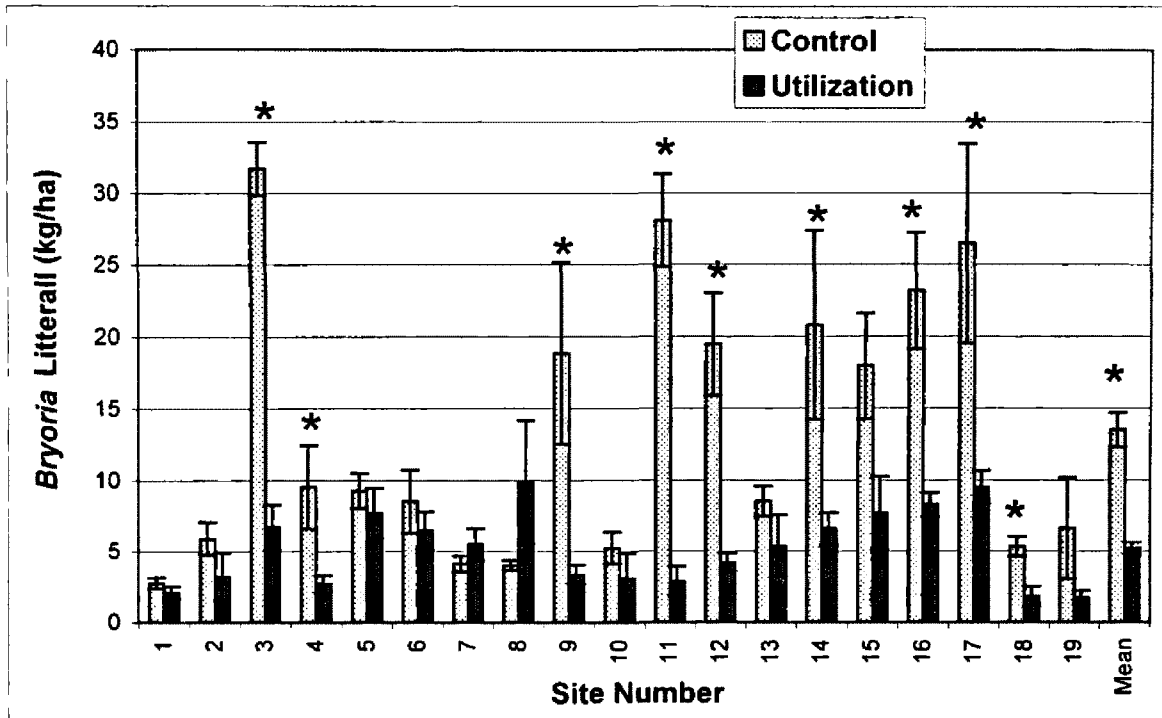
Lichen availability for plots sampled for both winters (two-year plots) was not significantly different between winter 1996-97 and winter 1997-98 for all sites combined, nor significant for any individual sites ( $P \leq 0.05$ ). The average quantity available for winter 1996-97 was 11.3 kg/ha and 10.5 kg/ha for two-year plots for winter 1997-98 (Table 1).

Quantities for lichens consumed on two-year plots was not significantly different between winter 1996-97 and winter 1997-98 for all sites combined, nor significant for any individual sites ( $P \leq 0.05$ ) (Fig. 5). The average quantity consumed for winter 1996-97 was 8.2 kg/ha and 6.6 kg/ha for two-year plots for winter 1997-98 (Table 1).

Percent of available lichens consumed on two-year plots was significantly greater during winter 1996-97 than winter 1997-98 for all sites combined, as well as 1 individual site ( $P \leq 0.05$ ) (Fig. 5). The average percent of available lichens consumed for winter 1996-97 was 58% and 41% for two-year plots during winter 1997-98 (Table 1).

### **Relation Between Lichen Availability and Utilization**

Lichen quantity consumed and lichen quantity available showed strong positive relationships for both years. Ninety seven percent of the variation in lichen quantity consumed in winter 1996-97 was explained by lichen quantity available. Similarly, 95%



\* Significant at  $P < 0.05$

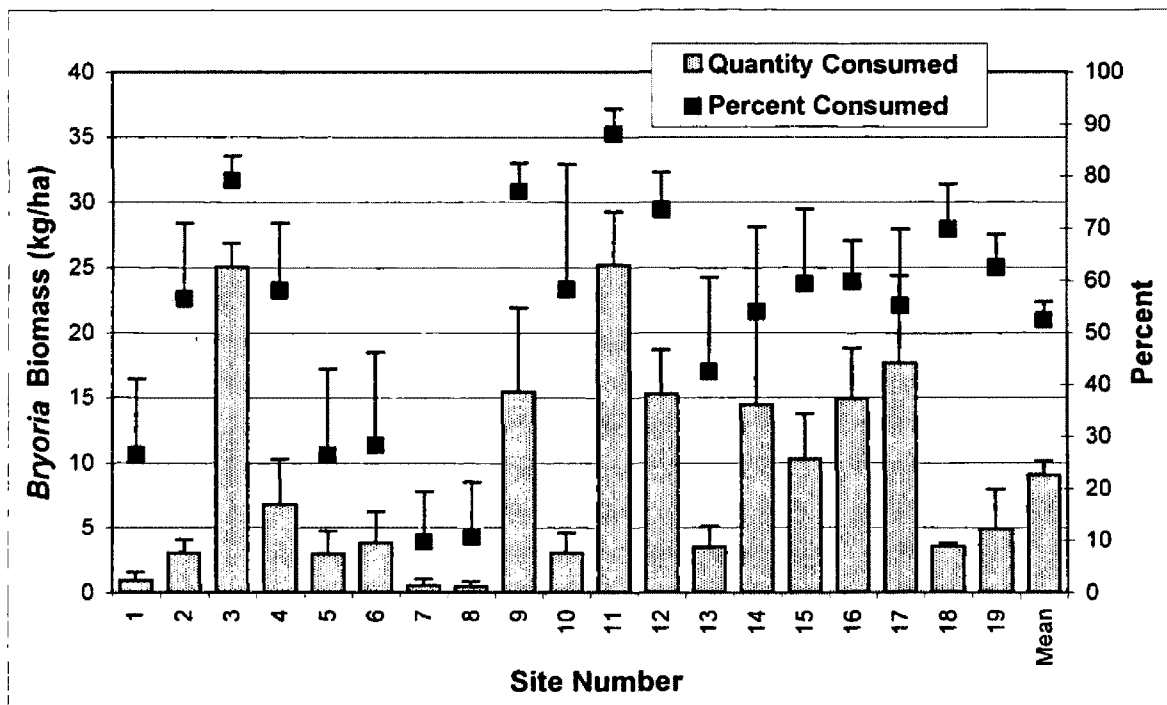
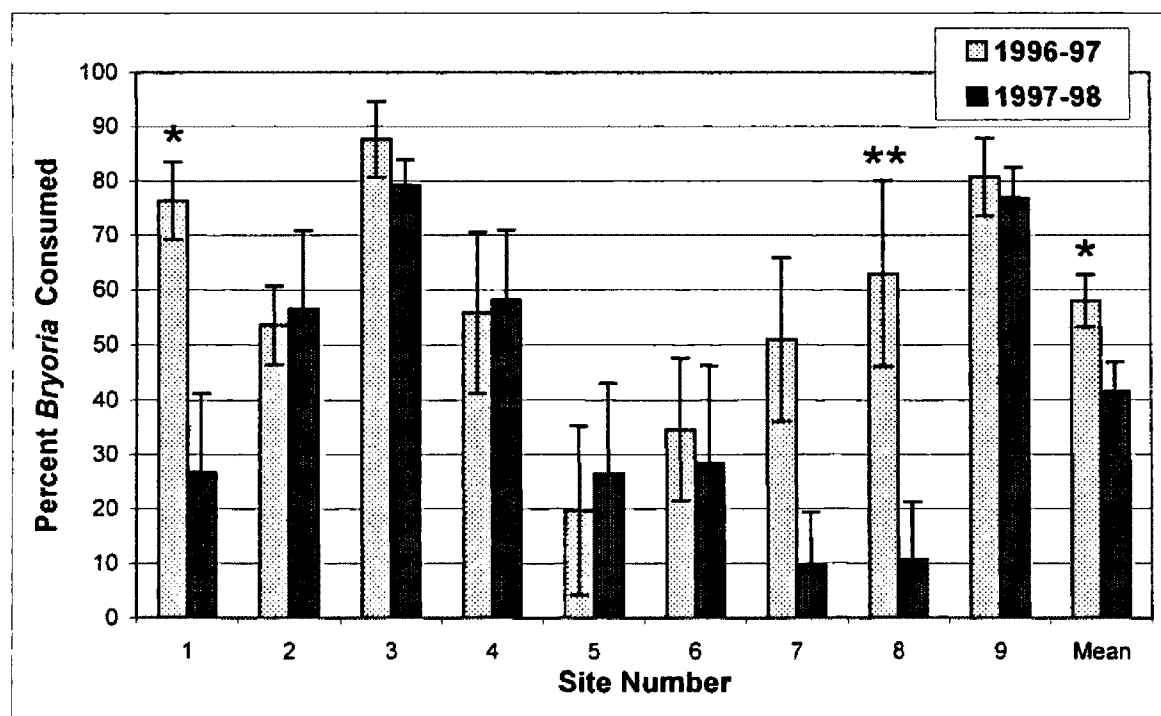
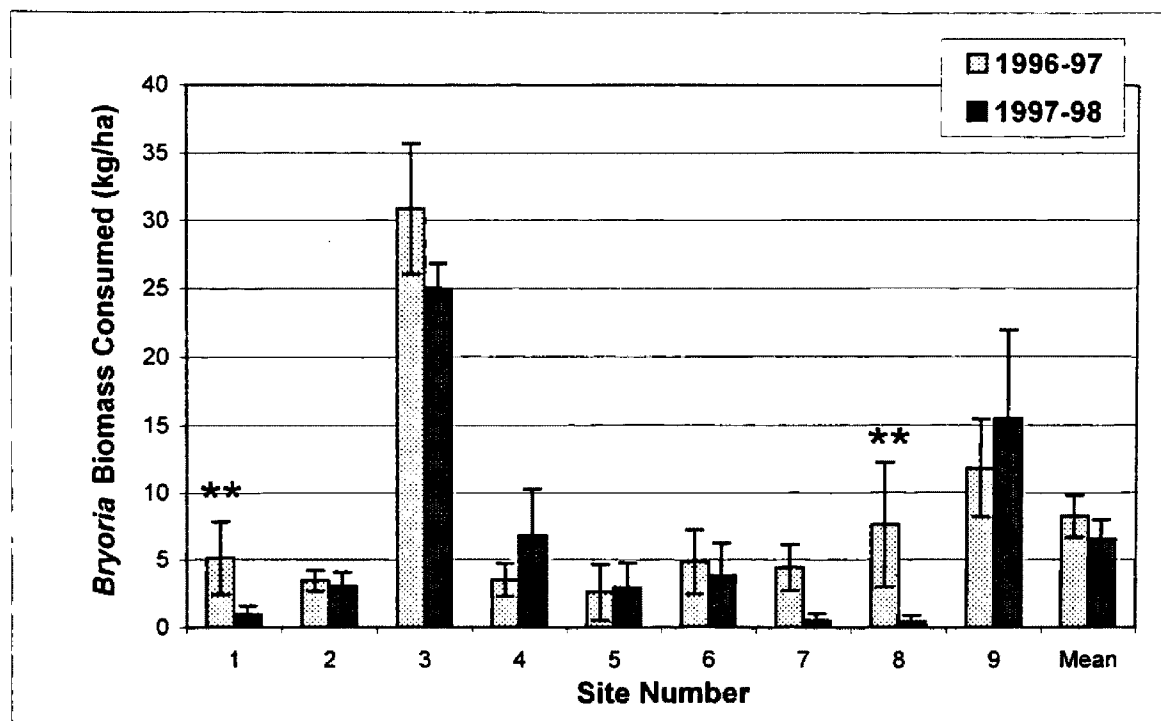


Fig. 4. Mean ( $\pm 1$  SE) *Bryoria* litterfall quantities inside and outside exclosures (top) and mean ( $\pm 1$  SE) *Bryoria* litterfall quantities consumed and percent of available *Bryoria* consumed (bottom) for winter 1997-98.

Table 1. *Bryoria* quantities available, consumed and percent of available *Bryoria* consumed by deer and elk.

Position	Site Number									Average	
	1	2	3	4	5	6	7	8	9		
1996-97											
Mean Quantity Available (kg/ha)	5.97	6.11	34.74	5.39	7.53	10.76	7.43	9.29	14.19	11.26	
Mean Quantity Consumed (kg/ha)	5.13	3.45	30.89	3.50	2.58	4.82	4.41	7.60	11.78	8.24	
Mean % Consumed	76.37%	53.60%	87.59%	55.83%	19.67%	34.54%	50.86%	63.02%	80.74%	58.02%	
										N=45	
1997-98											
Mean Quantity Available (kg/ha)	2.75	5.90	31.72	9.51	9.24	8.50	4.09	4.00	18.82	10.50	
Mean Quantity Consumed (kg/ha)	0.93	3.04	25.03	6.79	2.94	3.82	0.51	0.43	15.46	6.55	
Mean % Consumed	26.61%	56.61%	79.17%	58.20%	26.45%	28.39%	9.69%	10.64%	76.88%	41.41%	
										N = 45	
P-value Between Years											
Quantity Available	0.31	1.00	0.55	0.15	0.69	0.55	0.15	0.42	0.69	0.59	
Quantity Consumed	0.06	0.84	0.42	0.69	1.00	0.42	0.10	0.06	1.00	0.09	
Mean % Consumed	0.03	0.22	0.22	1.00	1.00	0.55	0.10	0.06	0.84	0.02	
										N = 45	
	Site Number									1 - 19	
	10	11	12	13	14	15	16	17	18		19
1997-98											
Mean Quantity Available (kg/ha)	5.19	28.08	19.45	8.49	20.79	17.93	23.16	26.50	5.33	6.61	13.48
Mean Quantity Consumed (kg/ha)	3.06	25.20	15.26	3.48	14.50	10.24	14.93	17.72	3.52	4.89	9.04
Mean % Consumed	58.36%	88.04%	73.47%	42.45%	54.04%	59.41%	59.87%	55.27%	69.79%	62.49%	52.41%
										N = 95	



\*Significant at  $P < 0.05$

\*\* Significant at  $P < 0.06$

Fig. 5. Mean ( $\pm 1$  SE) *Bryoria* litterfall quantities consumed (top) and mean ( $\pm 1$  SE) percent of available *Bryoria* consumed (bottom) for two-year plots for winters 1996-97 and 1997-98.

of the variation in lichen quantity consumed in winter 1997-98 was explained by lichen quantity available (Fig. 6). These data indicate that deer and elk consumed lichens in direct proportion to their availability. As availability increased, consumption increased. In this study, the data did not plateau. Deer and elk did not show a saturation point at which they consumed a smaller proportion of lichens once availability reached a certain concentration.

A regression of percent of available lichens consumed against lichen quantity available revealed that for winter 1997-98, percent of available lichens consumed increased linearly with quantity available ( $R^2 = 0.42$ ,  $p = 0.003$ ), but the relationship was not as strong as that between quantity consumed and quantity available. These results demonstrate that deer and elk utilized a greater proportion of lichens at sites with greater quantities available. The same regression using data from 1996-97 does not reveal a distinct pattern, probably due to the smaller sample size ( $R^2 = 0.29$ ,  $p = 0.135$ ) (Fig. 6). Most data points for two-year plots clustered at the left side of both graphs. The additional ten sites for 1997-98 increased the linear relationship.

### **Relation Between Utilization and Stand Characteristics**

Two variables, percent slope and basal area/ha of all live trees 13.0 – 22.9 cm dbh, explained 73.90% of the variation in mean lichen quantity consumed in winter 1996-97. These two independent variables also explained 64.6% of the variation in lichen quantity available for winter 1996-97 (Table 2). However, the  $R^2$  values for the individual regressions were quite low (Fig. 7), suggesting that other variables influenced lichen availability and consumption during that winter.

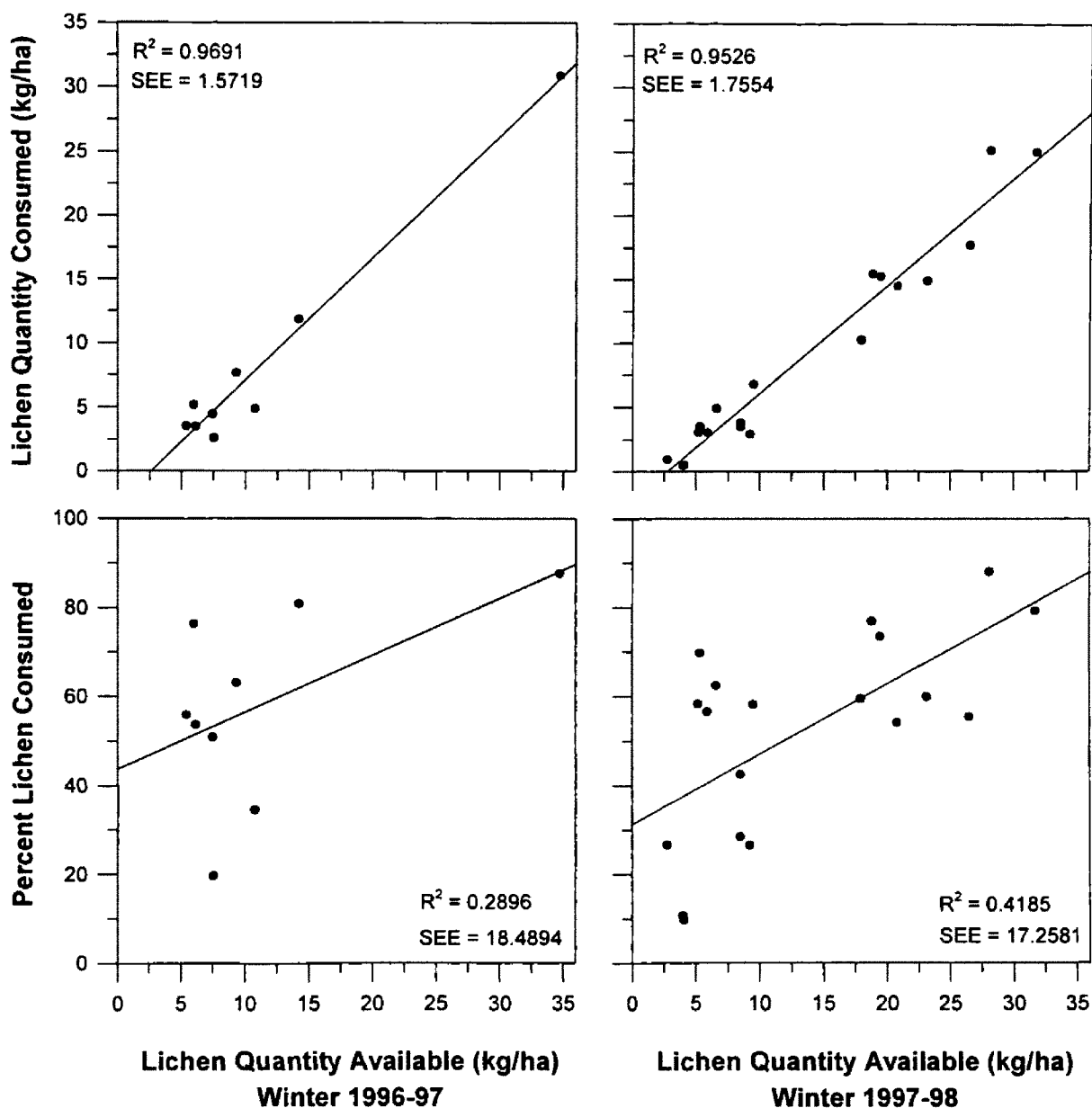


Fig. 6. Relationship between *Bryoria* quantity available, *Bryoria* quantity consumed, and percent of available *Bryoria* consumed for winters 1996-97 and 1997-98 (SEE: Standard Error of the Estimate).

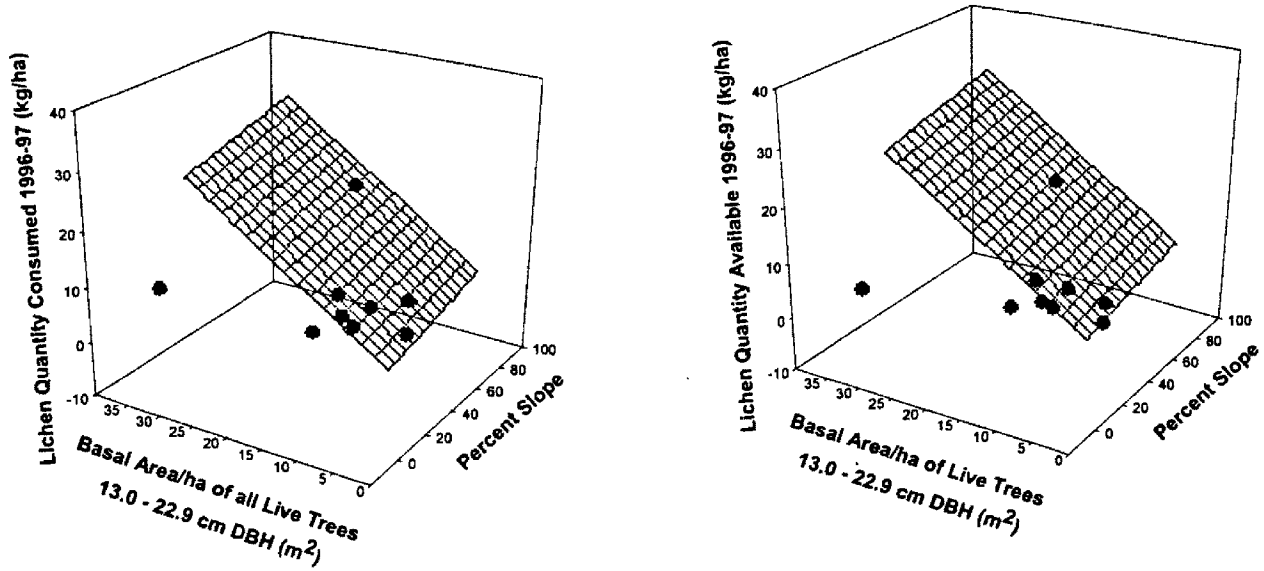
Table 2. Regression equations and associated statistics for biomass of *Bryoria* consumed and biomass of *Bryoria* available for winters 1996-97 and 1997-98 (SEE: Standard Error of the Estimate).

Winter 1996-97	R <sup>2</sup>	SEE	P-value		Fig. No.	
			Multiple Reg.			
			Eq.1	Eq.2		
1) <i>Bryoria</i> Consumed (kg/ha) = 27.36 - 0.73(x <sub>1</sub> ) - 0.60(x <sub>2</sub> )	0.739	5.278	---	---	7	
2) <i>Bryoria</i> Consumed (kg/ha) = 27.00 - 0.73(x <sub>1</sub> ) - 8.30*10 <sup>-3</sup> (x <sub>3</sub> )	0.731	5.356	---	---	---	
x <sub>1</sub> = Percent slope	0.388	7.479	0.009	0.009	0.073	7
x <sub>2</sub> = Basal area/ha of live trees 13.0 - 22.9 cm DBH	0.102	9.059	0.030	---	0.403	7
x <sub>3</sub> = Number of snags/ha	0.030	9.415	---	0.033	0.658	---
1) <i>Bryoria</i> Available (kg/ha) = 29.66 - 0.71(x <sub>1</sub> ) - 0.56(x <sub>2</sub> )	0.646	6.338	---	---	---	7
2) <i>Bryoria</i> Available (kg/ha) = 22.41 - 0.58(x <sub>1</sub> ) - 2.86*10 <sup>-2</sup> (x <sub>3</sub> )	0.382	8.378	---	---	---	---
x <sub>1</sub> = Percent slope	0.356	7.916	0.021	0.105	0.090	7
x <sub>2</sub> = Basal area/ha of live trees 13.0 - 22.9 cm DBH	0.077	9.478	0.068	---	0.468	7
x <sub>3</sub> = Number of snags/ha	0.008	9.826	---	0.635	0.815	---
<hr/>						
Winter 1997-98	R <sup>2</sup>	SEE	P-value		Fig. No.	
			Multiple Reg.	Indiv. Reg.		
<i>Bryoria</i> Consumed (kg/ha) = 0.93 + 2.65(x <sub>1</sub> ) - 0.400(x <sub>2</sub> )	0.407	6.588	---	---	7	
x <sub>1</sub> = Age of dominant tree layer	0.191	7.465	0.022	0.061	7	
x <sub>2</sub> = Basal area/ha of all live trees ≥ 1.4 m tall	0.167	7.573	0.028	0.082	7	
<i>Bryoria</i> Available (kg/ha) = 1.169 + 3.40(x <sub>1</sub> ) - 0.466(x <sub>2</sub> )	0.457	7.281	---	---	7	
x <sub>1</sub> = Age of dominant tree layer	0.242	8.349	0.009	0.032	7	
x <sub>2</sub> = Basal area/ha of all live trees ≥ 1.4 m tall	0.162	8.780	0.023	0.088	7	



For winter 1997-98, age of the dominant tree layer and basal area/ha of all trees  $\geq$  1.4 m tall explained 40.7% of the variation in lichen quantity consumed. These two independent variables also explained 45.7% of the variation in lichen quantity available for winter 1997-98 (Table 2). The relatively low  $R^2$  values for the multiple regression and the individual regressions (Fig. 7) again suggest that other variables influenced lichen availability and consumption during that winter.

**Winter 1996-97**



**Winter 1997-98**

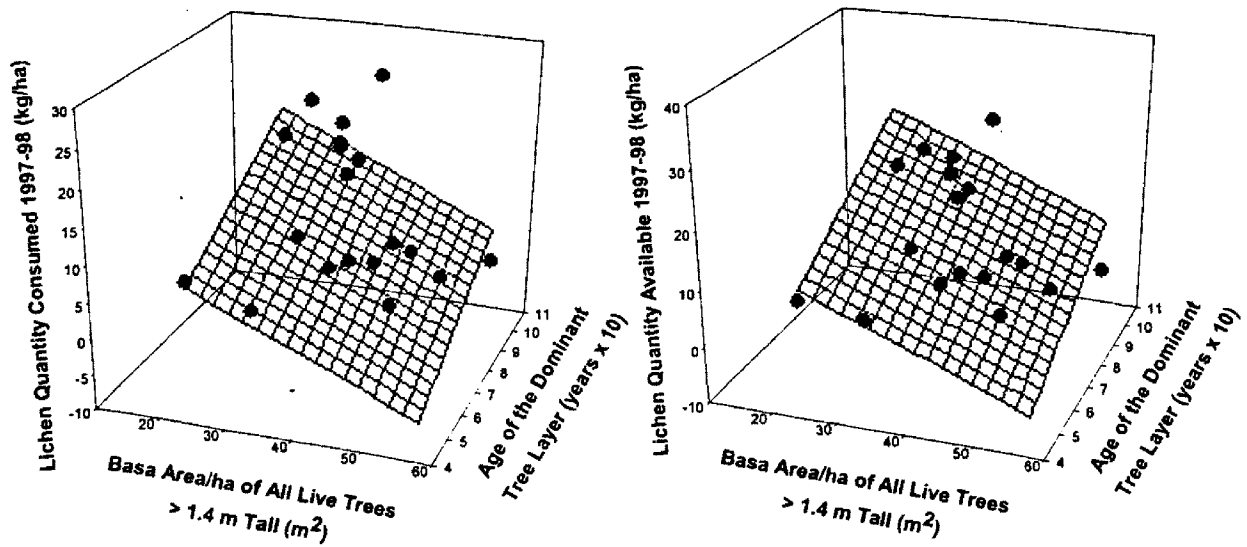


Fig. 7. *Bryoria* quantity consumed and *Bryoria* quantity available versus independent variables for winter 1996-97 and 1997-98.

## DISCUSSION

### Use of Lichen Litterfall by Deer and Elk

Results from this study indicate that lichen litterfall provides a substantial source of forage for deer and elk on winter ranges in west-central Montana. Values for lichen litterfall available as forage were as high as 34.7 kg/ha. These results are in general agreement with Stevenson (1978), Rochelle (1980), Hodgman and Bowyer (1985), and Ditchkoff and Servello (1998) (Table 3). Ditchkoff and Servello (1998) estimated that 4.1 kg/ha of *Usnea* spp. and *Evernia* spp. were available as forage in mature forest stands for white-tailed deer in central Maine in winter. These lichens were not a significant source of forage when suspended in the trees, but became available as litterfall. Although lichens constituted only 6.1% of the total biomass available as litterfall forage in that study, they made up 30.6% of the total energy available to deer. This study revealed that *Bryoria* litterfall rates in west-central Montana were somewhat higher, with an overall average of 12.2 kg/ha across both years. Ditchkoff and Servello (1998) concluded that the inclusion of even relatively small amounts of high quality forages such as lichens may allow deer to raise overall diet quality during winter and maintain adequate food intake on browse diets.

Hodgman and Bowyer (1985) reported that 56.1 – 63.1% of available lichens were consumed at feeding stations by white-tailed deer in late winter and early spring in Maine. When values were averaged for each year in this study, consumption values were similar (52.4 – 58.0%).

Table 3. Comparison of arboreal lichen litterfall rates and consumption values among deer studies.

Source	Area	Forest Type	Ungulate Species	Lichen species	Lichen Litterfall Available (kg/ha)	Time period of sampling	Quantity Utilized (kg/ha)	Percent Utilized
Ditchkoff and Servello (1998)	Central Maine	Mixed conifer and hardwood	White-tailed deer	<i>Usnea</i> spp. <i>Evernia</i> spp.	4.13	1 Jan. - 31 March	-----	-----
Hodgman and Bowyer (1985)	Maine	Mixed conifer and hardwood	White-tailed deer	<i>Usnea laricina</i> <i>Evernia mesomorpha</i>	-----	24 March - 13 May	-----	56.1 - 63.1%
Rochelle (1980)	Northern Vancouver Island	Coastal conifer	Columbian black-tailed deer	<i>Alectoria</i> spp. <i>Bryoria</i> spp.	13.2 - 115.3	Winter (180 days)	-----	80.1 - 81.6%
Stevenson (1978)	Northern Vancouver Island	Coastal conifer	Columbian black-tailed deer	<i>Alectoria</i> spp. <i>Bryoria</i> spp.	31.9 - 151.2	Nov. - May	16.7 - 80.0	36.7 - 52.9%
This Study	West-central Montana	Continental conifer	White-tailed deer, mule deer, elk	<i>Bryoria</i> spp. <i>Usnea</i> spp.	2.75 - 34.74	Jan. - May Dec. - May	0.43 - 30.89	9.69 - 88.04%

Rochelle (1980) found that a significant portion of the winter diet of Columbian black-tailed deer on Vancouver Island was composed of *Alectoria* spp. In that study, *Alectoria* was found in 100% of 12 rumens collected and constituted 35.5% of rumen volume. In addition, *Alectoria* made up 86.0% of the available forage litterfall, and lichen litterfall quantities inside ungulate exclosures were approximately 5 times greater than outside. Stevenson (1978), also examining Columbian black-tailed deer on Vancouver Island, determined that *Alectoria* quantities were significantly greater inside than outside exclosures for all sites and attributed the difference to removal by herbivores. *Alectoria* litterfall values were 31.9 – 151.2 kg/ha, utilization values were 16.7 – 80.0 kg/ha and percent utilized was 36.7 – 52.9 of available lichen litterfall. In my study, *Bryoria* availability values (2.8 – 34.7 kg/ha) and utilization values (0.4 – 30.9 kg/ha) were somewhat lower than Stevenson (1978), probably due to the greater biomass of standing crop of arboreal lichens on Vancouver Island. Values for percent of lichens utilized in my study (9.7 – 88.0%) were of comparable magnitude to those found by Stevenson (1978), although Montana values were more variable. This may be attributable to more variability in lichen use by deer and elk in Montana. It should also be noted that the sample size in my study (19 exclosures) was much larger than Stevenson's (3 exclosures), which may also explain the greater variation. When utilization values for my study were pooled by year, consumption was 52.4 - 58.0%, which was very similar to Stevenson (1978).

Several additional studies refer to lichens in the diet of deer. Cowan (1945) observed 100% frequency of *Usnea barbata* in 15 rumen samples of Columbian black-tailed deer on southern Vancouver Island and estimated that lichens constituted 36% of

the winter diet. DeNio (1938) estimated that lichens and mosses constituted 7.3% of the winter diet of mule deer and white-tailed deer and averaged 1.3% of rumen volume for samples taken on winter ranges on 17 National Forests, mainly in western Montana and northern Idaho. Hildebrand (1967) noted that lichens appeared in high frequency in white-tailed deer rumen samples taken during winter months in the Swan Valley in northwest Montana. This, in combination with the hair-like nature of lichens, led Hildebrand (1967) to conclude that lichens form a greater proportion of the diet than is often indicated by rumen samples. Baty (1995) observed lichen use by both deer and elk on winter range in west-central Montana, but used fecal pellet techniques to determine food habits. Quantifying lichen use through fecal analysis is not currently possible because arboreal lichens are up to 85% digestible (B. Davitt, pers. comm.).

Little published evidence is available to indicate that lichens form a major component of the winter diet of elk, although several studies mention lichens as contributing to the diet. DeNio (1938) found that lichens and mosses constituted 3.61% of the winter diet of elk and averaged 5.25% of rumen volume. Hash (1973) determined that arboreal lichens were more important than forbs throughout the winter and spring for elk in northern Idaho. He found that arboreal lichens accounted for 2.4% of elk winter diets and occurred in 20 of 57 elk rumens collected. Cliff (1939) reported the use of *Alectoria fremontii* by elk during winter in the Blue Mountains of Oregon. Kufeld (1973) summarized Cliff's findings, rating this species as low in value compared to other elk forage. Marcum (1975) found that *Alectoria americana* constituted 3.0% of rumen volume and occurred in 33.0% of 36 rumens collected from hunter-killed elk in west-central Montana during October and November.

Results of use of lichens by different ungulate species in the current study were difficult to assess. Due to the sampling procedure used, it was not possible to separate animal use of lichen litterfall according to mule deer, white-tailed deer and elk. However, speculation about species use is possible through information from previous studies (Baty 1995) and current knowledge about spatial and habitat partitioning among ungulates on winter ranges in west-central Montana. White-tailed deer utilized lichens whenever they become available, regardless of winter temperatures and snow conditions, although use probably increased when snow conditions restricted movement and deer remained in heavily timbered areas. Three of 4 exclosures (sites 14 – 17) assembled in an area known to be used almost exclusively by white-tailed deer had significant differences in lichen litterfall between control and utilization sites for winter 1997-98 and all of these sites had greater than 50% of lichen litterfall utilized.

Baty (1995) estimated that spatial overlap between elk and white-tailed deer increased 25% and overlap between elk and mule deer increased 14% on the BCWMA when winter resources were limited due to a removal of substantial amounts of bunchgrass forage by a 1991 wildfire. The severe winter of 1996-97 resulted in a similar effect. Bunchgrass forage in meadows was largely unavailable because of deep and crusted snow, so elk dispersed into forested habitats. The Montana Department of Fish, Wildlife and Parks (unpublished data 1997) found greatest spatial overlap between elk and mule deer (96.3%) because some mule deer were displaced from open shrubfields buried with crusted snow, and were concentrated with elk and other mule deer in forested types. This increase in elk and mule deer numbers in forested types may explain why lichen utilization was greater during the severe winter of 1996-97 than the more moderate

winter of 1997-98. Because of the high amount of spatial overlap, it was not possible to estimate quantities of lichen litterfall consumed by each species. However, Baty (1995) observed all three ungulate species foraging on arboreal lichen litterfall on the BCWMA.

The results indicate that lichen litterfall provided a consistent source of ungulate forage between winters, even when weather conditions differed dramatically. Two-year plots at control sites for the severe winter of 1996-97 averaged 11.26 kg/ha of *Bryoria* litterfall, and 10.50 kg/ha for the relatively mild winter of 1997-98, a difference of < 1.0 kg/ha between a severe and mild winter. Little evidence exists relating lichen litterfall rates to weather patterns between years. Rochelle (1980) determined that availability of lichen litterfall was greatest in February and March and was dependent on intermittent winter storms, but he found no relationship between snow depth and deposition rates of forage litterfall. Similarly, Stevenson (1978) recorded maximum litterfall rates in late winter, but found no relationship between litterfall rates and weather patterns or snow depth. Cowan (1945) noted that arboreal lichens were made available to black-tailed deer by strong winds and snow damage to mature trees. Winter storms probably also influence lichen litterfall deposition rates in the northern Rockies. Similar to Rochelle (1980) and Stevenson (1978), snow depth did not appear to influence lichen litterfall rates as evidenced by the similarity in litterfall rates between severe and mild winters.

Timing and quantity of lichen litterfall may be increasingly important as winter progresses. Body condition of deer and elk generally deteriorates and reaches a low point just before spring vegetation growth begins (DeNio 1938). If litterfall rates are highest in late winter, as Rochelle (1980) and Stevenson (1978) observed, then maximum availability of lichen litterfall probably coincides with the period of maximum stress for



animals. In addition, lichen litterfall that may have been previously buried by snow would become available to ungulates as snow melt commences. Arboreal lichen use by white-tailed deer in Maine was greatest from late March to April (Hodgman and Bowyer 1985). In addition, Ditchkoff and Servello (1998) observed that litterfall covered by snow periodically resurfaced during winter thaw periods, making them available as forage in midwinter.

Windthrown trees may also be an important source of lichens during winter and early spring. Rominger and Oldemeyer (1990) determined that a primary source of arboreal lichens for early winter woodland caribou in the Selkirk Mountains was provided by recently fallen trees. Similarly, Detrick (1985) and Edwards et al. (1960) postulated that trees that fall with regularity in mature forests may be an important source of arboreal lichens for woodland caribou. In the current study, a windthrown Douglas-fir tree was found in late May on the BCWMA. Observation of surrounding trees showed considerable *Bryoria* biomass in the standing trees, but only trace amounts on the downed tree. Pellets and trampled vegetation around the downed tree indicated that deer and elk had fed heavily on arboreal lichens, but did not feed heavily on the green needles.

### **Nutrition and Foraging Ecology**

Digestible energy and protein appear to be most limiting to large herbivores in winter (Berteaux et al. 1998). The literature provides a wide variety of nutrition studies in relation to energy and protein content of lichens used as forage by deer and caribou (Table 4). Rochelle (1980) conducted extensive in vitro digestibility trials with Columbian black-tailed deer inoculum. He found that *Alectoria sarmentosa* was the most

Table 4. Comparative digestibility, protein content and energy content of arboreal fruticose lichens in studies with deer and caribou.

Source	Area	Ungulate Species	Lichen Species	Technique	Percent Digestibility	Percent Protein	Energy Content (kcal/g)
Ditchkoff and Servello (1998)	Central Maine	White-tailed deer	<i>Usnea</i> spp. <i>Evernia</i> spp.	-----	-----	-----	2.86
Hodgman and Bowyer (1985)	Maine	White-tailed deer	<i>Usnea laricina</i> <i>Evernia</i> <i>mesomorpha</i>	In Vitro	-----	<i>U. laricina</i> - 7.3 <i>E. mesomorpha</i> - 5.1	<i>U. laricina</i> - 4.012 <i>E. mesomorpha</i> - 3.966
Jenks and Leslie (1988)	Maine	White-tailed deer	<i>Usnea</i> spp.	In Vitro In Vivo Estimate	In Vitro - 43.9 In Vivo - 67.3	-----	-----
Robbins (1987)	Southern Vancouver Island	Mule Deer	<i>Alectoria sarmentosa</i>	In Vivo	85.0	2.0	-----
Rochelle (1980)	Northern Vancouver Island	Columbian black-tailed deer	<i>Alectoria</i> spp. <i>Bryoria</i> spp.	In Vitro	72.5 ± 4.5	2.0	1.32
Rominger et al. (1996)	Northeast Washington	Woodland Caribou	<i>Alectoria sarmentosa</i> <i>Bryoria</i> spp.	In Vivo	82.0	<i>A. sarmentosa</i> - 2.0 <i>Bryoria</i> - 4.4	-----

digestible forage item ( $72.5 \pm 4.5\%$ ) and dry matter digestibility (DMD) varied little by season. Other forage species examined generally had the lowest DMD in winter.

Rochelle (1980) attributed the high digestibility of lichens to the different types of structural carbohydrates (e.g. hemicellulose rather than cellulose) and less lignin than other forage species. *A. sarmentosa* contained less than 2% protein, well below the 6-8% required for ungulate maintenance (Van Soest 1982). Caloric value for *A. sarmentosa* (1.1 kcal/0.8g) was among the lowest of any forage species examined by Rochelle (1980).

The rate at which forage species are digested, as well as the extent to which it is digested determines its value to ruminants (Rochelle 1980). Rochelle (1980) found that *A. sarmentosa* may be of less value to deer than other forage species because it would leave the rumen prior to being fully digested. However, he also estimated that *A. sarmentosa* increased digestibility of mixed diets 5-15% above levels expected from combined digestibilities of component species. This suggests that lichens were acting as a carbohydrate source, which would enable deer to use recycled urea more efficiently (Jenks and Leslie 1988) and improve the degree to which the entire diet is utilized (Rochelle 1980).

Rominger et al (1996) determined that woodland caribou showed a preference for *Bryoria* spp. over *A. sarmentosa* and speculated that it was because *Bryoria* had a crude protein content of 4.4% compared with 2.0% in *A. sarmentosa*. He also conducted in vivo digestibility trials and found arboreal lichens to be 82% digestible (ADMD). This is in agreement with Robbins (1987) who conducted in vivo digestibility trials with mule deer and found *A. sarmentosa* to be 85% digestible and 2% crude protein, but found no

synergistic affects when lichen was added to the diet. Deer fed on a diet of 100% *A. sarmentosa* became anorectic.

Arboreal lichens of the genera *Alectoria* and *Bryoria* contain usnic and vulpinic acids, which have antibacterial properties and may retard digestive processes in the rumen. Non-lichen forage supplements may be essential to dilute lichen toxins, or higher-protein forage may be necessary to stimulate microbial activity and increase passage rates (Robbins 1987, Rominger and Oldemeyer 1990).

Several studies have been conducted on lichen use by white-tailed deer in Maine. Jenks and Leslie (1988) estimated that *Usnea* spp. was 43.9% digestible for in vitro methods and 67.3% DMD for modified in vivo methods. Hodgman and Bowyer (1985) found that *Usnea laricina* and *Evernia mesomorpha* averaged 7.3 and 5.1% crude protein content respectively, and 4.01 and 3.97 kcal/g energetic content respectively. They concluded that the combination of moderate crude protein and energy values coupled with high digestibility make *Usnea* and *Evernia* suitable winter forage. Ditchkoff and Servello (1998) estimated *Usnea* spp. and *Evernia* spp. at 2.86 kcal/g energetic content.

The relatively high energy content and high digestibility of arboreal lichens may explain why it was selected in high proportion relative to its availability in this study. Recent results from domesticated species suggest that herbivores have the ability to select their food according to both energy and protein content, and tend to maximize the ingestion of these nutrients according to their needs (Berteaux et al. 1998). Small ruminants such as deer meet their relatively high metabolic requirements by having a small rumen volume, short rumen retention time, high fermentation rate, and tend to choose more soluble, more digestible diets than larger ungulates (Hanley 1982, Hobbs et

al. 1983). Elk diets generally contain larger amounts of fiber and smaller amounts of soluble carbohydrates relative to deer. In addition, elk have been shown to be less selective for forage in winter than deer (Hobbs et al. 1983).

Energy available to ungulates is lowest in winter (Moen 1976) when the energy costs of activity are greatest (Parker et al. 1996). Individuals meet their energy requirements from catabolism of body reserves and ingestion of woody browse which is low in energy content (Berteaux et al. 1998). Ingestion of some lichen species may increase fermentative efficiency and overall digestibility of the diet (Jenks and Leslie 1988). In experimental winter feeding trials, Berteaux et al. (1998) observed that white-tailed deer in Quebec consumed more foods high in digestible energy and at each level of digestible energy, they consumed less of the foods high in crude protein. Thus, winter use of arboreal lichens by deer and elk probably relates to the nutritive value of these epiphytes (Hodgman and Bowyer 1985).

### **Relation Between Utilization and Stand Characteristics**

This study demonstrates that deer and elk increased the quantity and proportion of lichens consumed as increased amounts of lichen became available. It is not clear if deer and elk foraged in these areas because of the increased amount of lichen litterfall, or if other variables determined habitat selection, or a combination of both. However, the strong linear relation between lichen availability and lichens consumed suggests that deer and elk were showing some selectivity for stands favoring high rates of lichen litterfall. Rochelle (1978) and Stevenson (1980) both determined that Columbian black-tailed deer selected winter range sites favorable to high amounts of lichen litterfall. Similarly,

Rominger et al. (1996) found that woodland caribou selected forest stands where *Bryoria* was the dominant arboreal lichen and biomass was high.

In this study, percent slope and basal area of the codominant tree layer (13.0 – 22.9 cm DBH) explained most of the variation in lichen quantity consumed and lichen quantity available for winter 1996-97. The greatest quantities of lichen litterfall were available on slopes < 20% and basal area of the codominant tree layer was < 10m<sup>2</sup>/ha. Deer and elk consumed the greatest quantities and proportions of available lichens on these sites. The inverse relationships of both independent variables to lichen quantity available and lichen quantity consumed demonstrates that as slope and basal area of the codominant tree layer increased, lichen quantity available decreased and deer and elk consumed lower quantities and proportions of those lichens. Deer and elk may have favored slopes < 20% because of decreased snow depths compared to slopes > 20%. In addition, these ungulates may have foraged in areas with relatively low tree density as a means of predator avoidance. Rominger (1996) found an inverse relationship between tree density and foraging movement of woodland caribou. As tree density increased, caribou spent less time foraging at each tree and moved more quickly between trees. He attributed this to behavior independent of foraging and speculated that reduced visibility in stands with higher tree densities induced more frequent movement as a predator avoidance mechanism.

For winter 1997-98, less than 50% of the variation in lichen quantity consumed and lichen quantity available were explained by tree stand variables. This demonstrates that variables other than those measured in this study impacted availability of lichens, as well as habitat selection and foraging behavior of deer and elk during that winter.

However, more than 40% of the variation in lichen quantity consumed and lichen quantity available was explained by age of the dominant tree layer and basal area/ha of all live trees > 1.4m tall. The largest quantities of lichens were available on sites where age of the dominant tree layer was  $\geq 100$  years and basal area of all live trees was < 40 m<sup>2</sup>/ha. Deer and elk consumed the greatest quantities of lichens on these sites. These sites may have been selected because large trees provide snow intercept and decreased snow depth on the ground, thereby decreasing energetic costs to deer and elk. Selection of sites with low tree density may again be attributed to predator avoidance.

The fact that the same independent variables explain approximately the same amount of variation in lichen quantity available and lichen quantity consumed for each winter further suggests that deer and elk selected foraging sites favorable to high rates of lichen litterfall. These independent variables probably do not go far in explaining the controlling factors in lichen litterfall distribution. Rather, they serve to further demonstrate the relation between availability and consumption and provide variables that may explain foraging site selection by deer and elk. Stand structure variables and microclimate variables and their relations with lichen biomass are explored extensively in Chapter II.

It is apparent from this study that arboreal lichen litterfall forms a substantial part of the winter diet of deer and elk in the northern Rocky Mountains. Deer and elk consumed high quantities of lichens and consumed them in high proportion relative to availability in areas where lichen litterfall rates were high. Deer and elk also showed some preference for stands with high rates of lichen litterfall. During the severe winter of 1996-97, deer and elk utilized stands with increased rates of lichen litterfall. The

relationship was similar for the relatively mild winter of 1997-98, but less variation in lichen availability and consumption for that year was explained by the variables recorded in this study.



## CHAPTER II: INFLUENCE OF FOREST STRUCTURE ON THE OCCURRENCE AND BIOMASS OF ARBOREAL LICHENS

### INTRODUCTION

Structure and dynamics of western forests are crucial in determining the presence and abundance of arboreal lichens (Pike et al. 1977, Eversman 1982, Lesica et al. 1991, McCune 1993, Pipp 1998). Recent management prescriptions of coniferous forests often include procedures to alter stand densities and reestablish park-like stands in the foothills of the intermountain West. In addition, logging has altered the presettlement stand age mosaic by systematically converting old growth to second growth. As a result, some species have become more common, while others have decreased. Although many species can occur in stands of all ages, others are more restricted (Lesica et al. 1991). This may be particularly true for epiphytic lichens, which are highly sensitive to changes in forest structure and microclimate (Eversman 1982, McCune and Antos 1982, Lesica et al. 1991, McCune 1993, Renhorn et al 1997, Pipp 1998).

Lichens play a wide range of ecological functions in coniferous forests. Arboreal pendulant lichens provide a major winter forage source for deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) in northern latitudes (Stevenson 1978, Rochelle 1980, Jenks and Leslie 1989, Gray and Servello 1995). Lichens also provide food for flying squirrels (*Glaucomys sabrinus*), caribou (*Rangifer tarandus*), and invertebrates (Rundel 1978, Maser et al. 1985, Hayward and Rosentreter 1994, Rominger et al. 1996). Lichens also play an integral role in nutrient cycling. This role is especially important in the coastal Pacific Northwest where high lichen biomass and rapid litterfall provide an input of nitrogen and minerals into the ecosystem (Nash 1996).

Little is known how silvicultural practices influence lichen growth, production, reproduction and availability as forage. The effects of logging and stand structure on lichens currently receive little consideration by wildlife biologists who are responsible for advising land managers about ways to maintain or enhance wildlife habitat values. Federal and state management agencies should understand how utilization of lichens affects the short-term and long-term prospects and appropriate harvest rates for migratory elk and deer populations. Further, these agencies and others should understand how current and proposed forestry operations throughout the mountainous West may affect the forested forage base in an attempt to develop compatible management practices.

In this study, I quantified total arboreal lichen biomass in several second growth forest types in west-central Montana to determine the relation of lichen biomass to stand age, composition, and structure, and to determine the effects of microclimate on patterns of lichen biomass and distribution.

## **STUDY AREA**

The study was located in west-central Montana, on and near the Blackfoot-Clearwater Wildlife Management Area (BCWMA) and the Lubrecht Experimental Forest (LEF). These sites were chosen because they represent a broad range of managed forests in west-central Montana and provide deer and elk winter range.

The BCWMA is approximately 70 km northeast of Missoula, Montana (Fig. 8). Elevations ranged from 1,200 – 1,700 m and topography was predominantly gentle, with slopes  $\leq 20\%$ . Sixty-three percent of the area was forested. The forest overstory was dominated by second growth Douglas-fir (*Pseudotsuga menziesii*) stands  $> 12$  m tall with

sparse canopies and well developed shrub and Douglas-fir sapling understories. These stands remained after extensive logging over the past 60 or more years. Mature ponderosa pine (*Pinus ponderosa*) stands were common along the western boundary of the study area and along forest-bunchgrass ecotones. Mixed stands of western larch (*Larix occidentalis*), sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*) were typical of cool or moist sites (Baty 1995). Additional study sites were located on the Lolo National Forest adjacent to the BCWMA. These study sites were similar in elevation and topography as those on the BCWMA.

LEF is located approximately 55 km northeast of Missoula, Montana and 15 km southwest of the BCWMA (Fig. 8). Elevations ranged from 1,070 – 1,700 m and topography was varied, ranging from benches to near-vertical slopes and cliffs. Most of the area was forested and typically composed of Douglas-fir and western larch on moist north slopes and Douglas-fir and ponderosa pine on dry southern slopes and benches. Sub-alpine fir, Englemann spruce and lodgepole pine were typical of cool or moist sites, generally at elevations above 1,400 m. The forest overstory was dominated by second growth Douglas-fir and ponderosa pine stands >12 m tall with sparse canopies. Extensive logging in the area occurred from 1885 - 1934 (Berner 1985). Experimental timber harvest methods have been applied to much of the LEF since that time.

The study sites were historically fire-adapted ecosystems, with mean fire intervals of 5 – 25 years in low elevation ponderosa pine forests to 90 – 130 years in lower elevation subalpine forests (Fischer and Bradley 1987). Fire was an important agent in controlling density and species composition in these forests. In drier, low elevation

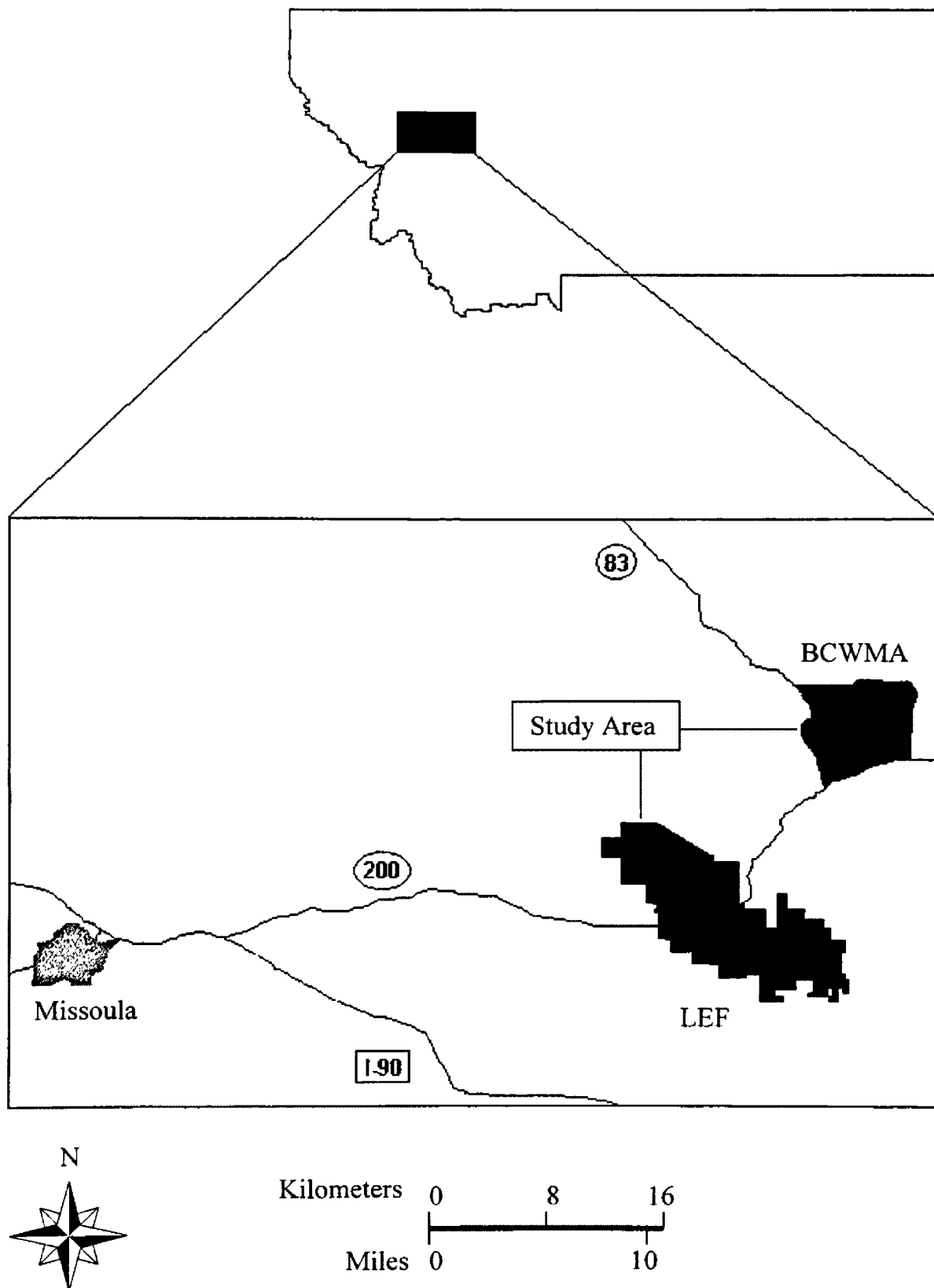


Fig. 8. Study area location in western Montana (BCWMA: Blackfoot – Clearwater Wildlife Management Area, LEF: Lubrecht Experimental Forest).

forests, frequent low or moderate intensity fires favored larch and ponderosa pine over Douglas-fir in stands where these species occurred. Fire suppression during the 20<sup>th</sup> Century has resulted in Douglas-fir regeneration beneath the overstory canopy in many of these forest types. In lower subalpine forests, periodic fire probably maintained an overstory of Douglas-fir and lodgepole pine. A dense understory of subalpine fir and spruce has resulted from fire suppression in these forests (Fischer and Bradley 1987).

Climate of the study areas is continental; characteristic weather patterns originate from the Pacific Ocean, and air masses move from west to east. Mean monthly temperatures range from  $-7.0^{\circ}$  C in January to  $16.8^{\circ}$  C in July and daily temperature fluctuations are wide. Annual precipitation ranges from 30 – 75 cm with a mean of about 45 cm. Summers are hot and dry, with over 66% of the annual precipitation falling from December through June. Snow depth is generally greatest in February with a mean of 58.4 cm.

## **METHODS**

### **Site Selection**

Productivity sites used for arboreal lichen sampling were established in several forest types. Forest types were selected in predetermined forested stands according to: (1) US Forest Service (USFS) Fire Groups (Fischer and Bradley 1987); (2) stand structure classes (Pfister 1994); and (3) percent canopy cover. The USFS Fire Groups are based on dominant trees and moisture gradients. Each Fire Group is a compilation of several habitat types specific to Montana (Pfister et al. 1997). Pfister et al. (1977) used

the presence of tree and undergrowth species to classify potential forest communities. Stand structure classes are a cross-sectional view of observable distinct canopy layers. Each layer must have 15% canopy cover to be recognized. They include single layer, 2 recognizable layers, 3 recognizable layers, and multiple layers where layers are not distinct, but obviously multi-storied. Canopy cover was used to classify open and closed canopy stands. Fifty percent canopy cover was chosen as the dividing point between open and closed canopy stands for the study area (P. Alaback pers. comm.). These three classification methods provided the ability to examine sites that differed by canopy architecture, moisture gradient, dominance class and potential solar radiation available to arboreal lichens. Several studies indicate that these variables have a significant impact on arboreal fruticose lichen abundance (Stevenson 1978, Eversman 1982, McCune and Antos 1982, Lesica et al. 1991, McCune 1993, Pipp 1998). The objective was to sample a wide array of forest types by selecting forested stands in each Fire Group, stand structure class and canopy cover class found on the study area.

Preliminary production stand types and their locations were determined by analyzing vegetation data collected on the study area by Baty (1995), vegetation inventories, and analysis of aerial photos of the study site. Final stand selection was determined by on-sight inspections. A total of 21 productivity sites were located in 1997 and 24 in 1998 for a total of 45 sites. Age of overstory trees ranged from 65 – 140 years. These sites were located within 6 different Fire Groups found on the study area. When combined with the 4 tree structure classes and 2 canopy cover classes, a total of 48 possible stand types could have theoretically been sampled. For some of the drier Fire Groups (2, 4 and 5), it was not possible to find sites that had > 50% canopy cover

because such stands in these Fire Groups probably do not exist in the managed forests that were sampled. Because of the patchy distribution of trees on the study area, small clumps of trees may have met the criteria for > 50% canopy cover, but such sites could not be found on the scale necessary for sampling (i.e. minimum of 60 m x 58 m site). In total, 17 stand types were sampled (Table 5).

I initially attempted to sample three replicates per forest type. However, canopy cover for stands > 50% was first sampled at 20 or 30 random points when the site was inspected for inclusion in the study. If this yielded > 50% canopy cover the site was included. Canopy cover values used in analysis were later measured when lichen litterfall was collected. This resulted in some stands that were initially categorized as > 50% canopy cover, but were later found to have < 50% canopy cover.

## **Field Methods**

Within each production stand, a 2,400 m<sup>2</sup> area (48 m x 50 m) was laid out so that no part of the rectangle was < 10 m from the stand edge. Four 50 m parallel transects were placed at random intervals within the rectangle. This allowed for random sampling while assuring that no large areas of the sample area were excluded (P. Alaback, pers. comm.). Transect intervals were measured from the 48 m baseline.

Each transect had five plots located at random distances for a total of 20 plots per productivity site. Plots measured 2 x 6 m and were located perpendicular to each transect. McCune (1994) hypothesized that rectangular plots would result in lower standard errors than equal area circular plots due to the patchy litterfall of arboreal lichens. Again, random intervals were used to assure that no large areas were excluded.

Table 5. Number and distribution of study sites based on USFS Fire Groups, tree stand layers and percent canopy cover. Bold numbers indicate the number of sample sites within each forest type.

Fire Group	Description	Less than 50% Canopy Cover				Greater than 50% Canopy Cover			
		1 layer	2 layer	3 layer	Multiple layer	1 layer	2 layer	3 layer	Multiple layer
2	Warm, dry ponderosa pine sites.	<b>3</b>							
4	Warm, dry Douglas-fir sites.	<b>3</b>	<b>3</b>	<b>3</b>					
5	Cool, dry Douglas-fir sites.		<b>1</b>		<b>2</b>				
6	Moist Douglas-fir sites.	<b>2</b>	<b>5</b>	<b>3</b>	<b>4</b>		<b>2</b>	<b>2</b>	<b>3</b>
8	Dry, lower subalpine sites.		<b>3</b>						
9	Moist, lower subalpine sites.		<b>3</b>		<b>2</b>				<b>1</b>



Distances were measured from the 50 m baseline and were calculated so that plots did not overlap. A random number table was used to determine placement of plots and transects.

Lichen litterfall collection was based on the methods of McCune (1994), who used arboreal lichen litterfall as a measure of the total standing crop of arboreal lichens. He found a ratio of approximately 1:100 between lichen litterfall collected in late summer and total arboreal lichen biomass. Lichen litterfall was collected either on the ground or hanging in the understory up to 2 m, but not attached to, or growing on any substrate. This also included lichens attached to fallen branches up to 10 cm diameter at the base. During late August and September of 1997 and 1998, lichen litterfall was collected within each plot.

Lichens were collected from plots using a 2 m x 2 m PVC plastic plot frame, which was rotated over once in each direction from the transect for a total plot size of 2 m x 6 m. Lichens were bagged, labeled and air dried for storage. Later they were cleaned of all foreign matter and sorted by genera. Samples were dried at 60°C for 24 hours and weighed to the nearest 0.01 gram.

Detailed stand variables recorded for each control and utilization stand were habitat type, stand age, height of lichen browse line, tree diameter and selected tree heights. These measurements were taken on a 1,000 m<sup>2</sup> fixed area circular plot centered in the middle of the 2,400 m<sup>2</sup> sample site. Each stand was assigned a habitat type based on the presence of tree and undergrowth species (Pfister et al. 1977). Stand age was determined by increment boring the two largest trees from each distinct canopy layer (Pfister 1995). The distance from the ground to the lichen browse line was measured on a tree deemed representative of the plot. All trees > 1.4 m in height were measured for

diameter at 1.4 m height (DBH) and a visual estimate of pendant lichen biomass was assigned to each tree. In addition, tree species were recorded so that species composition and densities could be determined. Tree heights were measured for two trees per canopy layer by taking the percent slope for the top and bottom of the tree from a known distance and calculated using trigonometric hypsometry (Hays et al. 1981). All trees  $\leq 1.4$  m were tallied by species. DBH and species for snags  $\geq 13.00$  cm DBH were recorded as well. Topographic measurements taken for each productivity site were elevation, slope and aspect.

Percent overstory canopy cover was measured once at plot center for each of the twenty productivity plots using a moosehorn coverscope (Garrison 1949), which has been shown to be more accurate than spherical densimeters (Bunnell and Vales 1990). In addition, lichen presence or absence in trees above the plot were recorded for each of the 25 points on the coverscope.

### **Analytical Methods**

For analysis, the four stand structure classes were combined into two groups: (1) stands with one or two distinct tree layers; and (2) stands with three or multiple tree layers. Each of the 45 sample sites was placed into one of these two groups. Regressions were then analyzed individually for each group. This approach helped to differentiate lichen biomass at sites with very different canopy architecture and better distinguish which stand level variables were correlated with lichen biomass. In total, 25 sites were 1 or 2 layer and 20 sites were 3 or multi-layer. Regressions of lichen biomass against stand characteristics for all sites combined were also analyzed.

The standard error of the mean DBH of all live trees was calculated as a measure of structural diversity (P. Alaback pers. comm.). A large standard deviation indicated a structurally diverse stand.

DBH measurements were converted to the quadratic mean DBH to decrease the influence of small trees. The formula used was:

$$QMDBH = 2 \times \sqrt{\frac{BA}{n \times \pi}} \quad (\text{Eqn. 1})$$

where  $BA$  is the basal area in  $\text{cm}^2$  and  $n$  is the number of trees/ha.

Measurements of slope and aspect together with solar radiation tables (Buffo et al. 1972) were used to determine annual potential solar radiation on each site. For computer analysis, aspect was converted to departure in degrees from due north.

Two diversity indices were computed to measure tree species diversity; the Shannon – Weiner diversity index and Simpson’s diversity index. The Shannon – Weiner diversity index is biased towards measuring richness over evenness:

$$H' = -\sum p_i \ln p_i \quad (\text{Eqn. 2})$$

where  $p_i$  is the proportion of individuals in the  $i$ th category.

Simpson’s index is weighted towards dominance. I used the form appropriate to a finite community (Magurran 1988):

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)} \quad (\text{Eqn. 3})$$

where  $n_i$  is the number of individuals in the  $i$ th category and  $N$  is the total number of individuals.

Lichen quantities between all layer types were compared using a one-way analysis of variance. Tukey's b test was used to assess differences between individual layer types. Differences in lichen biomass between grouped layer types were assessed using a T-test for 2 independent samples. I used multiple linear regression analysis to determine which stand level variables were most useful in distinguishing lichen biomass between stands. In this study regression was used to measure association between lichen biomass, stand structure, and environmental variables, not to forecast lichen biomass values for a given set of independent variables. Assumptions of multiple linear regression include selection of the appropriate model, independence, homoscedasticity, normality of dependent variables and no outliers (Ryan 1997). Each dependent variable model was assessed for violations of these assumptions according to Norusis (1995). Percent canopy cover was transformed to arcsin of percent canopy cover to obtain a more normal distribution of residuals. Assumptions for other variables and models were met. All data were analyzed using SPSS 8.0 (1998). Nomenclature of lichens follows McCune and Goward (1995).

## RESULTS

The most abundant arboreal lichen species found in the study area were *Bryoria* spp. (primarily *B. fremontii*) and *Nodobryoria* spp. (primarily *N. abbreviata*). These two genera are functionally and physically similar (McCune and Goward 1995). Personal observation and informal feeding trials suggest that deer and elk do not differentiate between the two genera. For these reasons and in an effort to conserve time, these two genera were not separated for analysis and are referred to collectively as *Bryoria*. Other fruticose lichens common to the study area include *Usnea* spp., a lichen considered to be palatable for ungulates (Stevenson 1978, Ditchkoff and Servello 1998), and *Letharia* spp. (primarily *L. vulpina*), a lichen which contains vulpinic acid (Vitt et al 1988). *Letharia* was not considered to be a forage item because of its toxicity and a lack of evidence to indicate any use as forage. Only arboreal pendulant lichens were considered for examination because they constitute the vast majority of arboreal lichen biomass in forests of western Montana. In addition, there is no evidence to indicate that deer or elk forage on any other lichens in the northern Rocky Mountains (R. Baty, C.L. Marcum, M. Thompson, pers. comm.). For these reasons lichen analysis for the study was limited to *Bryoria* and *Usnea*.

### Relation Between Canopy Layers and Lichen Biomass

Estimates of standing crop of lichens and associated stand and environmental variables are listed in Table 6. The mean standing crop of *Bryoria* biomass was greatest in 2 layer sites (417.3 kg/ha), followed by multi-layer sites (402.6 kg/ha), 1 layer sites (161.1 kg/ha) and 3 layer sites (143.9 kg/ha). The mean for 1 and 2 layer sites combined

Table 6. Biomass of *Bryoria* and *Usnea* standing crop and relevant stand characteristics for 45 sample sites categorized by number of canopy tree layers. Note: Sites 4, 7 and 13 were removed from analysis.

No. of Canopy Layers	Canopy Cover (%)	Fire Group	<i>Bryoria</i> Biomass (kg/ha)	<i>Usnea</i> Biomass (kg/ha)	Elevation (m)	Potential Solar Radiation (cal./cm <sup>2</sup> /yr.)	No. of snags/ha	Mean DBH of all live trees $\geq 13.0$ cm DBH	Basal Area/ha of larch (m <sup>2</sup> )	Standard Deviation of Mean DBH	Site Number
1	32	4	20.08	0.00	1250	172506	0	30.95	0.00	11.51	24
1	33	6	105.37	0.00	1440	172506	20	26.25	0.00	8.89	8
1	34	4	183.75	0.12	1342	160288	40	36.56	0.00	8.86	9
1	34	6	300.50	0.67	1293	158285	0	25.51	13.30	6.10	6
1	34	4	291.83	0.00	1220	168185	10	56.67	0.00	23.29	11
1	39	2	215.83	0.00	1263	164585	50	41.47	0.00	10.17	3
1	40	2	30.79	0.00	1269	182405	0	50.96	0.00	18.26	1
1	45	2	140.71	0.21	1281	138370	10	32.63	0.00	14.69	2
Mean	36.28	----	161.11	0.13	1294.75	164641.12	16.25	37.62	1.66	12.72	----
S.E.	1.41	----	37.89	0.05	24.20	4631.74	6.80	4.01	1.66	2.01	----
2	19	4	292.37	0.00	1244	178718	0	30.89	0.00	15.29	35
2	20	9	160.25	0.75	1574	181830	50	26.05	0.00	8.07	21
2	26	6	180.79	0.00	1257	169229	10	37.92	5.76	11.98	33
2	27	8	346.71	1.25	1562	176399	30	24.94	4.25	11.51	22
2	30	9	286.04	8.50	1574	178236	60	26.32	1.48	7.20	19
2	32	5	158.17	0.00	1263	180632	0	31.88	0.00	10.90	38
2	33	6	146.47	0.00	1257	148135	10	40.39	5.84	21.05	5
2	33	6	251.17	0.83	1257	171920	20	19.84	2.90	15.51	31
2	35	6	406.71	1.29	1257	171503	10	32.24	6.48	7.67	32
2	36	9	168.79	3.71	1574	179019	30	25.06	0.62	6.77	20
2	39	8	257.08	0.46	1568	173443	80	22.03	0.04	5.06	18
2	42	4	389.46	0.00	1244	180477	10	25.27	0.00	11.69	36
2	48	8	424.46	0.17	1562	174641	20	25.06	5.98	6.59	15
2	49	6	926.62	0.00	1165	138221	80	29.66	6.45	8.97	43
2	49	4	425.58	0.00	1244	180477	10	25.22	3.45	8.17	34
2	56	6	874.79	0.96	1177	102296	30	23.94	11.00	7.26	45
2	67	6	1398.71	0.54	1168	144100	60	26.16	14.76	7.12	44
Mean	37.80	----	417.30	1.09	1349.82	166428.03	30.00	27.82	4.06	10.05	----
S.E.	12.46	----	79.97	0.50	41.17	5027.41	6.23	1.27	0.99	0.97	----

Table 6. Continued.

No. of Canopy Layers	Canopy Cover (%)	Fire Group	Bryoria Biomass (kg/ha)	Usnea Biomass (kg/ha)	Elevation (m)	Potential Solar Radiation (cal./cm <sup>2</sup> /yr.)	No. of snags/ha	Mean DBH of all live trees ≥13.0cm DBH	Basal Area/ha of larch (m <sup>2</sup> )	Standard Deviation of Mean DBH	Site Number
3	25	6	47.25	0.00	1269	146102	0	33.31	5.29	10.66	28
3	25	6	101.08	0.00	1269	146102	10	29.01	4.36	9.95	29
3	26	4	230.50	0.00	1104	169828	0	24.60	0.00	10.55	41
3	28	4	363.71	0.00	1104	169828	0	26.20	0.00	9.02	40
3	29	4	180.96	0.00	1104	169828	0	23.30	0.00	7.94	42
3	45	6	168.21	1.87	1269	146102	0	29.49	12.90	7.47	30
3	49	6	121.54	19.92	1568	144100	0	27.63	0.00	10.32	47
3	57	6	54.92	14.58	1574	152538	10	30.68	0.00	13.05	46
3	75	6	26.58	22.58	1586	135310	30	30.79	0.00	12.89	48
Mean	39.89	----	143.86	6.55	1316.33	153304.26	5.56	28.33	2.51	10.21	----
S.E.	6.00	----	35.58	3.20	69.16	4384.03	3.38	1.07	1.48	0.64	----
Multi	24	5	58.17	0.21	1269	167304	0	25.75	0.00	6.48	39
Multi	31	5	350.21	0.00	1257	184205	0	28.09	0.00	11.53	37
Multi	32	9	279.12	9.50	1568	176399	100	25.10	0.75	5.84	17
Multi	33	6	6.79	17.00	1293	116333	2	35.07	0.00	13.22	27
Multi	46	9	159.25	6.29	1568	169828	40	23.75	4.97	6.83	16
Multi	48	6	8.50	14.96	1305	137288	0	28.97	0.02	12.02	25
Multi	49	6	10.04	47.71	1293	91386	10	25.20	0.57	11.65	26
Multi	51	9	118.21	0.00	1568	171618	120	24.96	2.44	6.59	14
Multi	52	6	1557.58	3.54	1226	150803	50	25.89	21.49	17.79	12
Multi	61	6	733.83	0.00	1458	176943	100	22.94	4.84	7.33	10
Multi	61	6	1147.12	1.46	1318	153753	10	22.54	25.24	14.09	23
Mean	44.25	----	402.62	9.15	1374.82	154169.14	39.27	26.21	5.48	10.31	----
S.E.	3.82	----	157.85	4.28	41.29	8690.11	14.06	1.06	2.73	1.18	----
<b>ALL SITES</b>											
Mean	39.52	----	313.48	3.98	1339.44	160488.99	24.93	29.27	3.67	10.62	----
S.E.	2.49	----	53.16	1.89	23.16	3165.89	5.23	1.64	1.44	1.18	----

(335.5 kg/ha) was greater than that for 3 and multi-layer sites combined (286.2 kg/ha) (Fig. 9). There was no significant difference in *Bryoria* biomass between all individual tree layers nor a significant difference in *Bryoria* biomass between grouped tree layers ( $P \leq 0.05$ ).

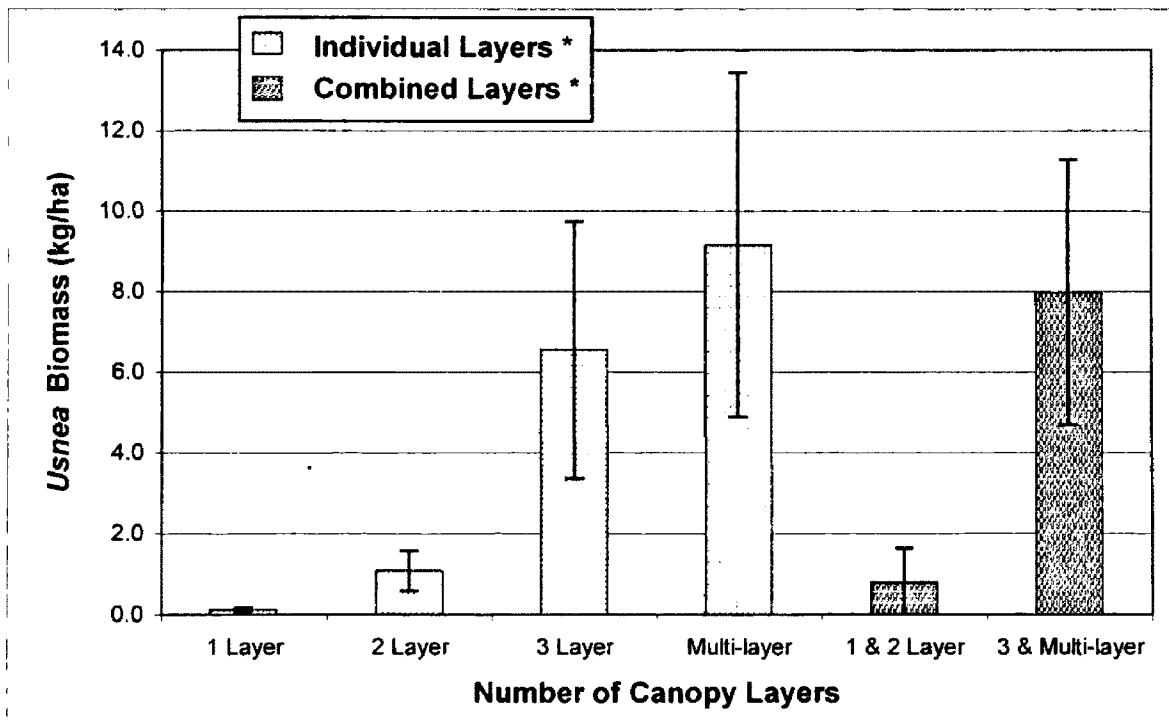
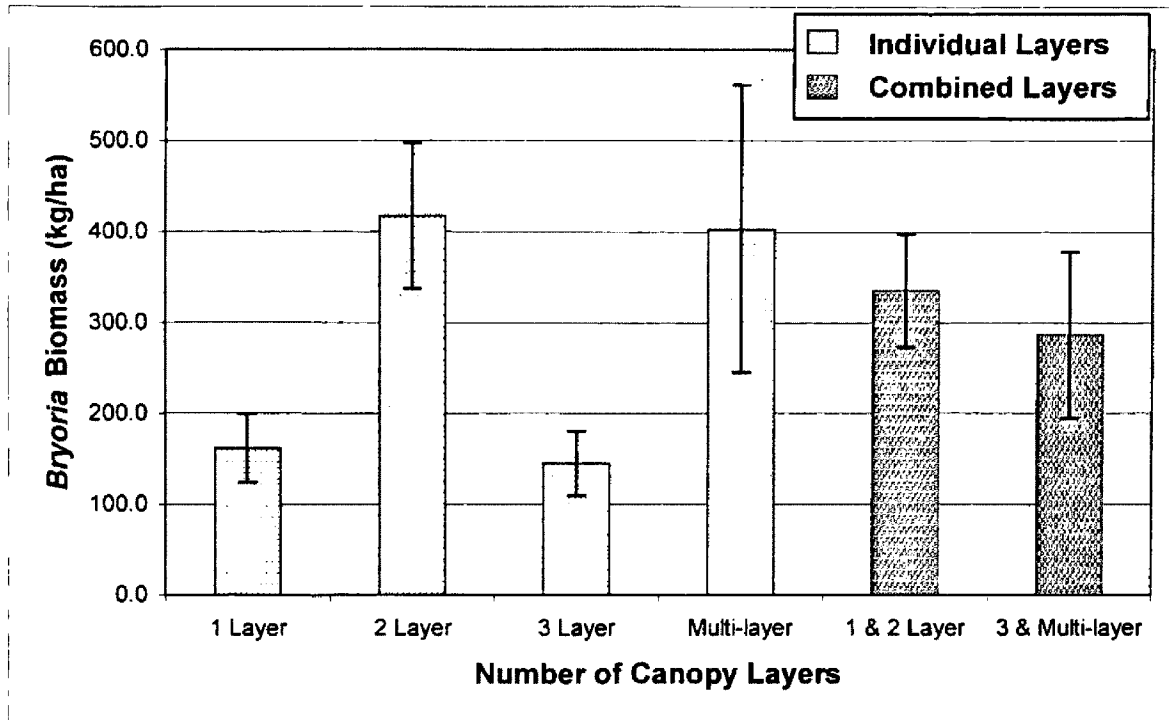
Values for standing crop of *Usnea* were much less in all stand types. Multi-layer sites had the greatest mean of *Usnea* (9.2 kg/ha), followed by 3 layer sites (6.6 kg/ha), 2 layer sites (1.1 kg/ha) and 1 layer sites (0.1 kg/ha). The mean for 3 and multi-layer sites combined (8.0 kg/ha) was greater than that for 1 and 2 layer sites combined (0.8 kg/ha) (Fig. 9). There was a significant difference in *Usnea* biomass between all individual tree layers, but post hoc tests did not show a significant difference between specific tree layers ( $P \leq 0.05$ ). In addition, there was a significant difference in *Usnea* biomass between grouped tree layers ( $P \leq 0.05$ ).

Visual estimates of standing crop of pendulant lichens did not provide accurate estimates of lichen biomass. Lichen hits counted using the moosehorn coverscope regressed against total standing crop of pendulant lichens resulted in an  $R^2$  of 0.35. Visual estimates of lichen biomass assigned to each tree regressed against total standing crop of pendulant lichens resulted in an  $R^2$  of 0.31.

### **Relation Between Stand Characteristics and Lichen Biomass**

Regression equations and associated statistics are summarized in Table 7. Two or 3 possible regression equations are presented for each group, with the exception of *Usnea* biomass. Only one acceptable model for *Usnea* was developed.





\* Significant at  $P < 0.05$

Fig. 9. Mean ( $\pm 1$  SE) standing crop of *Bryoria* biomass (top) and mean ( $\pm 1$  SE) *Usnea* biomass (bottom) estimated from litterfall in forested stands differentiated by overstory tree layers.

Table 7. Regression equations and associated statistics for biomass of *Bryoria* and *Usnea* standing crop in forest stands differentiated by number of tree canopy layers. (SEE: Standard Error of the Estimate.)

1 and 2 Layer Sites	R <sup>2</sup>	SEE	P-value		Fig. No.
			Multiple Reg.	Indiv. Reg.	
1) <i>Bryoria</i> Biomass (kg/ha) = -301.08 + 33.35(x <sub>1</sub> ) + 933.57(x <sub>2</sub> ) + 4.28(x <sub>3</sub> )	0.806	145.490	Eq.1	Eq.2	—
2) <i>Bryoria</i> Biomass (kg/ha) = -246.62 + 33.72(x <sub>1</sub> ) + 1054.43(x <sub>2</sub> )	0.690	179.540	—	—	—
x <sub>1</sub> = Basal area/ha of larch (m <sup>2</sup> )	0.530	216.145	0.000	0.002	0.000
x <sub>2</sub> = Arcsin of percent canopy cover	0.518	218.827	0.002	0.003	0.000
x <sub>3</sub> = Number of snags/ha	0.211	280.069	0.002	—	0.021
<hr/>					
3 and Multi-Layer Sites	R <sup>2</sup>	SEE	P-value		Fig. No.
			Multiple Reg.	Indiv. Reg.	
1) <i>Bryoria</i> Biomass (kg/ha) = 1029.65 + 31.09(x <sub>1</sub> ) - 50.15(x <sub>2</sub> ) + 47.76(x <sub>3</sub> )	0.811	193.544	Eq.1	Eq.2	—
2) <i>Bryoria</i> Biomass (kg/ha) = 935.78 + 41.81(x <sub>1</sub> ) - 30.291(x <sub>2</sub> )	0.728	225.151	—	—	—
x <sub>1</sub> = Basal area/ha of larch (m <sup>2</sup> )	0.665	242.567	0.001	0.000	0.000
x <sub>2</sub> = Mean DBH of live trees (m <sup>2</sup> )	0.196	375.928	0.004	0.065	0.051
x <sub>3</sub> = Standard Deviation of Mean DBH	0.206	373.459	0.018	—	0.044
<hr/>					
3 and Multi-Layer Sites	R <sup>2</sup>	SEE	P-value		Fig. No.
			Multiple Reg.	Indiv. Reg.	
<i>Usnea</i> Biomass (kg/ha) = 45.26 - 4.35(x <sub>1</sub> ) + 6.69*10 <sup>-3</sup> (x <sub>2</sub> )	0.747	6.434	—	—	—
x <sub>1</sub> = Potential annual radiation (cal/cm <sup>2</sup> /yr)	0.652	7.331	0.000	0.000	13
x <sub>2</sub> = Elevation (m)	0.089	11.868	0.022	0.203	13

Table 7. Continued

All Sites	R <sup>2</sup>	SEE	P-value			Fig. No.
			Multiple Reg.	Indiv. Reg.		
<i>Bryoria</i> Biomass (kg/ha) = 1018.12 + 40.71(x <sub>1</sub> ) + 4.75(x <sub>2</sub> ) - 0.22(x <sub>3</sub> )	0.740	186.187	Eq.1	Eq.2	—	—
<i>Bryoria</i> Biomass (kg/ha) = 72.16 + 45.09(x <sub>1</sub> ) + 3.04(x <sub>2</sub> )	0.665	209.052	—	—	—	—
x <sub>1</sub> = Basal area/ha of larch (m <sup>2</sup> )	0.593	227.753	0.000	0.000	0.000	12
x <sub>2</sub> = Number of snags/ha	0.110	336.650	0.000	0.004	0.026	12
x <sub>3</sub> = Elevation (m)	0.065	345.138	0.001	—	0.092	12

For all *Bryoria* regressions, basal area of western larch showed a strong positive relationship with *Bryoria* biomass. Additional independent variables used to explain *Bryoria* biomass for 1 and 2 layer sites were arcsin of percent canopy cover and number of snags/ha (Fig. 10). For 3 and multi-layer sites, additional independent variables were mean DBH of live trees and standard deviation (SD) of mean DBH of live trees (Fig. 11). It should be noted that the independent variable mean DBH of live trees was not the quadratic mean DBH, but DBH values as measured on each site. For all sites combined, additional independent variables were number of snags/ha and elevation (Fig. 12). Regressions of biomass values of *Usnea* were conducted only for 3 and multi-layer sites. The very low biomass values of *Usnea* in 1 and 2 layer sites did not warrant further analysis. The independent variables potential annual radiation and elevation were used to explain variation in *Usnea* biomass (Fig. 13).

Independence between variables is a problem in multiple linear regression equations with ecological data because it is difficult, if not impossible, to completely separate independent variables from overlapping in a natural system. However, coefficient correlations and covariances were examined for each regression model and determined to be acceptable. Coefficient correlations were greatest between basal area of larch and canopy cover (-.513) for 1 and 2 layer sites, basal area of larch and SD of mean tree DBH (-.544) for 3 and multi-layer sites, and basal area of larch and snags/ha (-.482) for all sites combined. In addition, residuals for all models were found to be normally distributed within the tolerances required for multiple regression and the assumption of equal variances (heteroscedasticity) were met (Norusis 1995).

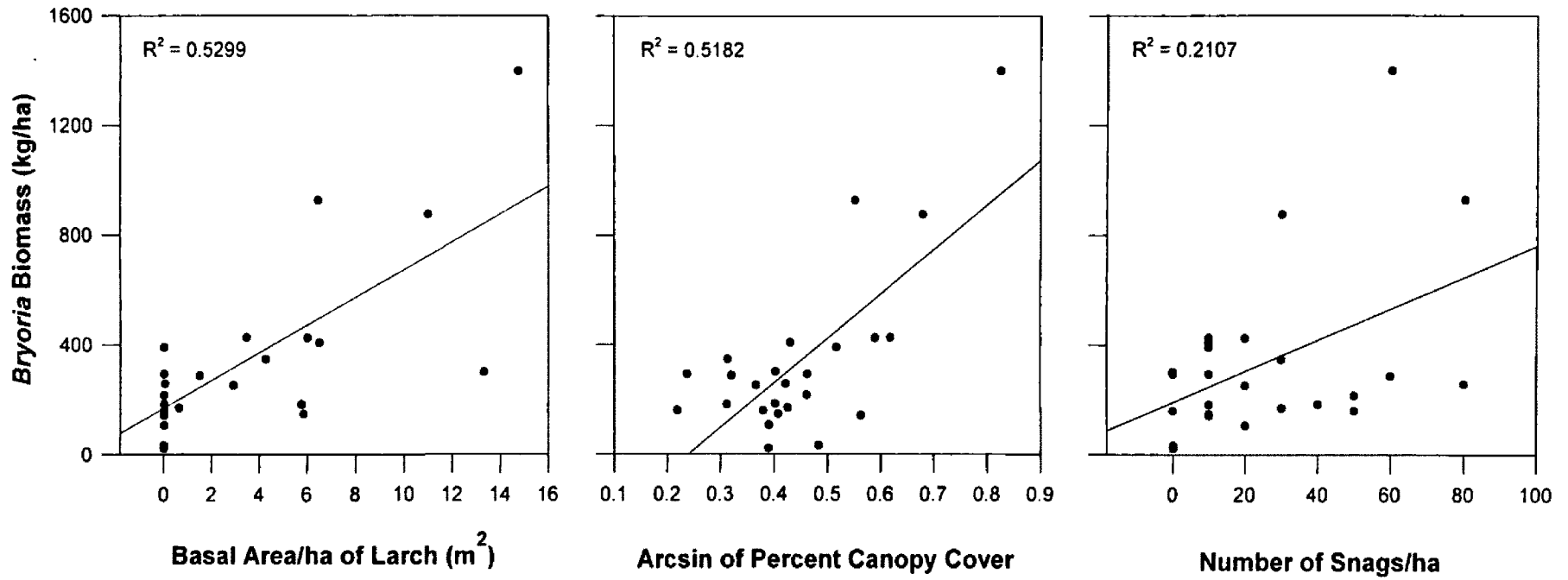


Fig. 10. Biomass of *Bryoria* standing crop versus 3 independent variables for study sites with 1 and 2 tree canopy layers.

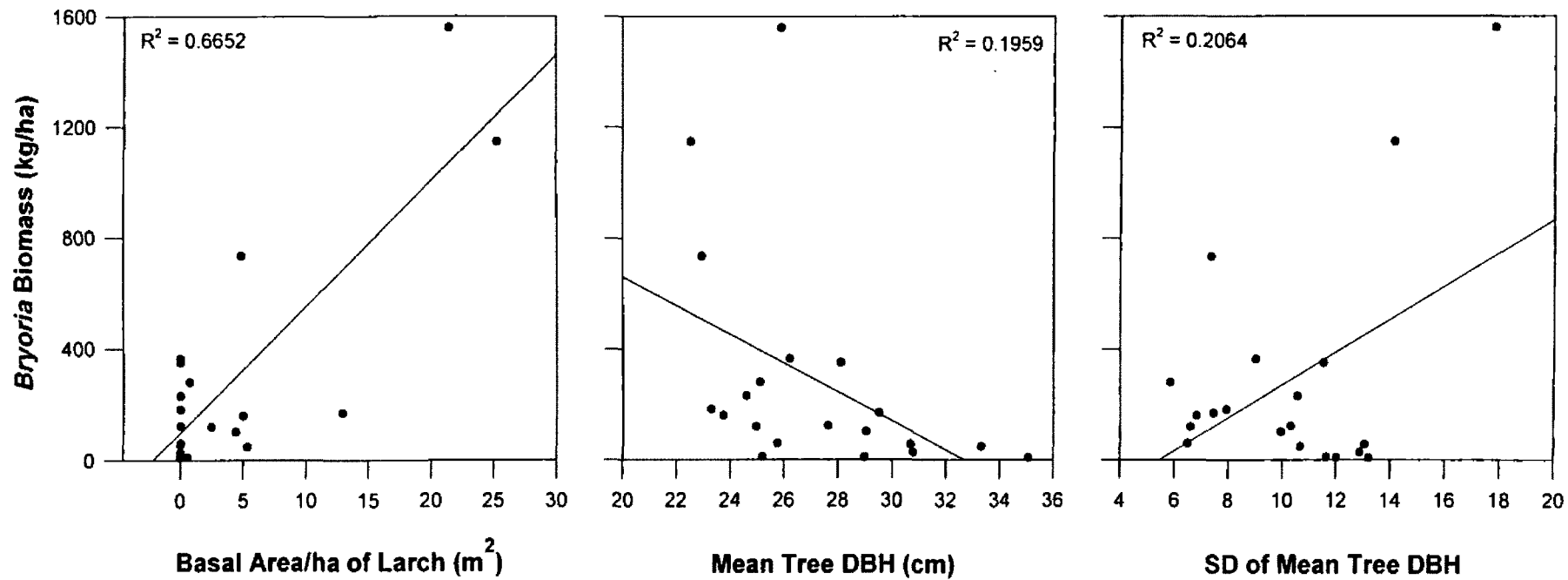


Fig. 11. Biomass of *Bryoria* standing crop versus 3 independent variables for study sites with 3 and multiple canopy layers.

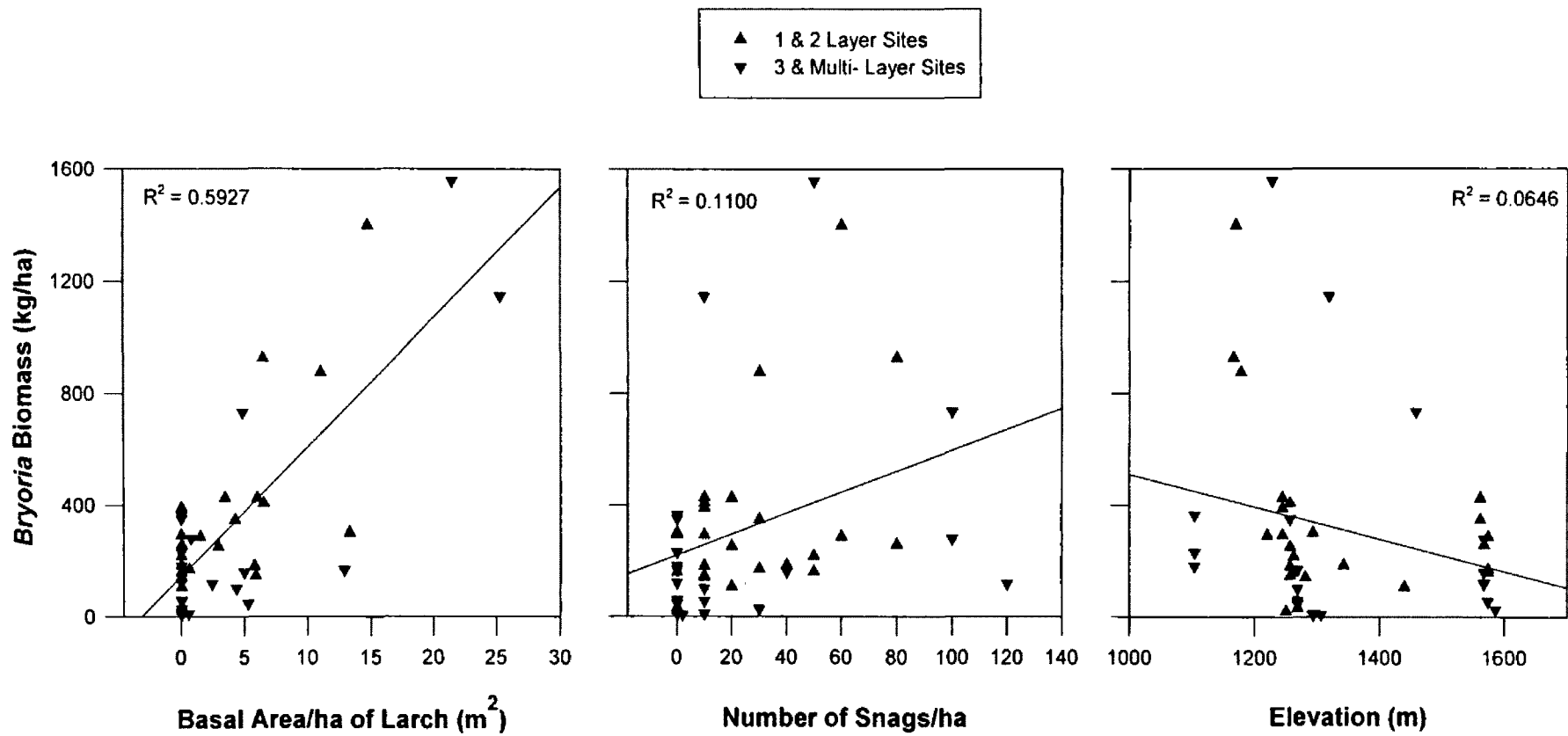


Fig. 12. Biomass of *Bryoria* standing crop versus 3 independent variables for all study sites combined.

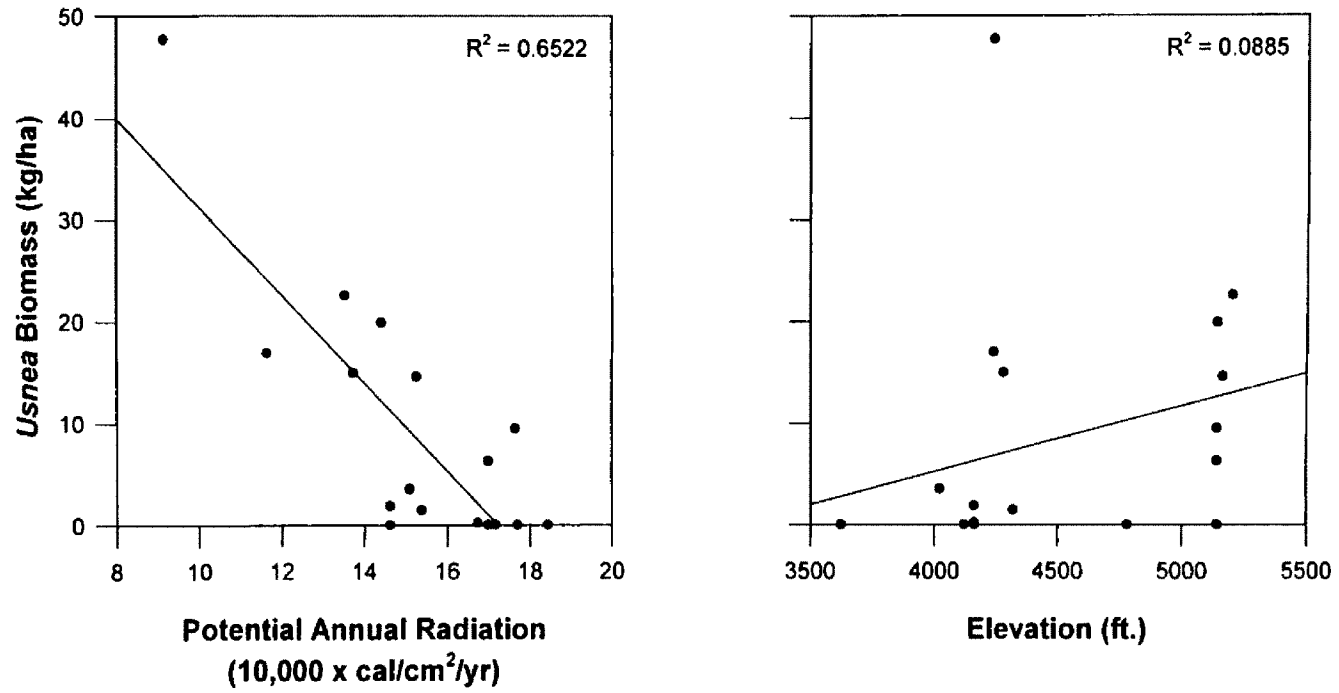


Fig. 13. Biomass of *Usnea* standing crop versus 2 independent variables for sites with 3 and multiple tree canopy layers.



## DISCUSSION

### Ecology of Alectorioid Lichens

*Bryoria* spp. and *Usnea* spp. are Alectorioid lichens, a group composed of all pendulous species in the genera *Alectoria*, *Bryoria* and *Usnea*. *Bryoria* and *Usnea* are primarily cold-climate genera, and most species are either northern or associated with mountains (Brodo and Hawksworth 1977). Some of the more important ecological factors determining the abundance of Alectorioid lichens within their geographical range are solar energy, water, nutrients, substrate characteristics, dispersal opportunities, and time (Brodo and Hawksworth 1977). Factors that contribute to the removal of lichens, such as breakage through the action of wind and rain, and consumption by animals, are also important (Stevenson 1978).

In the humid west coast forests, the dominant genus of Alectorioid lichen is *Alectoria*, which appears to be limited by light availability. In areas with a more continental climate, such as western Montana, humidity is more frequently a limiting factor for Alectorioid lichens (Stevenson 1978). McCune and Antos (1982) determined that *Bryoria* spp. in the Swan Valley of western Montana were most common in stands characterized by open irregular canopies of larch and Douglas-fir, often on well-lit slopes with frequent wetting and drying. A more open canopy allows more moisture throughfall, but rapid drying is promoted by the greater penetration of sunlight and freer air circulation. Closed canopies smooth fluctuations in humidity and air temperature and reduce throughfall and light in the understory. This effect of throughfall may be especially important in west-central Montana, and other areas of moderate precipitation,

because of the potential for proportionately greater interception of moisture by the canopy than in areas with heavier precipitation (McCune and Antos 1982).

Air pollution is thought to be an important factor in the present distribution of several species of *Bryoria* in Europe, and the occurrence of Alectorioid lichens in cities and industrial areas is limited (Brodo and Hawksworth 1977). Sheridan et al. (1976) found that biomass values of *Alectoria (Bryoria) fremontii* were much lower at experimental sites up to 16 km from a pulp mill near Missoula, Montana. No known sources of pollution potentially limiting to lichen growth and vitality were located near my study area.

The most common substrates of corticolous Alectorioid lichens are coniferous trees and trees with similar bark characteristics such as birch (Brodo and Hawksworth 1977). It is not clear whether these lichens prefer acidic bark due to a physiological requirement, or whether they require the climate and general environment of coniferous forests and simply occupy the most available substrate (Stevenson 1978). Brodo and Hawksworth (1977) noted that these lichens utilize a wide variety of trees within each forest type, suggesting that the latter possibility is more likely. Moisture capacity, mineral content, pH, physical texture, and stability are bark characteristics potentially important in determining suitability of a tree as a substrate (Brodo 1973).

The establishment of a lichen species in an area depends on the availability of viable propagules, either sexual or vegetative. Spore producing structures are rather rare among *Bryoria* and most species depend mainly on vegetative methods of propagation (Brodo and Hawksworth 1977). Vegetative reproduction by windblown thallus

fragments is of major importance in short-range dispersal, but there is some evidence that species of *Alectoria* and *Bryoria* that produce soredia (clumps of algal cells surrounded by fungal hyphae) have an advantage in long-range dispersal over species that do not (Stevenson 1978). Esseen (1984) found that *Bryoria* and *Alectoria* had the potential for greater vegetative dispersal distances than *Usnea longissima* because *Bryoria* and *Alectoria* disperse mainly by small fragments, allowing greater transport distances by wind. Fragmentation and isolation of old forest stands by human settlement, agriculture and logging may severely restrict the distribution of some lichen species that cannot disperse effectively over long distances (Stevenson 1978).

The abundance of *Bryoria* in a suitable forest site depends on how much time has been available for establishment and growth of lichens. Growth rates of lichens are generally slow compared to other plant groups. Stevenson (1978) and Lesica et al. (1991) determined that *Alectoria* spp. were more common in old growth stands while *Bryoria* spp. were more common in second growth, suggesting that *Bryoria* is more photophylic. In addition, *Bryoria* may be better adapted to edge environments than *Alectoria*. Esseen and Renhorn (1998) observed that *Alectoria* abundance was markedly reduced up to 50 m into the forest following clearcut logging and attributed the decrease to fragmentation by wind, photoinhibition and increased evaporation. *Bryoria* may have stronger thalli, which are less prone to breakage in wind and may avoid desiccation by increasing the dormant time coupled with an increased growth rate when conditions are favorable. Edge lichens also receive more nutrient and pollutant deposits than interior species (Esseen and Renhorn 1998). *Bryoria* may be more efficient at extracting

nutrients and less prone to damage from pollutants than *Alectoria*. Eversman (1982) determined that *Usnea* spp. were pioneer lichens, being the first lichens to occupy ponderosa pine stands following fire. These conclusions are consistent with the findings in my study, in which all sites were second growth and the only pendulant lichens found were *Bryoria* and *Usnea*. It is unclear, however, if *Alectoria* would inhabit my study site given adequate time. These sites are much drier than sites examined by Stevenson (1978) and Lesica et al. (1991) and are fire adapted ecosystems.

Impacts of fire on arboreal lichen biomass are poorly understood. Detrick (1985) determined that following a low intensity fire, 40 years were required to restore arboreal lichen biomass levels to pre-fire levels in high elevation forests of northern Idaho and northeast Washington. High intensity fires and clear-cut logging showed similar effects, where even after 80 years of recovery lichen biomass was insignificant. Detrick (1985) concluded that when complete tree removal occurred on a site, a time span of more than 100 years was required before lichens recovered to measurable levels. In my study, one site had undergone a low intensity ground fire in October, 1991. It was a one layer site in Fire Group 4, dominated by large Douglas-fir and ponderosa pine. It appeared that the fire had little or no impact on the standing crop of *Bryoria* (183.75 kg/ha). Fire may actually benefit ungulates that forage on arboreal lichens by removing small trees that restrict lichen litterfall from reaching the ground, where it is available as forage. In addition my observations indicated that small trees (< 13 cm DBH and < 3 m tall) inoculated with *Bryoria* from larger overstory trees, did not support lichen growth. This was probably do to an inhospitable microclimate in the small trees. Several studies have

demonstrated that microclimate is dramatically different at different heights in a tree, and lichen distribution and abundance follows a similar pattern, presumably because of these differences in microclimate (Stevenson 1978, McCune 1993, Eversman 1982, Lesica et al. 1991, Pipp 1998). Stevenson (1978) and Eversman (1982) both showed that arboreal pendant lichen biomass decreased drastically below about 2 m, at which point the microclimate was inhospitable to lichens. However, these sites may have been available for use by deer, which may have foraged on lichens within their reach.

### **Comparison With Other Studies**

This study differs significantly from most other bryophyte studies in that I only examined lichen biomass in second growth forests. Most other studies with comparable objectives compared managed stands with old growth stands. In addition, the few studies of lichens that have been conducted in the northern Rocky Mountains have been concerned primarily with lichen species richness and distribution, rather than examining biomass. Studies to determine lichen biomass in different forested areas have been conducted primarily in western Washington, Oregon and British Columbia, or at high elevations in northern Idaho. Forests in these climates tend to be more continuous than west-central Montana, where the tree distribution tends to occur in patches. Because of a dramatically different climate and forest types, results from those studies have limited applicability to this study. Surprisingly, however, several of the variables that I determined to be correlated with lichen biomass are similar to those found in studies conducted in different climates and forest ecosystems.

## Lichen Biomass Values

Values for standing crop of arboreal lichens in my study were of comparable magnitude to Stevenson (1978), who estimated *Alectoria* standing crop at 21.0 – 1,528.0 kg/ha for 14 study sites. Values for *Bryoria* in my study ranged from 6.8 – 1,557.6 kg/ha for 45 study sites. However, my values were substantially higher than McCune (1993) who estimated the standing crop of Alectorioid lichens in western Washington and Oregon at 27.2 – 163.3 kg/ha.

The methods used to arrive at total standing crop of arboreal lichens (McCune 1994) were developed in western Washington and Oregon, where climate and forest stands are substantially different than in the northern Rockies. For this reason, my values may be less accurate. McCune (1994) estimated a 1:100 ratio between lichen litterfall collected in late summer and lichen standing crop. It is unclear if litterfall rates in western Montana represent a similar proportion of standing crop as they do in western Washington and Oregon. If litterfall rates in western Montana were greater than 1% of the standing crop during my study, then my estimates of lichen standing crop would be overestimated. Decomposition rates of lichen litterfall on the forest floor may have also influenced estimates of standing crop. McCune's methods (1994) assume that lichen litterfall from the previous winter and spring would decompose by the time litterfall is collected in late summer. The drier climate in western Montana may result in a slower decomposition rate for lichen litterfall on the forest floor, thereby inflating estimates of lichen standing crop. At a minimum, values between stands in my study yield relative values, so that stands with the greatest litterfall had the greatest standing crop.

## Stand Structure and Microclimate

Stand structure variables and microclimate variables in my study are also comparable to other studies. In forests on northeast Vancouver Island, Stevenson (1978) determined that slope, elevation, potential solar radiation, height of the codominant tree layer, canopy cover and degrees from south were correlated with *Alectoria* biomass. *Alectoria* biomass values were greatest on steeper slopes and southern aspects, probably due to the increased solar energy on those sites (Stevenson 1978). In my study, slope and aspect were not significant in any part of the study. Microclimate in the canopy of trees on southern and northern aspects may be similar on my study site, or *Bryoria* is less sensitive to changes in solar radiation than other lichen species.

Stevenson (1978) found that *Alectoria* biomass increased with increased elevation and increased potential solar radiation. In my study, elevation was positively correlated with *Usnea* and potential solar radiation showed a negative relationship, demonstrating that *Usnea* biomass was higher in stands with low amounts of solar radiation at relatively high elevations. In addition, elevation showed a negative relationship with *Bryoria* biomass for all sites combined. The relationship was relatively weak ( $R^2 = 0.07$ ), but significant when regressed with basal area of larch and snag number, suggesting that *Bryoria* biomass was greater at low elevations when snags and larch were abundant. The number of snags probably provides increased surface area and provides an adequate substrate for *Bryoria* attachment. In addition, snags provide openings in the canopy, which benefit photophilic species such as *Bryoria* but seem to decrease growth and vitality of lichens adapted to forest interiors. Pipp (1998) found that snag density was

negatively correlated with lichen biomass in mature and old-growth forests of western Washington.

Stevenson (1978) found that canopy cover was negatively correlated with *Alectoria* biomass. My study resulted in the opposite relationship, demonstrating that canopy cover was positively correlated with *Bryoria* biomass for 1 and 2 layer sites. This suggests that when structural diversity is low (e.g. 1 or 2 tree layers), canopy cover is a necessary component for *Bryoria* growth and abundance, but less so when structural diversity is higher (e.g. 3 or multi-tree layers).

Rochelle (1980) speculated that greater tree densities and smaller tree diameters at mid-elevation sites compared to low elevation sites on Vancouver Island would provide greater area and more valuable sites for lichen attachment. My study agrees with Stevenson (1978) in concluding that there is not a discernible relationship between basal area of all trees and lichen biomass. However, my data showed a negative relationship between tree DBH and *Bryoria* biomass for 3 and multi-layer sites when basal area of larch and structural diversity were high. In these sites, structural diversity was high relative to other sites because of its multi-storied nature. Standard deviation of mean tree diameter was positively correlated with *Bryoria* biomass in these stands, further suggesting that structural diversity is an important component in the distribution and abundance of *Bryoria*.

Age of the dominant tree layer did not strongly influence *Bryoria* biomass for any stand types in my study. Recent studies have shown that forest structure is a better determinant of lichen biomass and species richness than age alone (Peck and McCune



1997, Pipp 1998). My study generally agrees with these conclusions, even for the relatively young forests that were sampled. However, tree species diversity as measured by Simpson's Diversity Index and the Shannon – Weiner Diversity Index did not correlate with lichen biomass, suggesting that lichen biomass on my study area was a function of structural diversity rather than substrate diversity.

Stand structure variables may also explain the large differences in *Bryoria* biomass between individual tree layers. Two layer sites had about 2.5 times as much *Bryoria* biomass as 1 layer sites. This may be due to the greater number of snags in 2 layer sites (30/ha) versus 1 layer sites (16/ha) and the greater basal area of larch in 2 layer sites (4.06 m<sup>2</sup>/ha) compared to 1 layer sites (1.66 m<sup>2</sup>/ha). Similarly, multi-layer sites had about 2.8 times as much *Bryoria* biomass as 3 layer sites. Basal area of larch in multi-layer sites averaged 5.48 m<sup>2</sup>/ha, whereas 3 layer sites averaged only 2.51 m<sup>2</sup>/ha.

### **Lichen Correlation with Western Larch**

Basal area of larch explained more variation in *Bryoria* biomass than any other single variable in my study. However, it is unclear if the correlation between larch and lichen biomass is due to larch providing a suitable substrate and microclimate for lichen growth, or if the relationship is due to other environmental or macroclimate variables favorable to both, but not measured in this study. This is particularly difficult to interpret because forest measures, such as basal area of a particular tree species, integrate the effects of many environmental variables. However, a wide range of environmental variables thought to influence lichen biomass were measured in this study, suggesting that larch may provide a suitable substrate and microclimate for *Bryoria*. In addition,

larch are deciduous and, therefore, provide more light lower in the canopy than other conifers. This may benefit photophylic lichens such as *Bryoria*.

On the other hand, Brodo and Hawksworth (1977) suggested that Alectorioid lichens occupy the most available substrates in conifer stands and are not species specific with regard to substrate. In addition, larch tend to shed dead limbs as they age. It is possible that trees that do not rapidly shed dead branches (e.g. Douglas-fir) provide a better substrate for lichens than self-pruning trees (e.g. lodgepole pine and western larch), but this hypothesis has not been evaluated. Basal area of Douglas-fir did not show a strong positive relationship with lichen biomass in my study. Detrick (1985) determined that subalpine fir was the most important lichen producing tree species for woodland caribou because it retains its branches, providing more substrate for lichens. These studies suggest that some environmental variable(s) not measured in this study may impact both *Bryoria* biomass and basal area of larch.

### **Between Year Variations**

Pipp (1998) found significant differences in epiphyte litterfall between years at the same plots. This may have occurred in my study, but sites were only sampled once, either in 1997 or 1998. Therefore, I could not determine if litterfall rates were greater for one year. If litterfall rates were different between years, then independent variables I determined to be correlated with lichen biomass may be a product of different litterfall rates between years rather than actual differences in stand structure and microclimate. However, I did not find significant differences in litterfall rates between winter 1996-97

and winter 1997-98 (see chapter 1). In addition, McCune (1994) did not find significant differences in lichen litterfall rates for late summer sample periods between 2 years.

### **Availability To Deer and Elk**

Assuming that lichen biomass is in a steady state in the forest, then litterfall provides a rough estimate of the annual turnover if the standing crop of lichens is known (Stevenson 1979). Esseen (1985) reported turnover rates of between 7.0 and 10.0% and cited other studies reporting turnover rates between 10.5 and 25.0%. Stevenson (1979) reported annual turnover of 10.5 – 16.1% of the standing crop for *Alectoria* and *Bryoria* on Vancouver Island. Using the turnover rates from Stevenson (1979) for my study, 1.0 – 250.78 kg/ha of *Bryoria* would be available each year as forage for deer and elk, most of this falling in the winter. For *Usnea*, 0.0 – 7.7 kg/ha/yr. would be available as forage. This represents a substantial forage source for deer and elk on winter ranges in west-central Montana.

## SYNTHESIS

My study demonstrates that pendulant arboreal lichens form a substantial part of the winter diet of deer and elk in west-central Montana. In addition, these lichens are found in high quantities in these forests relative to similar studies conducted elsewhere in western North America. The amount of lichen litterfall consumed by deer and elk seems to have been driven by lichen availability rather than by deer and elk foraging on lichens opportunistically in habitats selected according to other criteria. In other words, it appears that deer and elk selected sites specific to high rates of lichen litterfall, although this remains speculative.

Differences in independent variables that explained lichen quantity available to deer and elk in Chapter I and estimates of lichen standing crop in chapter II can probably be attributed to differences in sampling methods and sampling scale. Ungulate exclosures were established with specific regard to lichen biomass and in areas known to be used by deer and elk in the winter. In addition, the plots used for sampling at these sites were adjacent to one another so that the area sampled was 80 m<sup>2</sup>. Productivity sites used in Chapter II were established based on a specific set of stand structure and microclimate criteria. A total of 240 m<sup>2</sup> were sampled at each site. More importantly, the plots were distributed over a 2,400 m<sup>2</sup> area, thereby sampling on a much broader scale than in Chapter I. In addition, stand structure and microclimate variables were measured on a 400 m<sup>2</sup> plot for Chapter I and a 1,000 m<sup>2</sup> plot for Chapter II. For these reasons, independent variables that explained variation in lichen standing crop in Chapter

II are probably more accurate predictors of lichen quantity available to ungulates than variables used in Chapter I.

A few ungulate exclosures were located fairly close to productivity sites. This allowed for the comparison of standing crop estimated from late summer litterfall in productivity sites to standing crop estimated from winter litterfall within ungulate exclosures. Stevenson (1978) estimated that 10 – 16% of the lichen standing crop falls as litterfall each year, most of it in winter. Assuming that litterfall collected within exclosures in my study represented 10% of lichen standing crop, then the estimated value for standing crop of lichens would be 260.50 kg/ha for control site #17. This exclosure was in close proximity to productivity site #23, where the standing crop of lichens was estimated from late summer litterfall at > 1,100 kg/ha. These two estimates of lichen standing crop should be somewhat similar. Two possible explanations for this disparity are that lichen litterfall in the late summer is more than 1% of the standing crop, or that litterfall in the winter is less than 10% of the standing crop. The topic of estimating lichen standing crop from lichen litterfall deserves further attention in western Montana.

### **Further Studies**

There are several topics that should receive further study to aid in determining management objectives. I was unable to determine which ungulate species were foraging on lichen litterfall and in what quantities. More studies in this area have the potential to be very important to wildlife managers because it remains unclear if elk and mule deer forage heavily on lichen litterfall. This process would be simplified if a method was developed to relate lichen intake to a fecal pellet indicator. This may also allow for more

detailed studies of the nutritive values of lichens, particularly with regard to elk, for which no lichen nutrition studies have been conducted. In addition, it remains unclear if deer and elk select habitat based on the availability of lichens as forage or if they utilize lichens opportunistically, but do not expend additional energy to search for them.

Standing crop of lichen biomass may have been overestimated in my study because the methods I used were developed in a different forest ecosystem. However, this method is probably the simplest to implement and among the quickest to conduct. In addition, it has the potential to be fairly accurate compared to other methods of lichen standing crop estimation. A regression equation predicting standing crop from litterfall needs to be developed for the northern Rocky Mountains to increase the applicability of this method. This would entail collecting litterfall and then falling the surrounding trees to determine the standing crop. It is a time intensive process, but has the potential for widespread use. A possible alternative to falling trees would be to dye or otherwise mark lichens in the canopy and determine what percentage of those lichens fall during a given time period. If litterfall was collected throughout the stand, this percentage could then be extrapolated to the stand level and result in an estimate of lichen standing crop for the entire stand.

The reintroduction of fire to many forest ecosystems in the northern Rockies has the potential to alter lichen biomass and distribution. The effects of fire on lichens should be better understood before land managers implement landscape-level plans to reintroduce fire. The forest of western Montana are fire-adapted ecosystems, but fire intervals and intensities, and its impact on lichens remain unclear for many forest types.

## Management Recommendations

Management of lichens as a winter forage source for deer and elk deserves special attention by wildlife biologists and land managers. Management favoring high rates of lichen litterfall throughout deer and elk winter range will help to maintain healthy deer and elk populations. The strong positive correlation between western larch and *Bryoria* standing crop in all stand types suggests that the retention of large larch will favor lichen production. In addition, high overstory canopy cover and retention of large snags in stands with simple structure (1 or 2 canopy layers) will further enhance lichen production. In stands with more complex structure (3 or multi-layer) diversely sized trees will enhance structural diversity and, therefore, lichen biomass. Thinning of stands with dense Douglas-fir understories would allow potential lichen litterfall to reach the ground where it would be available as forage. Thinning would also allow more light to reach lower branches, which benefits photophylic lichens such as *Bryoria*.

Special consideration for overutilization of arboreal lichens is probably not necessary. From a management perspective, lichens cannot be overutilized by deer and elk because the vast majority of arboreal lichens are available only as litterfall.

## LITERATURE CITED

- Baty, G.R. 1995. Resource partitioning and browse use by sympatric elk, mule deer and white-tailed deer on a winter range in western Montana. M.S. Thesis, Univ. Montana, Missoula. 228 pp.
- Berner, K.L. 1985. Winter and spring habitat selection by white-tailed in a western Montana second-growth forest. M.S. Thesis, Univ. Montana, Missoula. 98 pp.
- Berteaux, D., M. Crete, J. Huot, J. Maltais, and J.P. Ouellet. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia* 115:84-92.
- Brodo, I.M. 1973. Substrate Ecology. pp. 401-441 in V. Ahmadjian and M.E. Hale, eds. *The Lichens*. Academic Press, New York, NY. 697 pp.
- \_\_\_\_\_, and D.L. Hawksworth. 1977. *Alectoria* and allied genera in North America. *Opera Botanica* 42:1-164.
- Buffo, J., J. Fritschen, and J.L. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60 degrees north latitude. USFS Research Paper PNW-142.
- Bunnell, F.L., and D.J. Vales. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. *Canadian Journal of Forest Resources* 20:101-107.
- Cliff, E.P. 1939. Relationship between elk and mule deer in the Blue Mountains of Oregon. *Transactions of the North American Wildlife Conference* 4:559-569.
- Cowan, I. McT. 1945. The ecological relationships of the food of the black-tailed deer, *Oidocoileus hemionus columbianus* (Richardson) in the coast forest region of southern Vancouver Island, B.C. *Ecological Monographs* 15:109-139.
- DeNio, R.M. 1938. Elk and Deer Foods and Feeding Habits. *Transactions of the North American Wildlife Conference* 3:421-427.
- Detrick, R. 1985. Arboreal lichens available to caribou, Selkirk Mountains, northern Idaho. Report to the Supervisor's Office, Idaho Panhandle National Forest, Coeur d'Alene, ID. 55 pp.
- Ditchkoff, S.S., and F.A. Servello. 1998. Litterfall: an overlooked food source for wintering white-tailed deer. *Journal of Wildlife Management* 62:250-255.
- Esseen, P.A. 1984. Litter fall of epiphytic macrolichens in two old *Picea abies* forests in Sweden. *Canadian Journal of Botany* 63:980-987.



- \_\_\_\_\_, and K.E. Renhorn. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* 12:1307-1317.
- Edwards, R.Y., J. Soos, and R.W. Ritchey. 1960. Quantitative observations on epidendric lichens used as food by caribou. *Ecology* 41:425-431.
- Eversman, S. 1982. Epiphytic lichens of a ponderosa pine forest in southeastern Montana. *The Bryologist* 85:204-213.
- Fischer, W.C., and A. F. Bradley. 1987. Fire Ecology of western Montana forest habitat types. USDA Forest Service General Technical Report INT-223. 95 pp.
- Garrison, G.A. 1949. Uses and modifications for "moosehorn" crown closure estimation. *Journal of Forestry* 47:733-735.
- Gray, P.B., and F.A. Servello. 1995. Energy intake relationships for white-tailed deer on winter browse diets. *Journal of Wildlife Management* 59:147-152.
- Hanley, T.A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35:146-151.
- Hash, H.S. 1973. Movements and food habits of the Lochsa elk. M.S. Thesis, Univ. Idaho, Moscow. 76 pp.
- Hays, R.L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. U.S.D.I. Fish and Wildlife Service. FWS/OBS-81/47. 111pp.
- Hayward, G.D., and R. Rosentreter. 1994. Lichens as nesting material for northern flying squirrels in the northern Rocky Mountains. *Journal of Mammalogy* 75:663-673.
- Hildebrand, P.R. 1967. Biology of white-tailed deer on winter ranges in the Swan Valley, Montana. M.S. Thesis, Univ. Montana, Missoula. 91 pp.
- Hobbs, N.T., D.L. Baker, and R.B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. *Journal of Wildlife Management* 47:1-16.
- Hodgman, T.P., and R.T. Bowyer. 1985. Winter use of arboreal lichens, Ascomycetes, by white-tailed deer, *Odocoileus virginianus*, in Maine. *The Canadian Field Naturalist* 99:313-316.
- Hoskins, L.W., and P.D. Dalke. 1955. Winter browse on the Pocatello Big Game Range in southeastern Idaho. *Journal of Wildlife Management* 19:215-225.

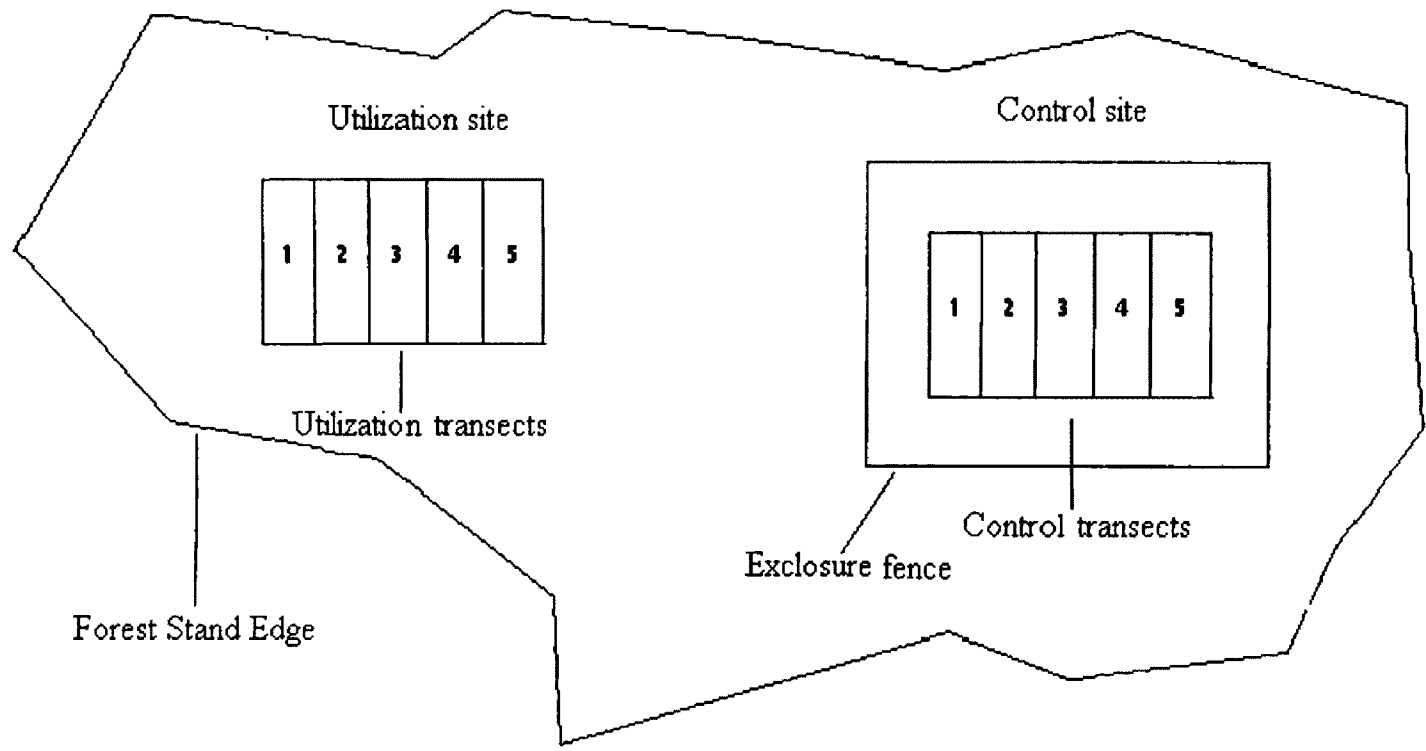
- Janke, D. 1977. White-tailed deer population characteristics, movements, and winter site selection in western Montana. M.S. Thesis, Univ. Montana, Missoula. 92 pp.
- Jenks, A.J., and D.M. Leslie Jr. 1988. Effect of lichen and in vitro methodology on digestibility of winter deer diets in Maine. *The Canadian Field-Naturalist* 102:216-220.
- \_\_\_\_\_, and \_\_\_\_\_. 1989. Digesta retention of winter diets in white-tailed deer (*Odocoileus virginianus*) fawns in Maine, U.S.A. *Canadian Journal of Zoology* 67:1500-1504.
- Kufeld, R.C. 1973. Foods eaten by the Rocky Mountain elk. *Journal of Range Management* 26:106-113.
- Lesica, P., B. McCune, S.V. Cooper, and W.C. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* 69:1745-1755.
- Magguran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.
- Marcum, C.L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph.D. Dissertation, Univ. Montana, Missoula. 188 pp.
- Maser, Z., C. Maser, and J.M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Canadian Journal of Zoology* 63:1084-1088.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *The Bryologist* 96:405-411.
- \_\_\_\_\_. 1994. Using epiphyte litter to estimate epiphyte biomass. *The Bryologist* 97:396-401.
- \_\_\_\_\_, and J.A. Antos. 1982. Epiphyte communities of the Swan Valley, Montana. *The Bryologist* 85:1-12.
- \_\_\_\_\_, and T. Goward. 1995. Macrolichens of the northern Rocky Mountains. Mad River Press, Eureka, California, USA.
- Moen, A.N. 1976. Energy conservation by white-tailed deer in the winter. *Ecology* 57:192-198.
- Montana Department of Fish Wildlife and Parks. 1997. Resource partitioning by sympatric elk and deer in a severe winter. Unpublished Data. MDFWP, Region 3, Missoula, MT.

- Morris, M.S., and J.E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. *Journal of Wildlife Management* 21:189-193.
- Nash, T.H., III. 1996. *Lichen Biology*. Cambridge University Press, Cambridge, Great Britain. 303 pp.
- Norusis, M.J. 1995 *SPSS 6.1 Guide to data analysis*. Prentice Hall, Engelwood Cliffs, NJ. 582 pp.
- Osborn, R.G., and J.A. Jenks. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. *Journal of Mammalogy* 79:437-447.
- Parker, K.L., M.P. Gillingham, T.A. Hanley, and C.T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Canadian Journal of Zoology* 74:442-450.
- Peck, J.E. and B. McCune. 1997. Remnant trees and canopy communities in western Oregon: A retrospective approach. *Ecological Applications* 7:57-63.
- Pfister, R. D. 1994. Stand structure and classification ; proposed common operational variables and classification for Bitterroot Ecosystem Management Project. Univ. Montana, Missoula.
- \_\_\_\_\_, B. L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. Forest habitat types of Montana. USDA Forest Service General Technical Report INT-34. 174 pp.
- Pike, L.H., R.A. Rydell, and W.C. Denison. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. *Canadian Journal of Forest Resources* 7:680-699.
- Pipp, A.K. 1998. Effects of forest age versus forest structure on epiphytic lichen biomass and diversity. M.S. Thesis, Univ. Montana, Missoula. 84 pp.
- Renhorn, K.E., P.A. Esseen, K. Palmqvist, and B. Sundberg. 1997. Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. *Oecologia* 109:1-9.
- Rochelle, J.A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Ph.D. Dissertation, Univ. British Columbia, Vancouver. 295 pp.
- Robbins, C.T. 1987. Digestibility of an arboreal lichen by mule deer. *Journal of Range Management* 40:491-492.

- Rominger, E.M., and J.L. Oldemeyer. 1990. Early-winter diet of woodland caribou in relation to snow accumulation. Selkirk Mountains, British Columbia, Canada. *Canadian Journal of Zoology* 68:2691:2694.
- \_\_\_\_\_, C.T. Robbins, and M.A. Evans. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. *Journal of Wildlife Management* 60:719-728.
- Rundel, P.W. 1978. The ecological role of secondary lichen substances. *Biochemical Systematics and Ecology* 6:157-170.
- Ryan, T.R. 1997. *Modern regression methods*. Wiley series in probability and statistics. Wiley and Sons, New York, NY. 515 pp.
- Stevenson, S.K. 1978. Distribution and abundance of arboreal lichens and their use as forage by black-tailed deer. M.S. Thesis, Univ. British Columbia, Vancouver. 148 pp.
- \_\_\_\_\_. 1979. Effects of selective logging on arboreal lichens used by Selkirk caribou. Fish & Wildlife Report No. R-2, Province of British Columbia, Ministry of Forests and Ministry of Environment. ISSN 0701-581X.
- Sheridan, R.P., C. Sanderson, and R. Kerr. 1976. Effects of pulp mill emissions on lichens in the Missoula Valley, Montana USA. *Bryologist* 79:248-252.
- Van Soest, P.J. 1982. *Nutritional ecology of the ruminant*. O and B Books, Corvallis, OR. 350 pp.
- Vitt, D.H., J.E. Marsh, and R.B. Bovey. 1988. *A photographic field guide to the mosses, lichens and ferns of northwest North America*. Lone Pine Publishing, Redmond, WA, USA.

### APPENDIX A

Diagram representing paired utilization transects and control transects within a forested stand. Numbers represent paired plots.



## APPENDIX B

Methods used to collect epiphyte lichen litterfall for utilization sites, control sites and productivity sites (McCune 1994).

- 1) Fragments less than 2 cm long were not collected.
- 2) If the epiphyte litter reestablished then it was not collected. This was determined by observing the thallus condition, orientation, and attachment to the substrate.
- 3) If the litter was attached to a fallen branch it was picked up unless the branch was attached to other branches with a diameter at its base of more than 10 cm. Litter attached to large fallen trees or branches was not collected.
- 4) Litter that was hung up in the understory at a height above 2 meters was not collected.
- 5) Fragments were quickly cleaned as they were bagged. A final cleaning was done in the lab.
- 6) If the litter was largely incorporated into the forest floor (attached by fungal hyphae and partly buried by other litter) or was decaying, it was not collected.

## APPENDIX C

Lichen biomass values and P-values for *Bryoria* spp. and *Usnea* spp. collected inside and outside ungulate exclosures for winters 1996-97 and 1997-98.

1996-97	<i>Bryoria</i> (kg/ha)			<i>Usnea</i> (kg/ha)		Lichen Total (kg/ha)
	A	B	Total	A	B	
Control 1	5.97	1.40	7.36	0.00	0.00	7.36
Utilization 1	0.84	0.10	0.94	0.00	0.00	0.94
p-value	0.00		0.00			0.00
Control 2	6.11	0.00	6.11	0.00	0.00	6.11
Utilization 2	2.66	0.00	2.66	0.00	0.00	2.66
p-value	0.00		0.00			0.00
Control 3	34.74	0.00	34.74	0.00	0.00	34.74
Utilization 3	3.85	0.00	3.85	0.00	0.00	3.85
p-value	0.00		0.00			0.00
Control 4	5.39	0.00	5.39	0.00	0.00	5.39
Utilization 4	1.89	0.00	1.89	0.01	0.00	1.89
p-value	0.01		0.01			0.01
Control 5	7.53	5.20	12.73	0.00	0.00	12.73
Utilization 5	8.43	0.26	8.69	0.00	0.01	8.69
p-value	0.78		0.46			0.46
Control 6	10.75	2.56	13.32	0.04	0.01	13.37
Utilization 6	5.93	0.00	5.93	0.00	0.00	5.94
p-value	0.18		0.11			0.11
Control 7	7.43	2.54	9.97	0.08	0.01	10.06
Utilization 7	3.43	1.43	4.86	0.01	0.01	4.87
p-value	0.05		0.02			0.02
Control 8	9.30	0.00	9.30	0.02	0.00	9.31
Utilization 8	1.70	0.00	1.70	0.31	0.00	2.01
p-value	0.01		0.01			0.01
Control 9	14.19	0.00	14.19	0.00	0.00	14.19
Utilization 9	2.40	0.00	2.40	0.00	0.00	2.41
p-value	0.00		0.00			0.00
Mean Control	11.27	1.30	6.28	0.02	0.00	12.58
Mean Utilization	3.46	0.20	1.83	0.04	0.00	3.69
p-value	0.00		0.00			0.00

## APPENDIX C. Continued

1997-98	<i>Bryoria</i> (kg/ha)			<i>Usnea</i> (kg/ha)		Lichen Total (kg/ha)
	A	B*	Total	A	B*	
Control 1	2.75	NA	2.75	0.00	NA	2.75
Utilization 1	2.11	NA	2.11	0.00	NA	2.11
p-value	0.25		0.25			0.25
Control 2	5.90	NA	5.90	0.00	NA	5.90
Utilization 2	3.22	NA	3.22	0.01	NA	3.23
p-value	0.09		0.09			0.09
Control 3	31.72	NA	31.72	0.00	NA	31.72
Utilization 3	6.69	NA	6.69	0.00	NA	6.69
p-value	0.01		0.01			0.01
Control 4	9.50	NA	9.50	0.08	NA	9.58
Utilization 4	2.71	NA	2.71	0.03	NA	2.74
p-value	0.01		0.01			0.01
Control 5	9.24	NA	9.24	0.00	NA	9.24
Utilization 5	7.67	NA	7.67	0.01	NA	7.67
p-value	0.39		0.39			0.40
Control 6	8.50	NA	8.50	0.03	NA	8.53
Utilization 6	6.46	NA	6.46	0.00	NA	6.46
p-value	0.64		0.64			0.63
Control 7	4.10	NA	4.10	0.01	NA	4.10
Utilization 7	5.47	NA	5.47	0.00	NA	5.47
p-value	0.35		0.35			0.35
Control 8	4.00	NA	4.00	0.02	NA	4.02
Utilization 8	9.83	NA	9.83	0.31	NA	10.14
p-value	0.25		0.25			0.24
Control 9	18.82	NA	18.82	0.02	NA	18.84
Utilization 9	3.36	NA	3.36	0.01	NA	3.37
p-value	0.00		0.00			0.00
Control 10	5.20	0.00	5.20	0.00	0.00	5.20
Utilization 10	3.07	0.00	3.07	0.00	0.00	3.07
p-value	0.29		0.29			0.29

\* B lichens were not available for sampling for Winter 1997-98 in two-year sites (1 - 10) as a result of their removal for sampling during the previous season.



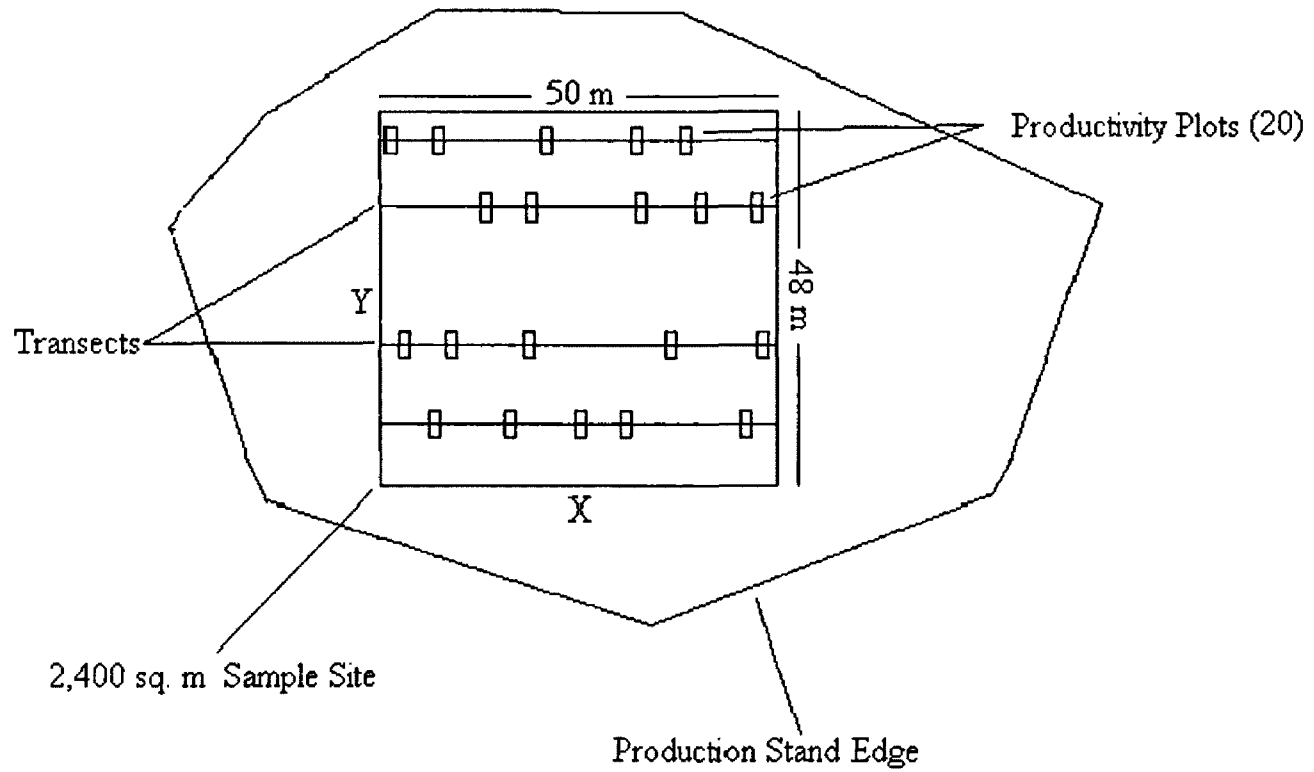
## APPENDIX C. Continued

1997-98	<i>Bryoria</i> (kg/ha)			<i>Usnea</i> (kg/ha)		Lichen Total (kg/ha)
	A	B*	Total	A	B*	
Control 11	28.08	0.00	28.08	0.02	0.00	28.11
Utilization 11	2.88	0.00	2.88	0.02	0.00	2.90
p-value	0.00		0.00			0.00
Control 12	19.45	0.00	19.45	0.00	0.00	19.45
Utilization 12	4.20	0.00	4.20	0.00	0.00	4.20
p-value	0.00		0.00			0.00
Control 13	8.49	0.00	8.49	0.03	0.00	8.52
Utilization 13	5.37	0.00	5.37	0.01	0.00	5.38
p-value	0.14		0.14			0.14
Control 14	20.79	0.00	20.79	0.00	0.00	20.79
Utilization 14	6.55	0.00	6.55	0.00	0.00	6.55
p-value	0.02		0.02			0.02
Control 15	17.92	0.00	17.92	0.00	0.00	17.92
Utilization 15	7.68	0.00	7.68	0.00	0.00	7.68
p-value	0.14		0.14			0.14
Control 16	23.16	0.00	23.16	0.00	0.00	23.16
Utilization 16	8.24	0.00	8.24	0.00	0.00	8.24
p-value	0.00		0.00			0.00
Control 17	26.50	0.00	26.50	0.00	0.00	26.50
Utilization 17	9.47	0.00	9.47	0.01	0.00	9.49
p-value	0.02		0.02			0.02
Control 18	5.33	0.72	6.05	0.06	0.02	6.14
Utilization 18	1.81	0.00	1.81	0.03	0.00	1.84
p-value	0.03		0.02			0.02
Control 19	6.61	0.59	7.20	0.02	0.00	7.22
Utilization 19	1.72	0.12	1.84	0.04	0.11	1.99
p-value	0.08		0.10			0.12
Mean Control	13.48	0.13	13.61	0.01	0.00	13.62
Mean Utilization	5.18	0.01	5.20	0.03	0.01	5.23
p-value	0.00		0.00			0.00

\* B lichens were not available for sampling for Winter 1997-98 in two-year sites (1 - 10) as a result of their removal for sampling during the previous season.

### APPENDIX D

Diagram representing a productivity stand with 20 random productivity plots along transects in a 2,400 m<sup>2</sup> sample site.



Independent variables measured, recorded, or calculated for each productivity site.

- Fire Group number
- Alpha tree species
- Basal area of the alpha tree species
- Age of the dominant tree layer
- Age of the codominant tree layer
- Age of the sub-dominant tree layer
- Elevation
- Percent Slope
- Aspect
- Degrees from North
- Potential Annual Radiation
- Canopy cover arcsin transformation
- Average DBH of all live trees  $\geq 13.0$  cm
- Standard deviation of the average tree DBH of all live trees  $\geq 13.0$  cm
- Quadratic mean DBH
- Simpson's Diversity Index
- Shannon-Wiener Diversity Index
- Basal area/ha of all live trees
- Basal area/ha of all live trees  $> 22.9$  cm DBH
- Mean DBH of all live trees  $> 22.9$  cm DBH
- Basal area/ha of all live trees 13.0 – 22.9 cm DBH
- Mean DBH of all live trees 13.0 – 22.9 cm DBH
- Basal area/ha of all live trees  $\geq 13.0$  cm DBH
- Number of snags/ha  $\geq 13.0$  cm DBH
- Mean snag DBH of all snags  $\geq 13.0$  cm DBH
- Mean number of stems/ha of all live trees  $\geq 1.4$  m tall
- Mean number of stems/ha of all live trees  $\geq 13.0$  cm DBH
- Mean number of stems/ha of all live trees  $\geq 23.0$  cm DBH
- Height of the dominant tree layer
- Height of the codominant tree layer
- Height of the subdominant tree layer
- Basal area/ha of all *Pinus ponderosa*
- Basal area/ha of all *Pseudotsuga menziesii*
- Basal area/ha of all *Larix occidentalis*
- Basal area/ha of all *Pinus contorta*
- Basal area/ha of all *Abies lasiocarpa*

Coefficient correlations for multiple linear regression equations for productivity sites grouped by stand structure class.

**1 and 2 Layer Sites – Bryoria as dependent variable.**

Model		Canopy Cover Arcsin Transformation	SNAG HEC	Basal area/ha of all LAOC
1	Correlations	Canopy Cover Arcsin Transformation	1.000	-.513
		SNAG_HEC	-.133	1.000
		Basal area/ha of all LAOC	-.513	-.014
Covariances	Canopy Cover Arcsin Transformation	65583.892	-41.419	-1029.531
	SNAG_HEC	-41.419	1.468	-.130
	Basal area/ha of all LAOC	-1029.531	-.130	61.395

**3 and Multi-layer Sites – Bryoria as dependent variable.**

Model		S.D. of DBH	Av. DBH of all live trees >13.0cm	Basal area/ha of all LAOC
1	Correlations	S.D. of DBH	1.000	-.544
		Av. DBH of all live trees >13.0cm	-.494	1.000
		Basal area/ha of all LAOC	-.544	.448
Covariances	S.D. of DBH	325.539	-135.384	-73.064
	Av. DBH of all live trees >13.0cm	-135.384	230.491	50.629
	Basal area/ha of all LAOC	-73.064	50.629	55.333

**All Sites – Bryoria as dependent variable.**

Model		SNAG HEC	Basal area/ha of all LAOC	ELEV M
1	Correlations	SNAG_HEC	1.000	-.482
		Basal area/ha of all LAOC	-.193	1.000
		ELEV_M	-.482	.255
Covariances	SNAG_HEC	1.057	-.989	-.104
	Basal area/ha of all LAOC	-.989	24.812	.266
	ELEV_M	-.104	.266	4.413E-02

**3 and multi-layer Sites – Usnea as dependent variable.**

Model		Yearly values of direct solar radiation	ELEV M
1	Correlations	Yearly values of direct solar radiation	1.000
		ELEV_M	-.013
Covariances	Yearly values of direct solar radiation	4.271E-09	-7.203E-09
	ELEV_M	-7.203E-09	7.552E-05